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Predicting eider predation potentials on mussels in Danish coastal areas — implications for mussel farming site-selection

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ABSTRACT: Selecting optimal locations for mussel farming is vital for the optimization of production yield and for the minimization of environmental impact. Although predation by sea ducks may induce large stock losses and hence severe economic loss for mussel farmers, predation potential is rarely included in site-selection tools. In this paper we present a GIS-based spatial model predicting the potential of eider predation on blue mussel farms in Danish coastal waters. The model incorporates national survey data on eiders, as well as knowledge of eider behavior and habitat preferences, and was calibrated with predated/non-predated observations of eiders from 9 experimental mussel farms or test lines in Danish coastal waters. Except for 1 case study area, our model successfully confirmed a higher predation potential at test sites where predation had been observed. Our resulting predation potential map revealed potentials ranging from very low in inner parts of narrow estuaries to very high in more open coastal areas. Integration of the predation map into an existing site-selection tool showed that areas optimal for mussel growth were also associated with the highest modelled predation potential. Nonetheless, it was possible to identify areas having a very low potential of predation and only a 10 % lower mussel production potential. These results underpin the potential for reducing production loss and increasing income by including predation potential in site-selection tools. In addition, the eider predation model can be used to identify and subsequently protect key foraging areas to support eider conservation.

KEY WORDS: Mussel aquaculture · Stock losses · Human–wildlife interaction · Production optimization · Conservation

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1. INTRODUCTION

Bivalve production is an expanding industry in terms of both biomass production and economy (Wijsman et al. 2019). The industry is optimized for human consumption but has recently also been proposed as an environmental measure to mitigate eutrophication in the marine environment and for feed production for animal husbandry (Petersen et al. 2014). When compared to monoculture of finfish, bivalve aquaculture has become very attractive since it does not require exogenous food input (Garen et al. 2004, Ferreira et al. 2009) and may provide goods and services beneficial for the marine environment and society (van der Schatte Olivier et al. 2020), including a low CO_2 footprint (Alonso et al. 2021). In recent years, mussel mitigation aquaculture optimized for nutrient removal has been proposed as a tool to improve marine water quality (Petersen et al. 2014, Timmermann et al. 2019) or as a compensation

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measure for marine point sources (i.e. finfish culture). Excess nutrient loadings often result in increased phytoplankton biomass and poor water quality in coastal regions. Through water filtration by the mussels and their subsequent harvesting, nutrients bound in mussel tissue are permanently removed from the aquatic environment. The productivity and yield of bivalve farming depends on bivalve species-specific characteristics as well as environmental conditions such as food supply, salinity and temperature. Several geographic information systems (GIS)-based site-selection tools have been developed for the purpose of optimal site selection for bivalve farming, mainly for human consumption (Brigolin et al. 2017). Moreover, a few site-selection tools optimized for nutrient mitigation have been developed (Gimpel et al. 2018, Holbach et al. 2020b). Site selection for marine aquaculture is an essential element of implementing the Maritime Spatial Planning Directive (MSPD) (Gimpel et al. 2018). While these studies evaluated the spatial variability of bivalve growth conditions, either based on fixed thresholds or seasonal average values of habitat factors or temporal dynamics (Holbach et al. 2020a), none of the applied methods account for potential loss of mussel biomass due to predation. Bivalves, especially mussels, are principal prey for several sea duck species including eiders *Somateria* spp. (Bustnes & Erikstad 1988, Houle et al. 2017). Eiders dive to feed on a variety of benthic invertebrates (Ydenberg & Guillemette 1991) and although they can dive down to 50 m, they generally prefer shallower waters (0 to 10 m) where benthic prey are most abundant (Guillemette et al. 1993) and accessible. They prefer small (<50 mm) mussels (Waltho & Coulson 2015) with a high meat to shell ratio and can selectively ingest the most optimal prey items based on size and quality (Varennes et al. 2015b). As mussel farms contain very high densities of mussels located in surface waters (0 to 10 m), with fast growth rates resulting in thin shells and high meat content (Buer et al. 2020), cultivated mussels are optimal as food sources and preferred by ducks (Hamilton et al. 1999). Hence, mussel farms may become a foraging hotspot for sea ducks (Kirk et al. 2007), potentially leading to large stock losses and resulting in severe economic loss for mussel farmers. Significant losses of both wild and cultivated mussels due to seabird predation is well documented (e.g. Hamilton 2000, Ross & Furness 2000), with losses in mussel abundance close to 50 % in an experimental study on the effect of eider predation in an intertidal community (Hamilton 2000). When sea ducks forage on mussels, especially in spring and autumn, they form large flocks (100s to 1000s of birds), which may cause substantial losses if no protection measures are put in action (Varennes et al. 2013).

Different types of protection measures such as nets (Varennes et al. 2013), chasing birds by boat, underwater noise (Ross et al. 2001) and protective socking (Dionne et al. 2006) have all been developed in order to reduce the impact of sea duck predation on cultivated mussels. While some of these measures may reduce stock loss to some degree, their effectiveness depends on knowledge of the potential of predation at a given farm site and appropriate investment and preparation (Dionne et al. 2006, Varennes et al. 2013). Hence, locations with a low predation potential might be more optimal for mussel production despite less favorable conditions for mussel growth. As predation may influence the harvest and production costs, predation potential should be an important component of site selection.

Danish coastal waters are highly suitable for blue mussel (*Mytilus edulis*) production (Holbach et al. 2020a) due to high primary production, optimal salinity conditions, sheltered micro-tidal estuaries and coastal waters with low contamination levels of toxins and *Escherichia coli* bacteria. Due to the favorable conditions for blue mussel growth, wild populations of blue mussels are widespread in Danish marine waters, with dense stocks in the Wadden Sea as well as in almost all semi-enclosed estuaries and bays. Whereas blue mussel dredging occurs in Limfjorden, the Wadden Sea, Isefjorden and along the east coast of Jutland, commercial blue mussel cultivation currently only occurs in Limfjorden. Due to technological improvements and societal need for sustainable food and animal feed production, mussel cultivation is likely to increase in the future.

Danish waters also constitute internationally important wintering and staging areas for sea ducks, especially for the Baltic/Wadden Sea flyway population of common eider *Somateria mollissima* (Desholm et al. 2002). Although midwinter counts suggest that the size of the common eider (hereafter 'eider') populations wintering in Danish waters has decreased from 800 000 birds to approximately 300 000 birds over the past 3 decades, Danish waters still support a large proportion of the wintering flyway population (Desholm et al. 2002). The reasons behind this severe and long-term decline are still unclear, but likely include the impacts of multiple stressors such as increasing predation by white-tailed eagles and epidemic disease, as well as reductions in wild mussel beds causing starvation and increased mortality, especially among female eiders (Christensen et al.

