



Assessing the potential for sea-based macroalgae cultivation and its application for nutrient removal in the Baltic Sea



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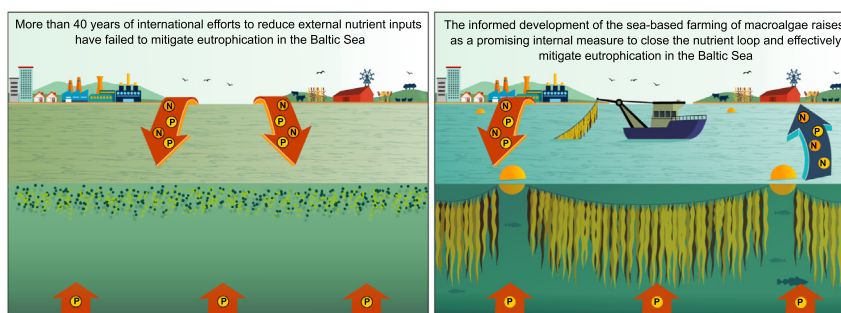
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HIGHLIGHTS

- Production potential of macroalgal farms is high in the Baltic Sea.
- Potential farm locations are widespread across the Baltic Sea.
- Different farmed species have different production hotspots.
- Macroalgal farms, when established, reduce eutrophication symptoms in the Baltic Sea.

GRAPHICAL ABSTRACT



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ABSTRACT

Marine eutrophication is a pervasive and growing threat to global sustainability. Macroalgal cultivation is a promising circular economy solution to achieve nutrient reduction and food security. However, the location of production hotspots is not well known. In this paper the production potential of macroalgae of high commercial value was predicted across the Baltic Sea region. In addition, the nutrient limitation within and adjacent to macroalgal farms was investigated to suggest optimal site-specific configuration of farms. The production potential of *Saccharina latissima* was largely driven by salinity and the highest production yields are expected in the westernmost Baltic Sea areas where salinity is >23. The direct and interactive effects of light availability, temperature, salinity and nutrient

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concentrations regulated the predicted changes in the production of *Ulva intestinalis* and *Fucus vesiculosus*. The western and southern Baltic Sea exhibited the highest farming potential for these species, with promising areas also in the eastern Baltic Sea. Macroalgal farming did not induce significant nutrient limitation. The expected spatial propagation of nutrient limitation caused by macroalgal farming was less than 100–250 m. Higher propagation distances were found in areas of low nutrient and low water exchange (e.g. offshore areas in the Baltic Proper) and smaller distances in areas of high nutrient and high water exchange (e.g. western Baltic Sea and Gulf of Riga). The generated maps provide the most sought-after input to support blue growth initiatives that foster the sustainable development of macroalgal cultivation and reduction of in situ nutrient loads in the Baltic Sea.

1. Introduction

The development of alternative methods to produce commodities such as food, feed, fuel, and pharmaceuticals is crucial to sustain the increasing human demand for natural resources. In this regard, marine ecosystems are often seen as a treasure trove to satisfy human needs (Hasselström et al., 2020; Rotter et al., 2021). Today more than 40% of the human population live near coastal areas and an increasing proportion relies on their services (Martínez et al., 2007; Neumann et al., 2015). As a result, these environments are subjected to an increasing diversity of impacts, thereby jeopardizing their sustainability (e.g. Dailianis et al., 2018; Gerovasileiou et al., 2019).

“Blue Growth” is a long-term initiative to support productive growth and the sustainable use of aquatic resources (FAO, 2018; World Commission on Environment and Development, 1987). Within the Blue Growth initiative, the cultivation of marine macroalgae is a promising enterprise in that it competes for neither arable land nor freshwater resources. Importantly, as macroalgae assimilate nutrients that are then removed from the marine environment upon harvest, macroalgal farming provides low-impact eutrophication remediation in coastal waterbodies currently degraded by excessive accumulation of nutrients (Campbell et al., 2019; Jiang et al., 2020).