1997, Garbus et al. 2018, Öst et al. 2018). Despite the apparent decline, eiders are the most abundant species of sea duck in inner Danish waters during winter (Holm et al. 2021). During autumn and winter, eiders consume up to 2–2.5 kg of their preferred prey, i.e. blue mussels, per day (Laursen 1987, Guillemette 1998). The birds identify suitable seafloor mussel beds or lines used for mussel farming by test diving. Once a mussel bed or line has been located, the flock of birds deplete the available mussels of preferred size and move on to a new location (Dunthorn 1971, Galbraith 1992, Larsen & Guillemette 2000, Ross & Furness 2000). Eiders are strictly marine species, with a preference for shallow coastal and saline (>15 psu) waters and with a high site fidelity to their wintering area (Beuth et al. 2017). Eiders rarely cross narrow land barriers to enter estuaries, although these may constitute attractive feeding grounds (Durinck et al. 1994, Petersen et al. 2010). This behavior results in a main winter distribution along the parts of the Danish coastline that are directly connected with the open sea, whereas estuaries that either have a narrow entrance or are too deep appear to be less attractive to eiders (Holm et al. 2021).

As eider predation can have significant influence on mussel production (Ross & Furness 2000) and result in significant stock loss if the problem is not addressed (Varennes et al. 2013), knowledge of the likelihood of eider presence and thus potential predation is an essential component in optimal site selection and management of mussel farms in coastal waters. Knowing the potential of eider predation across Danish waters is crucial in order to select areas of low eider predation for mussel farming and hence avoid stock losses or costly investments in protection measures. Mussel production in areas with a high eider predation potential may very well be profitable due to favorable conditions for mussel growth, but the profitability largely depends upon timely implementation of effective protection measures. The aim of this study was to develop a GIS-based spatial model capable of predicting the potential of eider predation when prey items in the form of mussel aquaculture are introduced to surface waters. Because of the high abundance of the species in inner Danish waters during winter and their strong preference for blue mussels as prey, the common eider is the most relevant species for investigating conflicts between sea ducks and mussel farming in the study area. However, the same modelling approach can equally well be applied to other species of sea duck. The model incorporates national surveys of eiders (Nielsen et al. 2019), as well as knowledge of eider behavior and habitat preferences, and is applied for Danish waters. The model outputs a GIS layer showing the potential of eider predation that can be incorporated into existing multi-criteria site-selection tools, allowing for a more realistic assessment of expected costs and yield of mussel farming at different locations. Hence, this study can become an important element of selecting suitable sites for marine aquaculture when implementing the MSPD. Despite the focus of this study on predation potential, the model can also have implications for the protection of eiders as a species, which has recently been uplisted to Near Threatened in Europe (BirdLife International 2018). Finally, the resulting predation potential map for eiders was evaluated against observations from field experiments with mussel longlines from 9 sites all located within Danish estuaries.

2. METHODS

In order to make comprehensive geographical references to the study area, we implemented a chessboard-like grid (25 × 25 km cells) with characters and numbers (*x*- and *y*-axis, respectively; see Fig. 1), so that individual cells or cell ranges can easily be referred to.

2.1. Study area

The study area is confined to marine areas around Denmark, from the near-coastal Danish parts of the Wadden Sea (B6:C3), to the fjords of west Jutland (A7:B10), Limfjorden (B10:F13), Kattegat (H15:K8) and inner Danish waters (E7:K2) including belts and estuaries, Øresund (L8:M6) and the western part of the Baltic Sea embracing the island of Bornholm (Q3:S6) (Fig. 1). The study area reflects the area that was surveyed for eiders during midwinter 2016 (Nielsen et al. 2019) and extends from 54.36 to 57.79° N and 8.12 to 15.45° E.

Spatial distinctions of land–water boundaries were based on the European coastline shape file (European Environmental Agency 2015) and the exclusive economic zones from the Maritime Boundaries Geodatabase (Flanders Marine Institute 2018). The background classification in Fig. 1 is based on nitrogen reduction efficiency classes for mussel mitigation farms based on Holbach et al. (2020b). The classes C1 to C5 were derived by setting the maximum modelled nitrogen reduction potential to 100 % and by