The contribution by Europe to the global production of algal biomass is scant (0.57% in 2016) and relies almost exclusively on the harvesting of wild stocks (98% of the European production in 2016), while aquaculture-based technologies supplies most of the global supply (97% of the global production in 2016, Araújo et al., 2019, 2021). Due to concerns over potential in situ environmental impacts of the harvesting of wild stocks (Camia et al., 2018; Thomas et al., 2019), the number of companies engaged in aquaculture-based initiatives and algal-derived products has increased rapidly throughout Europe (Camia et al., 2018; Araújo et al., 2021). Nevertheless, seaweed aquaculture in Europe is in an early stage of development (FAO et al., 2019). Securing space for macroalgae cultivation in Europe (and elsewhere) requires an identification of areas with the highest production potentials. To date, most studies have been case-specific and developed at small scales (e.g. Thomas et al., 2019; but see van der Molen et al., 2018 for a modelling exercise at a regional scale). However, the modelling frame should cover wider geographic ranges to provide meaningful evidence at the scales (i.e. national, regional) at which maritime spatial plans (MSP) are developed.

The Baltic Sea has a long and well-documented history of scientific research, high data density and multiple on-going cross-border collaborations supporting the effective management of marine resources (Reusch et al., 2018). Nevertheless, more than 97% of the marine area in the Baltic Sea is currently considered degraded by eutrophication (Helin, 2013; Fleming-Lehtinen et al., 2015; Andersen et al., 2017; Breitburg et al., 2018), primarily due to the legacy nitrogen and phosphorus (HELCOM, 2018). Nevertheless, the excessive eutrophication in the Baltic Sea can be regarded as a rich and cost-free source of nutrients for macroalgal cultivation. Here, aquaculture can make a positive contribution to nutrient removal; the harvesting of internally produced macroalgae offers a potential for efficient recirculation of nutrients from sea to land. Despite salinity constraints, several characteristics of the Baltic Sea favour macroalgal farming for eutrophication control. First, nutrient limitation is less likely than in many other marginal seas (Kotta et al., 2017). Second, external nutrient control is inadequate to solve the eutrophication problem in the

Baltic Sea (Savchuk, 2018; Murray et al., 2019; Kotta et al., 2020). Third, and most importantly, developed economies around the Baltic Sea support a healthy and waste-free macroalgal production industry; responsibly produced macroalgae are attractive for regional consumers concerned about food traceability and content (Barbier et al., 2019). The first macroalgal farms are limited to the westernmost parts of the Baltic Sea where robust technical solutions have recently been developed (Thomas et al., 2019).

This paper presents an analysis of a large collection of recent measurements of macroalgal growth in the Baltic Sea region which forms the basis for a new model chain to predict the production potential of seaweed species of high farming potential in the Baltic Sea region (*Saccharina latissima*, *Ulva intestinalis* and *Fucus vesiculosus*). This production potential was modelled as the statistical relationships between environmental variables and macroalgal growth yield over the entire Baltic Sea region. An analysis of the potential nutrient removal by cultivated macroalgae in hypothetical farms and surrounding areas subsequently determined the optimal spatial configuration of farms with no significant effects of nutrient limitation on macroalgal biomass yields. Nutrient availability was modelled as a function of hydrodynamics, nutrient concentrations in seawater and the rate of nutrient assimilation of the farmed macroalgae. The modelling results provide a factual large-scale assessment of the feasibility of macroalgal farming and the potential of macroalgal farms to reduce nutrient loads in the Baltic Sea.

2. Material and methods

2.1. Environmental control of macroalgal growth

Seaweed growth in natural assemblages is controlled by both abiotic and biotic factors (Field et al., 1998; Hauxwell et al., 2003). However, abiotic constraints are often dominant in macroalgal farms, owing to the effective internal control of fouling by nuisance algae and grazing (Titlyanov and Titlyanova, 2010). Light, nutrient availability, temperature and salinity are thus key factors that drive growth patterns of macroalgae (Breeman and Pakker, 1994; Field et al., 1998; Hauxwell et al., 2003; Binzer et al., 2006).

Light availability is defined by the amount of irradiance arriving at the sea surface, the optical characteristics of the water and the self-shading within algal assemblages. The first two variables define the light field above underwater canopies and the maximum photosynthetic rates of macroalgae (Kirk, 1994; Anthony et al., 2004). Self-shading is a critical biological limitation in natural macroalgal assemblages, because it establishes the actual threshold for realized photosynthesis (Binzer et al., 2006; Tait and Schiel, 2010). In macroalgal farms, however, this limitation is less severe, because algae are suspended in the water, thereby enabling maximum use of the natural resources (e.g. light, and nutrients) and the highest possible algal yield (Titlyanov and Titlyanova, 2010).