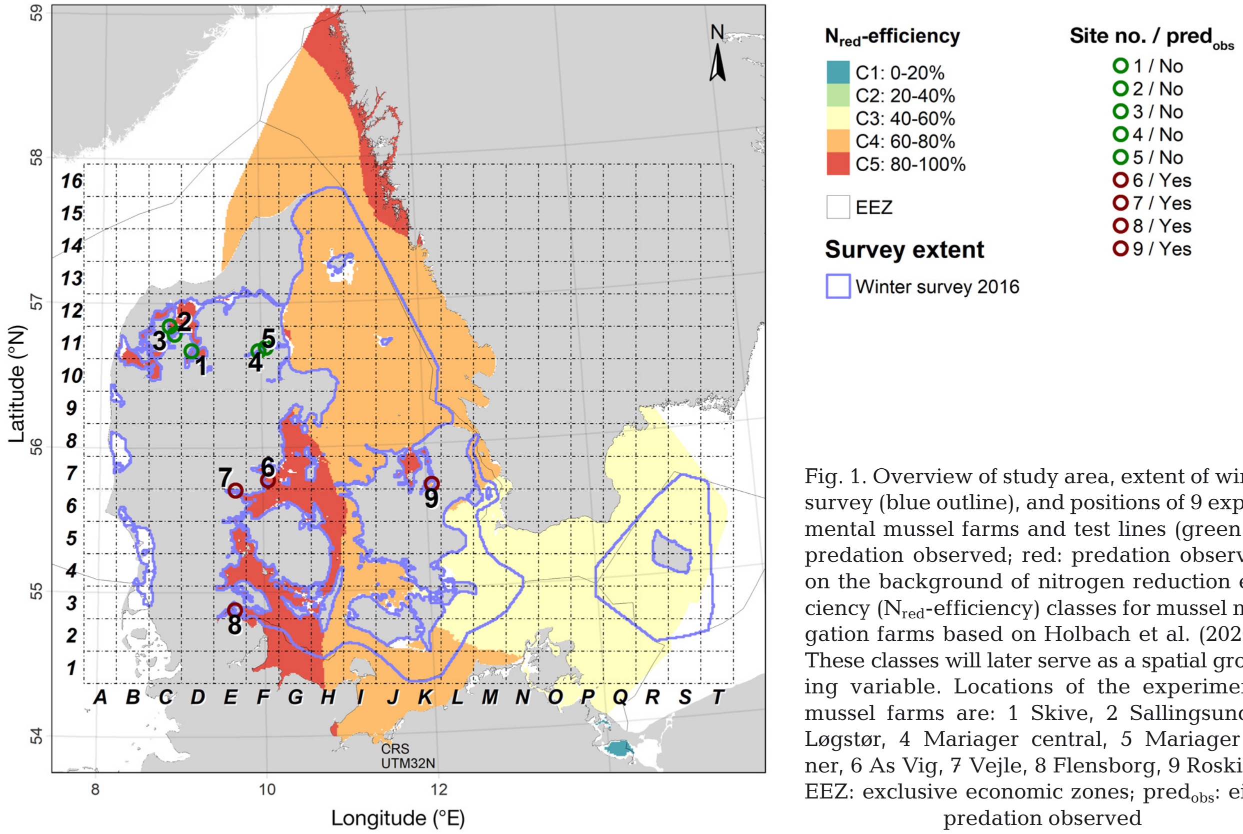

Fig. 1. Overview of study area, extent of winter survey (blue outline), and positions of 9 experimental mussel farms and test lines (green: no predation observed; red: predation observed) on the background of nitrogen reduction efficiency (N_{red}-efficiency) classes for mussel mitigation farms based on Holbach et al. (2020b). These classes will later serve as a spatial grouping variable. Locations of the experimental mussel farms are: 1 Skive, 2 Sallingsund, 3 Løgstør, 4 Mariager central, 5 Mariager inner, 6 As Vig, 7 Vejle, 8 Flensborg, 9 Roskilde. EEZ: exclusive economic zones; $pred_{obs}$: eider predation observed

dividing the range between 0 and 100% into 5 equal 20% intervals. These classes will later serve as spatial grouping variables in an application example of our eider predation potential model on mussel mitigation farm site selection.

2.2. Modelling approach

The theoretical potential of predation by eiders was modelled across the study area (Fig. 1) by combining 4 spatial layers of information: (1) predation base potential, (2) spatial winter distribution of eiders, (3) bathymetry (water depth suitability) and (4) cost-distance through water to open sea taking landscape barriers into account. These layers of spatial information were selected because they were expected to influence the probability of eider presence and, hence, predation on mussel mitigation farms or commercial mussel farms. The following sections will detail these spatial layers. All data layers were normalized to values between 0 and 1 before they were combined in the map overlay analysis. The layers were prepared in the UTM32N coordinate system as spatially aligned raster data with a resolution of 1 × 1 km.

2.2.1. Base predation potential and winter distribution of eider

The predation base potential layer and spatial winter distribution layer of eiders were modelled based on the 2016 midwinter aerial survey for eiders in Denmark (Nielsen et al. 2019). In these aircraft-borne surveys, counts of wintering eiders were performed as a combination of counts along pre-defined and evenly dispersed transect lines over the open sea, supported by more exploratory random flights inside the estuaries (Petersen & Nielsen 2011). The base potential layer is intended to reflect the potential of predation primarily during migration seasons as eiders may rest and forage during migration, but also through mid-winter displacements of eider flocks searching for yet unexploited mussel beds. We divided the study area into 8 primary water areas differing in their migratory flow of birds. For each of these areas, base predation potential was computed by tracking mid-winter abundances of eiders along primary migration routes according to known migration patterns (Noer 1991, Bønløkke et al. 2006). Abundances of migrating birds were weighted by 1/3 compared to winter abundances because passage of migratory flocks of eiders are likely to have a markedly lower predation potential compared to wintering flocks that remain in the same area for a longer period of time. Because the base potential layer is a rough measure of the predation potential in any given water area, we transferred base potential values to breaks of 5 % (5 %, 10 %, 15 % etc.), with 100 % and 5 % as the highest and lowest base potential, respectively. The final base potential p_{base} raster layer is normalized to values between 0 and 1 using a standard normalization procedure:

$$p_{\text{base}} = \frac{p_{\text{base}} - \min(p_{\text{base}})}{\max(p_{\text{base}}) - \min(p_{\text{base}})} \tag{1}$$

As eiders show high site fidelity to their wintering area (Beuth et al. 2017), the spatial winter distribution of eiders was included as a predictor. The winter distribution was modelled using the kernel density function implemented in ArcGIS with a search radius of 18 km (Esri 2017) based on the spatial location of observations and the recorded mid-winter abundance of eiders. The search radius was set to 18 km to account for local within-winter movements between mussel beds. The resulting data layer on potential by winter distribution p_{wint} is normalized to values between 0 and 1 using the same standard procedure as in Eq. (1):

$$p_{\text{wint}} = \frac{p_{\text{wint}} - \min(p_{\text{wint}})}{\max(p_{\text{wint}}) - \min(p_{\text{wint}})} \tag{2}$$

2.2.2. Bathymetric suitability

Bathymetric suitability for eiders was computed based on a digital bathymetry model covering the whole study area. For this model, 2 available bathymetry datasets were merged: (1) a Danish bathymetry model (Danish Geodata Agency 2010) with a spatial resolution of approximately 50 × 50 m and (2) the EMODnet Bathymetry DTM (EMODnet Bathymetry Consortium 2018) with a spatial resolution of approximately 100 × 100 m. Both were projected onto the model raster using the 'projectRaster' function of the 'raster' library (v. 3.5-11) in R (v. R-4.1.2) by calculating the mean bathymetry (bathy) for each cell. Then, both raster layers were merged using the merge() function of the 'raster' library in R, prioritizing the Danish bathymetry model due to the higher initial spatial resolution.

Although eiders are capable of diving >40 m, most diving takes place at depths <10 m (Guillemette et al. 1993). For this analysis, we defined a binary spatial parameter for potential related to bathymetry p_{bathy}, in which we considered shallow depths of ≤20 m suitable for foraging of eiders:

$$p_{\text{bathy}} = \begin{cases} 1; \text{bathy} \leq 20 \\ 0; \text{bathy} > 20 \end{cases} \tag{3}$$

2.2.3. Cost-distance through water to open sea

Eiders are generally marine birds and not comfortable with leaving the open marine environment (Waltho & Coulson 2015). Therefore, we hypothesized that increased distance through water from the open ocean and the presence of narrow passages will reduce the probability of encountering eiders. Both of these effects were integrated into a single layer called 'cost-distance'.

First, we defined the 'open ocean' as the area covered by all the marine water pixels with >5 km distance to the nearest coast plus a 5 km surrounding circular buffer. By this method, fjords and bays with less than 10 km entries to open oceans were excluded from the open ocean. It has been reported that eider

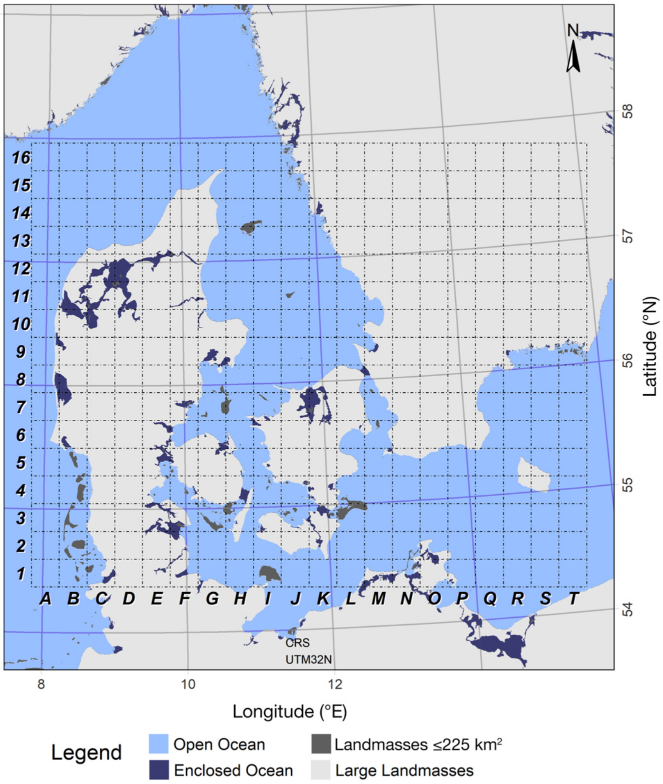

Fig. 2. Spatial definitions of open ocean, enclosed ocean and the 2 types of landmasses considered in the spatial model calculation

ducks in Scandinavia usually migrate at altitudes <30 m (Day et al. 2004). At 30 m altitude, the distance of the sea horizon is at approximately 20 km. Therefore, we concluded that it is possible for migrating eiders to recognize landmasses of 15 × 15 km (225 km^2) as islands, not part of the mainland. Hence, we only took into account larger landmasses with an area >225 km^2. The resulting spatial structure of open ocean, enclosed ocean, large landmasses and landmasses ≤225 km^2 is displayed in Fig. 2.

For all the remaining enclosed marine water pixels, we calculated an eider-conductance layer, based on the assumption that narrow passages would reduce the likelihood of an eider passage. We defined the eider-conductance ($\text{cond}_{\text{eider}}$) as:

$$\text{cond}_{\text{eider}} = \begin{cases} \dfrac{d_{\text{coast}}\,[\text{km}]}{10\text{ km}}; d_{\text{coast}} \leq 10\text{ km} \\ 1; d_{\text{coast}} > 10\text{ km} \end{cases} \tag{4}$$

where d_{coast} is the distance in km to the nearest coast. d_{coast} was determined with the 'gridDistance' function of the 'raster' library in R; d_{coast}, e.g. receives 0.5 conductance. This conductance layer was used to calculate a minimum cost-distance layer from the open into the enclosed ocean areas using the 'costDistance' function of the 'gdistance' library (v. 1.3-6) in R. The resulting cost-distance is a relative measure composed of both the distance through water plus an extra distance due to respective conductance values to be passed on the way. Cost-distance values were capped at 1000 distance units, which represents the 95th percentile of all pixels with a cost-distance >0. As a high cost-distance represents a low potential for eider predation, the cost-distance values were translated into distance-related potential values p_{dist} and normalized between 0 and 1 in the following way:

$$p_{\text{dist}}^{\text{norm}} = \frac{-d_{\text{cost}}}{\max(d_{\text{cost}})} + 1 \tag{5}$$

2.2.4. Predation potential by eiders

The combined layer predicting the predation potential of eiders on mussel farms in Danish waters p_{pred} emerges as a spatial overlay of the individual normalized data layers. The layers were combined in the following way:

$$p_{\text{pred}} = w1 \times p_{\text{base}}^{\text{norm}} + p_{\text{bathy}} \times \left(w2 \times p_{\text{wint}}^{\text{norm}} + w3 \times p_{\text{dist}}^{\text{norm}}\right) \tag{6}$$

where $w1$ to $w3$ are variable weights assigned to the respective individual spatial potential layers. To maintain the value range $0.1 \leq p_{\text{pred}} \leq 1$ and to assure that all layers were accounted for in the final predation potential assessment, these weights were limited by the following conditions: $0.1 \leq w \leq 0.8$ and $\sum_{i=1}^{3} w_i = 1$. The base potential was treated separately, as we assume that migrating eiders can actually appear anywhere, and the final predation potential should therefore never become 0. As stated above, the potential related to bathymetry is treated as a binary variable, which we applied to include/exclude effects of the remaining 2 layers.

2.3. Experimental mussel farms and model calibration

To identify suitable assignments of weights, we used the following approach for model calibration. The theoretical model for eider predation potential on farmed mussels was calibrated with empirical qualitative (predated/non-predated) observations of predation by eiders at 1 full-scale experimental mussel farm in Limfjorden and 8 test lines located in different estuaries and coasts around Denmark, as shown in Fig. 1. The mussel farm and test lines were established in spring 2017 and 2018 when longlines were deployed. The full-scale farm covered 18 ha with longlines whereas each of the 8 test lines consisted of a single, 100 m longline. Natural recruitment and settling of blue mussel larvae occurred at all locations and the growth of the mussels were followed for a year by biweekly to monthly monitoring of mussel wet and dry weight, shell length and mussel cover on spat collectors. Observations of eiders were performed by visual inspection at test sites during each monitoring campaign. The areas covered by eider monitoring were >6 km^2 of water surface surrounding the test line. Only eiders present on the water surface were counted. The presence of eiders was determined as visual observation of at least 1 eider during at least 1 monitoring campaign. At 4 out of the 9 test farms, eiders were present in the vicinity of the test lines, and in these cases, more than 10 eiders were observed. Predation of mussels, presumably by eiders, resulted in a significant loss (>50%) of mussel biomass between 2 monitoring campaigns. Theoretical values for eider predation at the location of each of the 9 test farms were then extracted and compared against the qualitative empirical observations (predated/non-predated). The individual weights ($w1$, $w2$, $w3$) were constrained to numbers in steps of 0.1 while complying with the conditions explained above for Eq. (6). Consequently, we derived 36 possible weight scenarios.

We applied all these 36 possible combinations of weights in Eq. (6) and extracted respective p_{pred} values for the 9 experimental mussel farm locations. A 1-sided *t*-test was applied to test for significantly ($p < 0.05$) higher p_{pred} values in the predated farms compared to the non-predated. All combinations of weights that passed this *t*-test were considered 'realistic' weight scenarios and the final weight scenario selection was subject to expert judgement and guided by the mapped eider distribution from the national survey. Finally, we derived a threshold value to differentiate between low and considerable p_{pred} as the maximum p_{pred} value for experimental test sites that had not suffered from predation by eiders.