Nutrient availability strongly affects the production of macroalgae (Raven and Hurd, 2012). Importantly, some macroalgal species can store nutrients in their tissues in order to circumvent temporal lack of nutrients (Lüning, 1990). Nevertheless, cultivated seaweeds grow better in areas with high nitrogen and phosphorous levels. Harvests in farms are inhibited, however, if macroalgae are cultivated too densely and/or the water exchange is insufficient to replenish the nutrient supply (Titlyanov and Titlyanova, 2010).

Temperature affects macroalgal production less than light and nutrients, unless the temperature is beyond the thermal tolerance of the species.

Within these limits, macroalgae exhibit relative uniform responses to temperature changes (Wiencke and tom Dieck, 1990). Even at extreme temperatures, a long-term acclimation of macroalgae is expected to significantly ease the constraints imposed by temperature (Nejrup et al., 2013).

Salinity is recognized as an important stressor that affects macroalgal habitats (Kaiser et al., 2011). The salinity gradients are most prominent in estuaries and/or semi-enclosed seas, such as the Baltic Sea, and are often characterized by a significant loss of marine taxa and a decrease of diversity towards low salinity conditions (e.g. Bonsdorff and Pearson, 1999). In such ecosystems, the salinity has a strong structuring role which may supersede the effect of other environmental variables, including nutrient availability, and this is especially true in areas where salinity conditions approach the species' tolerance limits (Krause-Jensen et al., 2007).

2.2. Standard macroalgal farms

Three seaweed species have high farming potential in the Baltic Sea region. The growth of *Saccharina latissima* is limited by overly high (>20 °C) or low temperatures (<5 °C) and by overly low salinity (<10–13) (Gerard et al., 1987; Spurkland and Iken, 2011; Nepper-Davidsen et al., 2019). Moreover, exposure to waves, turbidity and nutrient availability significantly affect the growth of *S. latissima*, although the exact responses to these variables are less known (Chapman et al., 1978; Mols-Mortensen et al., 2017). *Ulva intestinalis* is an opportunistic green alga that is widely distributed in littoral zones across the Baltic Sea. Due to its high production potential, *U. intestinalis* may form drifting algal mats in eutrophic embayments (Bäck et al., 2000). *U. intestinalis* tolerates a wide range of environmental conditions (e.g., salinity, temperature, light, pH, inorganic carbon) and, importantly, high nutrient availability enhances its resistance to environmental extremes. These properties have led to *U. intestinalis* being cultivated experimentally in the central (Gulf of Gdansk) and western parts (Hjarnø in Kattegat) of the Baltic Sea (Brzeska-Roszczyk et al., 2017; Christiansen, 2018). Salinity dictates the potential growth of the perennial brown alga *Fucus vesiculosus*, which in contrast to *S. latissima*, can inhabit almost the entire Baltic Sea region except for areas with salinity <4 (Barboza et al., 2019). In contrast to *U. intestinalis*, *F. vesiculosus* grows better under moderate nutrient enrichment. However, low performance at high nutrient levels is likely an indirect effect of biofouling (Wallentinus, 1984; Torn et al., 2006), which can be mitigated somewhat in algal farms (Meichssner et al., 2020). To date, a few small-scale experimental trials to farm *F. vesiculosus* in the Baltic Sea region have been initiated (Balina et al., 2018; Mikkelsen, 2019; Meichssner et al., 2020), but unlike *S. latissima* and *U. intestinalis*, robust technical solutions to cultivate *F. vesiculosus* remain lacking.