2.4. Effect of predation potential on site selection for mussel mitigation farms

To investigate the effect of the estimated predation potential by eider ducks on the optimal placement of mussel mitigation farms, we integrated the new spatial predation potential layer into the existing MYTIGATE — *Mytilus edulis* (Blue Mussel) Mitigation Farm Site Selection Tool for the Western Baltic Sea (Holbach et al. 2020a). MYTIGATE is based on 'A spatial model for nutrient mitigation potential of blue mussel farms in the western Baltic Sea' (Holbach et al. 2020b) and interactively integrates a set of potential exclusion and conflict criteria to calculate customized scenarios of optimal mitigation farm placement with respect to the individually selected criteria. The tool is based on the commonly applied suspended longline farm system (Taylor et al. 2019). Here, we used the source code of MYTIGATE to limit the spatial selection to the model domain of the predation potential layer. Further, we applied the following set of spatial exclusion criteria as implemented in MYTIGATE: Main Shipping Routes; Military Shooting Areas; Restrictions to Sail, Anchor and Fish; Cables and Pipelines. Minimum distances to harbors, towns, summerhouse areas and bathing sites were set to 1 km. The resulting spatial layer on nitrogen reduction potential was based on a longline farm with 2 m loop depth and 0.7 m loop interval, which requires a minimum water depth of 4 m (Holbach et al. 2020b). From this layer, we identified the areas of the top 10% nitrogen reduction potentials both before and after applying the derived threshold for low predation potential by eider ducks.

3. RESULTS

The modelled assessment of eider predation potential on mussel farms and natural mussel stocks resulted from a combination of 4 underlying data layers based on (1) predation base potential, (2) bathymetry (water depth suitability), (3) spatial winter distribution of eiders and (4) cost-distance through water to open sea accounting for both in-water distance and landscape barriers (Fig. 3). Layers (1) and (3) reflect the migration and within-winter movements and distribution of eiders, whereas layers (2) and (4) represent purely geographic features meant to represent habitat suitability of water areas for eider presence in Danish coastal waters.

The predation base potential layer, depicting the potential of eider predation throughout the migration season and due to within-winter movements, displayed the highest potentials in the south-western Baltic Sea and belts between Denmark and Germany (E4:M2; Fig. 3a). An intermediate predation potential was found in Kattegat (G15:K8) and around the island of Bornholm (Q3:S6). In central inner Danish waters, e.g. in southern Kattegat (E6:I7), Great Belt (H5:I6) and Aarhus Bight (G8:G9), the potential of predation by migrating or dislocated wintering birds was intermediate-low. Low base potentials were found in the Wadden Sea (B6:C3) and estuaries of western (A10:B7) and northern Jutland including Limfjord (B10:F13), but the absolute lowest base potentials were found in Øresund (L8:M6) and Køge Bight (L5:L6).

Bathymetric suitability for eider foraging was predicted for all the shallow near-coastal areas (Fig. 3b). Remaining areas include water areas too deep for foraging like the deep channels along Kattegat (H15:K9), Great Belt (H6:I4) and Little Belt (E4:G3), as well as deeper basins in the Baltic Sea (L3:N4, Q3:S6).

Densities of eiders, expressed by their distribution at mid-winter, were particularly high at 2 hotspots, resulting in high potentials of predation near those areas (Fig. 3c). These 2 density hotspots were located in Little Belt (E4:F6) and in the northern parts of Isefjord (J7:K8). In addition, considerable densities were also found in the waters south of Funen (F3:H3) and southwestern Zealand (I4:J4), along the coasts of eastern Jutland (F6:G13) and around the island of Læsø (H13:I14).

The predicted predation potential related to cost-distance to open sea is an integrated measure of the actual in-water distance and landscape barriers that eiders would have to pass on their way to potential

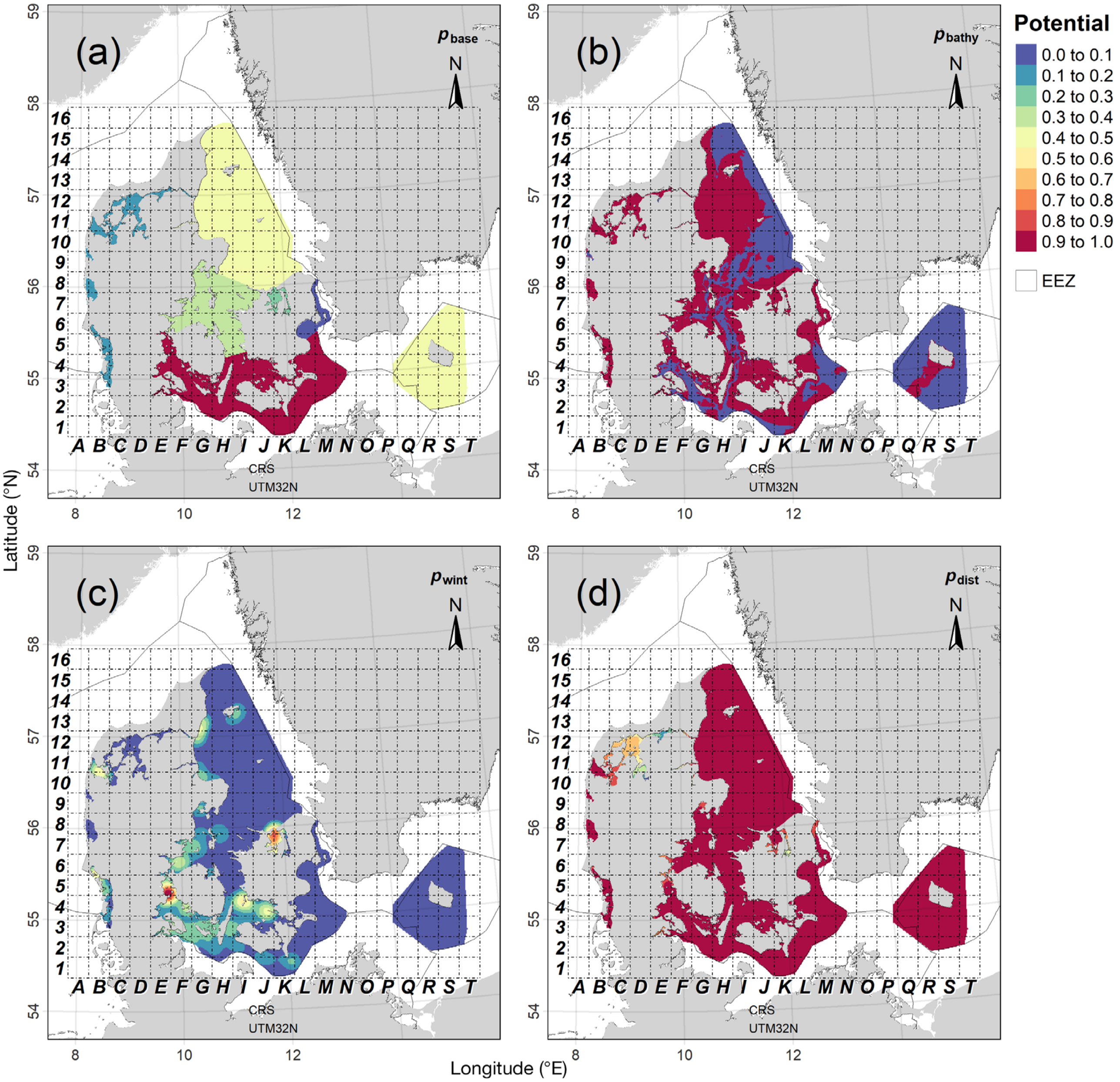

Fig. 3. The 4 underlying layers included in the combined assessment of eider predation potential on mussel farms and mussel stocks around Denmark. (a) Predation base potential, (b) bathymetric suitability, (c) spatial winter distribution of eiders and (d) potential related to cost-distance through water to open sea accounting for in-water distance and landscape barriers

mussel food sources. Therefore, the lowest predation potentials with respect to this layer were found inside the inner parts of estuaries with narrow passages (e.g. Limfjord D10:E13, Roskilde Fjord K6:K7 and Mariager Fjord F11), while maximum predation potentials were found in the open sea (Fig. 3d).

By applying all possible combinations of weights in Eq. (6) and subsequent *t*-tests (see Section 2.3), we identified 12 'realistic' weight scenarios out of a total of 36 possible weight scenarios. From these, we selected the following model equation as the most suitable model for estimating p_{pred} by eiders on mussel farms, according to our expert judgement guided by the mapped eider distribution from the national survey (Nielsen et al. 2019):

$$p_{\mathrm{pred}} = 0.5 \times p_{\mathrm{base}} + p_{\mathrm{bathy}} \times (0.3 \times p_{\mathrm{wint}} + 0.2 \times p_{\mathrm{dist}}) \quad (7)$$

The derived threshold to distinguish between low and considerable potential of predation by eiders was found to be 0.25. The final spatial distribution

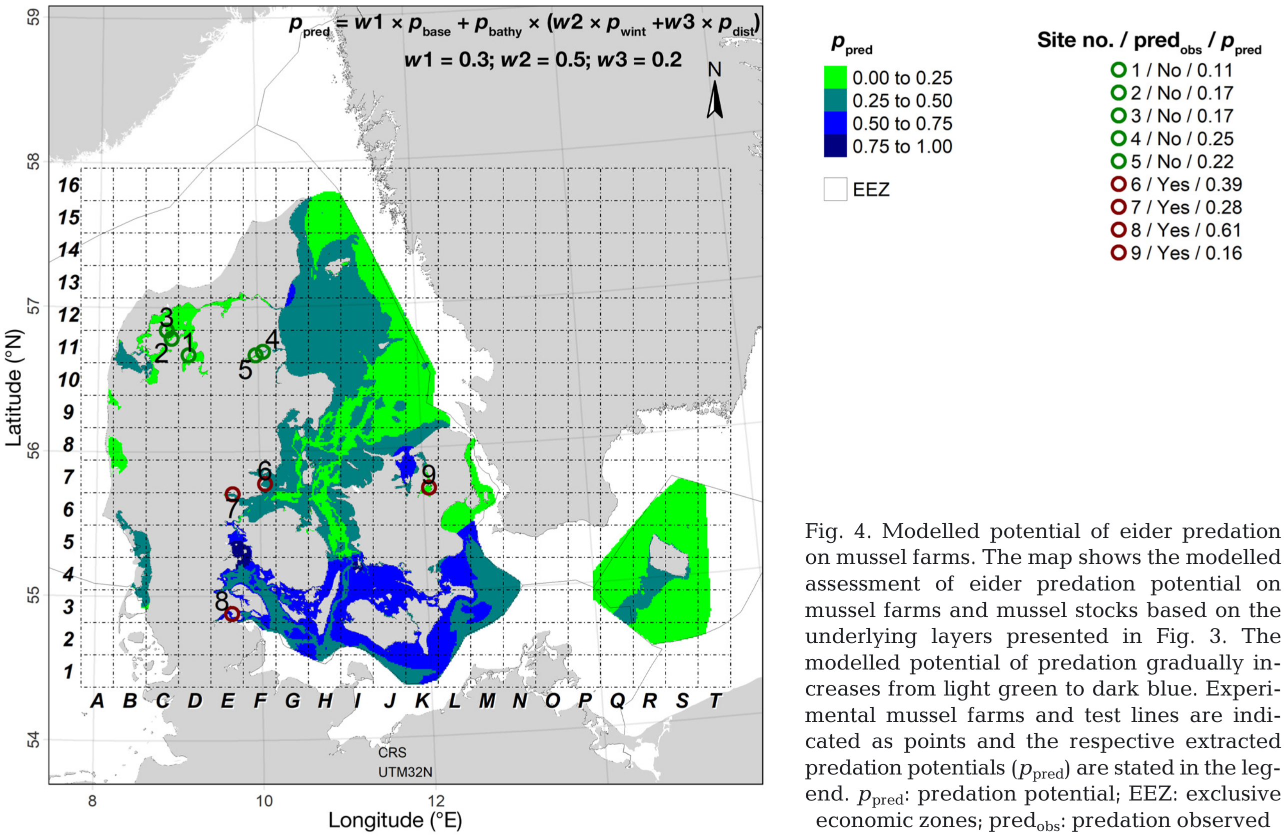

Fig. 4. Modelled potential of eider predation on mussel farms. The map shows the modelled assessment of eider predation potential on mussel farms and mussel stocks based on the underlying layers presented in Fig. 3. The modelled potential of predation gradually increases from light green to dark blue. Experimental mussel farms and test lines are indicated as points and the respective extracted predation potentials (p_{pred}) are stated in the legend. p_{pred}: predation potential; EEZ: exclusive economic zones; pred_{obs}: predation observed

of the estimated p_{pred} is presented in Fig. 4 together with extracted p_{pred} values for the 9 experimental test sites.

The resulting layer of predation potential predicts the spatial probability that migrating and wintering eiders are capable of locating and exploiting mussels farms and mussel stocks at a given location within the study area. In Fig. 4, dark blue areas have the highest theoretical predation potential, whereas the lowest potentials are found in the light green areas. The highest potentials (>0.75) identified by our model were found in Little Belt (E4:F5) and in a restricted area off the coast of southwestern Zealand (I4). Other high potential areas (≥0.50 and ≤0.75) were located at the intersection between Kattegat and Isefjord (J7:K8), in Great Belt (H4:I3) and the western Baltic Sea around southern Zealand and the islands of Lolland, Falster and Funen (E4:L1), and in Aalborg Bight (G12:G13).

Moderately lower predation potentials (>0.25 and <0.50) were found at many locations in inner Danish waters, for instance around Læsø (H13:I14), in large areas of Aalborg and Aarhus Bights (G8:G12), and off the coast of northwestern Zealand (I7:K8). The lowest (<0.25) modelled potential of predation was predicted for the deepest areas of Kattegat (H15:L9) and the Baltic Sea around Bornholm (Q3:S6), along with long and narrow estuaries such as Limfjord (C10:E12) and Roskilde Fjord (K6:K7).