2.2.1. *Saccharina latissima* farm

The cultivation of *S. latissima* has expanded along the European Atlantic coast in recent years to meet the increasing demands for fresh algal biomass by many quickly developing industries. The size of existing farms ranges from fully commercial scale (ca. 100 ha) to experimental scale (a few ha). The raft systems employed in the cultivation can be constructed using either horizontal (long-line) or hanging ropes (garland and vertical types), but in general horizontal ropes are preferred for kelp mariculture in environments with moderate to high degrees of water motion (Peteiro et al., 2016). In our model, a standard *S. latissima* farm consists of a horizontal long-line cultivation system at 1 m depth covering 5 ha (200 × 250 m). The system consists of a series of 65 long-lines running parallel to one another and separated by 4-m access corridors. This provides a total of 12 km of long-line upon which kelp can grow. A typical deployment season for *S. latissima* in the Baltic Sea region would be from November to May. The initial biomass of *S. latissima* in the farm is 6 g ww per 1 m long-line. This farm is harvested once at the end of the deployment in May.

2.2.2. *Ulva intestinalis* farm

There are currently no commercial *Ulva intestinalis* farms in Europe (Burg et al., 2013), but floating nets are used to cultivate this species in

Asia (Ohno and Critchley, 1993). Experimental farms in the Baltic Sea have used either horizontal ropes (long-line) at Hjarnø (Kattegat) or nets in the Gulf of Gdansk and ropes and nets in the St. Petersburg region (Gulf of Finland) (Kovaltchouk, 1996; Kruk-Dowgiało and Dubrawski, 1998; Brzeska-Roszczyk et al., 2017; Christiansen, 2018). In this model, a standard *U. intestinalis* cultivation farm covers 5 ha of sea area (200 × 250 m). The farm contains 65 horizontal parallel ropes, each 200 m long, placed within 1 m depth. The average distance between ropes is 4 m. This provides a total of 12 km of long-line upon which *U. intestinalis* can grow. A typical deployment season for *U. intestinalis* in the Baltic Sea region would be from May to September. One harvest cycle is 1 month and the species can be harvested 5 times in a growing season. The initial biomass of *U. intestinalis* in the farm is 20 g ww per 1 m long-line.

2.2.3. *Fucus vesiculosus* farm

No commercial *Fucus vesiculosus* farm operates at present. In the model, a standard *F. vesiculosus* cultivation system covers 5 ha sea area (200 × 250 m). The farm contains 65 lines of adjacently placed 1 m³ cages at 1 m depth. The cages are placed parallel to one another and separated by 4 m access corridors. This provides a total of 13,000 cages within which *F. vesiculosus* can grow. A typical deployment period for *F. vesiculosus* in the Baltic Sea region would be from May to September. The initial biomass of *F. vesiculosus* in the farm is 900 g ww per 1 m³ cage (Fucosan, 2020). This farm is harvested once at the end of the deployment period in September.

2.3. Environmental data and species growth data

A compilation of all available experimental data relevant to macroalgal cultivation for the Baltic Sea region into a harmonized geo-referenced database ($n_{\text{total}} = 3334$; $n_{\text{Saccharina latissima}} = 219$; $n_{\text{Ulva intestinalis}} = 200$, $n_{\text{Fucus vesiculosus}} = 2915$; see supplement data) was used to model the growth of the selected species along the key environmental gradients. This diverse database included measurements from the existing macroalgal farms as well as data obtained from experimental studies of macroalgal growth under controlled conditions.

The most relevant ecological variables were selected to attain the most robust predictions of the role of the environment on macroalgal growth. Ill-suited variable selection may cause a model to include irrelevant variables and lower its predictive power (Mac Nally, 2000). Earlier studies have shown that macroalgal cultivation depends mostly on temperature, salinity, wave exposure, light and nutrient availability in the water (Titlyanov and Titlyanova, 2010).

The utilization of dissolved organic nutrients is common in the microbial community, whereas seaweeds primarily acquire dissolved inorganic nutrients. Nevertheless, dissolved organic nutrients can be an important source of nutrients for some macroalgal species in some ecosystems, often associated with low inorganic nutrient concentrations (Van Engeland et al., 2011; Li et al., 2016; Alexandre and Santos, 2020). In the nutrient rich Baltic Sea ecosystem, however, it is likely that this mode of nutrient acquisition is not prevailing. The organic nutrients are often first assimilated by bacteria and then transformed by bacteria into inorganic nitrogen or phosphorus forms, which are subsequently taken up by the macroalgae. As there are too many unknowns on seaweed-bacteria interactions and considering large spatial scale of our models, in the current paper only dissolved inorganic nutrients was used to predict large-scale patterns of macroalgal production potential in the Baltic Sea region.