A comparison of the observed predation by eiders at the 9 experimental mussel farms and the modelled potential values (Fig. 4) showed that 3 out of 4 predated farms were located in areas above the 0.25 threshold. This validation applied to the mussel farms at Sites 6: As Vig, 7: Vejle and 8: Flensborg Fjord, whereas the mussel farm at Site 9: Roskilde Fjord was predated despite a modelled potential of predation below the 0.25 threshold (0.16). At test sites where no predation was observed, the modelled potential of predation was either equal to (4: Mariager central) or below (1: Skive, 2: Sallingsund, 3: Løgstør and 5: Mariager inner) the 0.25 threshold for predation.

Integrating the eider predation potential map into the mussel farm site-selection tool MYTIGATE revealed that water bodies that were optimal for mussel farming (C5 water bodies; Fig. 1) were also associated with the highest median potential of eider predation (0.33), the highest maximum potential (0.99) and the highest proportion (78%, derived from

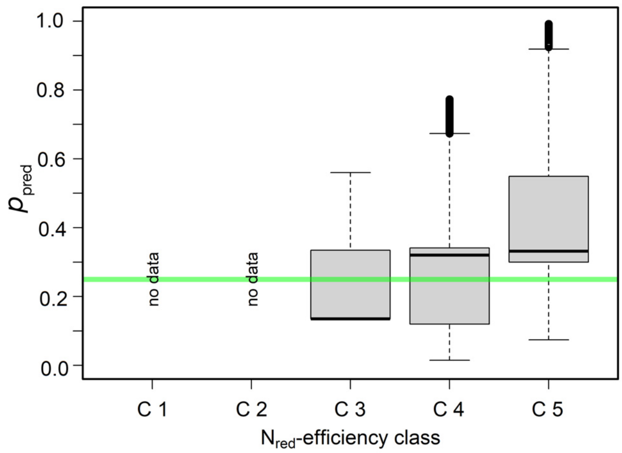

Fig. 5. Eider predation potential in water bodies categorized by low (C1) to high (C5) nitrogen reduction (N_{red}) potential of mussel mitigation farms (see Fig. 1). The eider duck survey extent does not cover the 2 lower nitrogen reduction classes C1 and C2. Within boxplots, black horizontal lines indicate median values of predation potential. Boxes mark the interquartile range and whiskers include all data within 1.5 interquartile ranges around the box. Horizontal green line: 0.25 threshold for low predation potential

background data of boxplots in Fig. 5) of areas with predation potential above the derived threshold of 0.25 (Fig. 5). For those water bodies in the mussel farming suitability classes of C4 and C3, 66 and 39%, respectively, of the areas were above the predation potential threshold (derived from background data of boxplots in Fig. 5). The maximum modelled predation potentials for these 2 classes were 0.77 (C4) and 0.56 (C3), respectively.

When a predation potential threshold of 0.25 was introduced into MYTIGATE to separate low-insignificant potential of predation from medium-high potential, the top 10% areas for nitrogen reduction shifted from areas around Funen (E6:G3) to more open areas in Kattegat (G8:I5), whereas optimal sites in Limfjorden (C10:F12) were unaffected by the inclusion of eider predation (Fig. 6). Because eiders are present in areas suitable for mussel production, relative potentials of predation can be used to guide site selection in the direction of less productive sites that have a lower associated potential of being found and predated by eiders. Inclusion of predation potentials in the MYTIGATE site-selection tool resulted in drastic displacement of the top 10% of the optimal locations for nitrogen reduction (Fig. 6) with a decrease of 10% in total harvest and nutrient extraction potential (derived from the numbers given for 'Red.-Potential [t-N]' in Fig. 6).

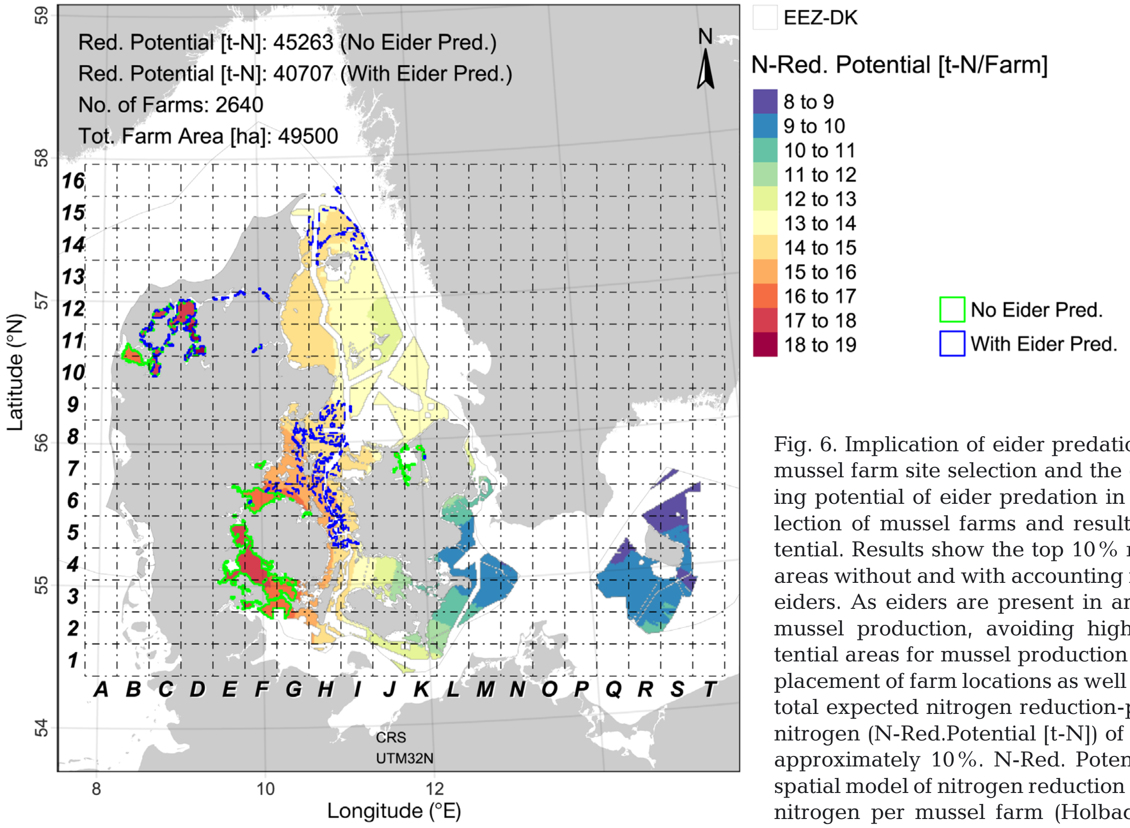

Fig. 6. Implication of eider predation potentials for mussel farm site selection and the effect of including potential of eider predation in optimal site selection of mussel farms and resulting harvest potential. Results show the top 10% most productive areas without and with accounting for predation by eiders. As eiders are present in areas suitable for mussel production, avoiding high predation potential areas for mussel production results in a displacement of farm locations as well as a decrease in total expected nitrogen reduction-potential in tons nitrogen (N-Red.Potential [t-N]) of mussel farms of approximately 10%. N-Red. Potential [t-N/Farm]: spatial model of nitrogen reduction potential in tons nitrogen per mussel farm (Holbach et al. 2020b)