Model inputs for the physical and biogeochemical conditions in the Baltic Sea were obtained from BALTICSEA_ANALYSIS_FORECAST_PHY_003_006, BALTICSEA_ANALYSIS_FORECAST_BIO_003_007 and BALTICSEA_ANALYSIS_FORECAST_WAV_003_010 within the Copernicus open access data portal (<http://marine.copernicus.eu/services-portfolio/access-to-products/>). These physical products covering the entire Baltic Sea area contain data with hourly resolution and 25 vertical levels. The biogeochemical data are provided with 6-hour resolution and 25 vertical levels. The horizontal grid in both products is regular in latitude and longitude and is approximately 1 nautical mile. The physical product is based on simulations with the HBM

ocean model HIROMB-BOOS-Model. The biogeochemical product is based on simulations performed with the BALMFC-ERGOM version of the biogeochemical model ERGOM, originally developed at IOW, Germany. The BALMFC-ERGOM version has been further developed at the Danish Meteorological Institute (DMI) and Bundesamt für Seeschifffahrt und Hydrographie (BSH). The BALMFC-ERGOM model is run online coupled with the HBM ocean model code. In our analyses, daily averages of environmental variables were used. Data for the global distribution of photosynthetically available radiation at the sea surface was obtained from Pfeifroth et al. (2017). This product covers the entire Baltic Sea area, is regular in latitude and longitude at a resolution of 0.05×0.05 degrees and contains data with daily resolution.

2.4. Modelling the growth yields of macroalgal farms along environmental gradients of the Baltic Sea

Growth models were based on algal dry weight yields estimated experimentally across the Baltic Sea as opposed to length measurements. This approach allowed the calculation of negative growth estimates during periods of resource limitation. Yields were normalized with the total incubation time (to produce data for daily yield).

Boosted Regression Trees (BRT; R 3.2.2. for Windows; Elith et al., 2008) were used to model the relationship between macroalgal growth yields and surface water temperature, salinity, irradiance, wave height, nitrates (NO_3^-) and phosphates (PO_4^{3-}) values obtained from the Copernicus products (see previous subsection). The established relationships were used to predict the macroalgal production potential for the entire harvest cycle of *S. latissima*, *U. intestinalis* and *F. vesiculosus* at the Baltic Sea scale.

In contrast to traditional regression techniques, BRT avoids starting with a data model, but rather uses an algorithm to ascertain the relationship between the response variable and its predictors (Elith et al., 2008). BRT models were used first to test if and how different environmental factors (predictors) contribute to the variability of measured dependent variables (training data). Then, BRT were used to predict potential production of macroalgae at the Baltic Sea scale based on the predictive model derived from the first step (model application). BRT models were then fitted using a learning rate, number of trees, and interaction depth set at 0.001, 3000, and 5, respectively. Once the plausible effects of environmental variables on dependent variables were ascertained, monotonic constraints were applied to better represent causality in the modelled relationships. The performance of the fitted models was evaluated using cross-validation statistics (Hastie et al., 2009). Standard errors for the predictions and pointwise standard errors for the partial dependence curves, produced using the R package “pdp” (Greenwell, 2017), were estimated using bootstrap (100 replications).

Unlike *S. latissima* and *U. intestinalis*, farm-scale estimates of the production potential of *F. vesiculosus* are unavailable. The only experimental *F. vesiculosus* farm in the Baltic Sea region consists of small plastic baskets with an edge length and volume of 28 cm and 14 L, respectively (Fucosan, 2020; Meichssner et al., 2020). When describing a standard macroalgal farm (see the subsection below), a similar caging approach was used, but with larger-volume cages (1 m³ each) to meet aquaculture requirements. However, algal self-shading in larger cages is expected to yield systematically lower algal growth than in smaller cages (Binzer et al., 2006). In order to account for light limitation in macroalgal canopies at farm scale, the predicted growth yields of *F. vesiculosus* (obtained from the previously described BRT procedure) were further corrected using an experimentally-driven function that predicts an expected reduction of *F. vesiculosus* growth along increasing biomass yield (Pärnoja et al., 2014).