4. DISCUSSION

4.1. Predicting eider predation potentials

Model results of eider predation potential on cultured mussels revealed huge spatial variability across Danish waters with no or only very minor risk of predation in inner parts of semi-enclosed estuaries such as Limfjorden (C10:F12) and Mariager Fjord (F11), and high predation potential in Little Belt (E4:F5) and the southern parts of Danish waters (G4:L1; Fig. 4). These findings support the expectations that eiders prefer shallow coastal waters in close connection with the open sea and that they only rarely cross larger landmasses or barriers and coincide with presence/absence observations of eiders at mussel longline field experiments (Fig. 4). Low predation potentials (≤0.25) were predicted at 6 test sites, and no eiders were observed at 5 of these. At the remaining 3 test sites, eiders were observed at or near the mussel lines, supporting a positive model validation as these locations received a high modelled predation potential. However, the model failed to predict the observed presence of eiders in Roskilde Fjord (Fig. 4). As eiders are not common in Roskilde Fjord, this was likely a flock of staging birds that had discovered the mussel test line by chance on the way to their winter location elsewhere in Danish waters. Although migration routes are included in the model, the predation potential along the routes might be underestimated. As eiders exhibit high site fidelity to their wintering area (Beuth et al. 2017), prefer shallow waters and avoid passing land barriers, the selected predictors for the potential occurrence of eiders seem robust. While it could be hypothesized that more food will attract consumers, which would result in higher eider abundances at locations with higher benthic biomass, this does not necessarily apply for eiders (Larsen & Guillemette 2000). For instance, in central Limfjord (C10:D12), which is optimal for blue mussel growth and production and has an intensive mussel fishery, eiders are rarely observed (R. S. Tjørnløv pers. obs.) and the model successfully predicts low potentials of predation in this area. The low occurrence of eiders in central Limfjord is likely due to the long and narrow strait (E12:G12) connecting the central part of Limfjorden with the open sea, which reduces the probability of encountering eiders. The overall good agreement between eider observations at mussel farms and model predictions indicate that the model captures the main features of potential habitats for eiders overwintering in Danish coastal waters and that the selected parameters addressing movement and habitat preferences are important characteristics for predicting the presence of eiders and the potential of predation. As mussel farming in Danish coastal waters is expected to increase in the coming years due to increased demand for sustainable food and livestock feed production, as well as for mitigation purposes (Petersen et al. 2021, European Commission 2012), more knowledge on the potential of predation by eiders and other sea ducks will become available and provide continuous validation of our results on the spatial potential of predation.

4.2. Implication for mussel farming site selection

The spatial variability in predation potential observed in this study implies that eider predation should be considered when selecting sites for mussel farming, as this could reduce biomass loss due to predation (Ross & Furness 2000) or avoid additional production costs for protection measures (Varennes et al. 2013). Most mussel farm site-selection tools focus on estimating growth potentials based on environmental conditions (Ferreira et al. 2007, Yin et al. 2018), and none of the existing tools take predation potentials into account. Most Danish coastal waters are very suitable for sustaining mussel growth (Holbach et al. 2020b), resulting in fast-growing mussels and a potential high yield if predation is avoided. However, predation by eiders may disrupt any harvest predictions and cost calculations, and change the optimal production site. By incorporating predation potential as a layer in site-selection tools such as MYTIGATE (Holbach et al. 2020a), it is possible to minimize or even avoid losses due to predation by eiders by choosing other locations with slightly less optimal conditions for mussel production (Fig. 6). Mussel production optimized for human consumption or mitigation purposes both depend on the harvested biomass. For food production, the harvested amount is directly linked to monetary gain, whereas the harvested mitigation mussels constitute the amount of nutrients permanently removed from the aquatic environment. Although eider predation on mussels undoubtedly transfers nutrients from short-lived mussels to long-lived birds, the fate of the nutrients becomes highly uncertain, partly because some of the nutrients ingested will be excreted by the birds. Using mussel farming as a management tool to mitigate eutrophication requires the certainty of permanent nutrient removal, which can only be provided by the harvested mussel biomass. Hence, in both cases (food production and mitigation), predation by eiders will decrease the biomass of harvested mussels and thus decrease the monetary or management value of mussel farming. Inclusion of predation potentials can thus guide site selection of mussel farming, as shown in this study where accounting for eider predation potentials resulted in a drastic displacement of the top 10% optimal locations (Fig. 6). Despite the value gained from our new model, it is still not possible to quantify the potential loss of biomass from mussel farms due to eiders. Therefore, the new layer can only be implemented as an exclusion criterion and not yet be used to re-estimate the expected harvest and nutrient reduction. Knowing the potential of predation by eiders could also be useful for mussel farmers located in high-potential areas, as protection of the farms would prevent stock losses. Several active and passive protection measures have been developed (Ross et al. 2001, Varennes et al. 2013) and even though protection does not prevent losses, it may significantly reduce the loss (Varennes et al. 2013).

4.3. Implication for eider conservation

Knowledge of potential eider habitats and foraging range are also an important part of eider conservation and management. Although eiders have been protected for decades as part of e.g. the EU bird directive and habitats directive, eider populations are declining (Ekroos et al. 2012). This imposes a need for improved management tools allowing for efficient protection of eider populations. Several environmental and anthropogenic-induced drivers, such as a decrease in wild blue mussel biomass (Laursen et al. 2009) or an increase in ship traffic (Schwemmer et al. 2011), could be responsible for the observed population decline. Thus, the predation potential map may facilitate identification of potential eider foraging habitats, which can be used to identify marine protected areas (Thaxter et al. 2012) or prohibit mussel dredging in habitats preferred by eiders.

4.4. Conclusion and future perspectives

This study provides the first attempt to model the distribution of eiders in Danish coastal waters taking into account site fidelity, migration routes and geotopographical habitat preferences. The parameterization of the current model is calibrated based on only a few qualitative predation observations. Although the approach and spatial model equation (Eq. 7) are capable of representing the majority of these observations, more reference points and preferably quantitative observations would be highly valuable for improving the quality and accuracy of the derived predation potential estimates. As monitoring data on eider observations only constitutes a snapshot of eider presence, habitat and eider distribution, modelling is important not only for mussel aquaculture but also for optimal eider conservation and impact assessment. The methodology developed in this study can easily be transferred to any other area occupied by eider ducks, provided that the necessary input datasets are available. Also, transfer to other bird species of interest is possible, if habitat preferences can be sufficiently described by similar spatial variables.

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