2.5. Assessing nutrient removal at macroalgal farms

Farmed macroalgae can extract large quantities of dissolved inorganic nutrients from seawater. These nutrients are transformed into macroalgal biomass and then removed from the marine environment upon harvest (Sfriso et al., 2020). The rates of nutrient removal vary largely among algal species, but also within species, mainly due to differences in the

prevailing environmental conditions. Algal growth is optimal given a sufficient nutrient supply. However, when the uptake of nutrients by algae exceeds the import of nutrients, algal growth may be nutrient-limited leading to suboptimal growth conditions. To describe this situation, nutrient limitation at farms should be modelled as a function of hydrodynamics, nutrient concentration in seawater and the actual capacity of nutrient uptake by algae. Such models provide the means to account for short-term dynamics of growth conditions and thereby suggest working solutions to avoid nutrient limitation within farms.

The nutrient limitation of macroalgae growth was modelled using the following linear relationship:

$$\frac{dB}{dt} = rf(N, P),$$

where B [kg] is macroalgal biomass in wet weight, r daily growth rate [kg/(day*m)] for *S. latissima* and *Ulva intestinalis*, [kg/(day*m³)] for *Fucus vesiculosus* and $f(N, P) \in \{0, 1\}$ is the nutrient limitation function [non-dimensional].

The nutrient limitation function was calculated as follows:

$$f(N, P) = \min(N_{lim}, P_{lim}),$$

and

$$N_{lim} = \frac{N^x}{KN^x + N^x},$$

$$P_{lim} = \frac{P^x}{(KN * rfr)^x + P^x},$$

where x is a scaling factor ($x = 1$ equivalent to Michaelis-Menten function), KN is the half saturation concentration of nitrogen and rfr is the Redfield ratio with $x = 0.9$, $KN = 1.2$, $rfr = 1/16$.

N and P are daily concentrations of inorganic nitrogen and phosphorus respectively at the model grid of 1 km². The concentrations were obtained from the coupled NEMO-ERGOM model (BALTICSEA_ANALYSISFORECAST_BIO_003_007). The N and P concentrations at the grid cell are affected by advection and diffusion due to hydrodynamics and local biogeochemical processes.

The macroalgal growth rates were obtained from the Boosted Regression Trees (BRT) models (see the subsection “Modelling the growth yields of macroalgal farms along environmental gradients of the Baltic Sea” above for further details). The daily recycling of nutrients was represented through the growth rate coefficient, r . The initial biomass of macroalgae was defined by the size of the macroalgae farm in the grid cell of 1 km². The modelling was performed for the realistic period of deployment defined for the different standard macroalgal farms (see the subsection “Standard macroalgal farms” above). The macroalgal wet biomass was converted to mass of removed N and P at the farm scale using the following conversion coefficients for N and P (share): *S. latissima* 0.640 and 0.120; *U. intestinalis* 0.114 and 0.017; *F. vesiculosus* 0.139 and 0.028, respectively.

The standard macroalgal farms described in this study are small and, in such settings, nutrient limitation is unlikely due to the high internal reserve of nutrients in the Baltic Sea. However, nutrient limitation may develop and farm production yields may decline, if too many small farms are located in the same area. The avoidance of this situation requires site-specific estimates of the minimum distance between standard macroalgal farms to assure optimal growth rates. This study used actual hydrodynamic data, expected site-specific growth potential of macroalgae (obtained from the BRT models above) and applied a simplified model framework to estimate the uptake of nutrients by algae and the plausible propagation of the effect of nutrient reduction in space. For this, the daily mean current velocity at each location was calculated using the NEMO model (BALTICSEA_ANALYSISFORECAST_PHY_003_006). These daily mean velocities were multiplied by time to obtain the distance of the uptake of nutrients by algae and the propagation of nutrient reduction in space within a day. The critical

distance between farms was calculated as the square root of the area from which farms removed more than 5% of the available nutrient stock from the control volume (upper 10 m water layer). Then, daily means were averaged over the entire deployment period of the macroalgal farms. This was then used as the maximum between-farm distance in which two macroalgal farms can effect each other in terms of nutrient availability.

3. Results

3.1. Spatial models

3.1.1. *Saccharina latissima*

The fitted BRT models accounted for 98.7% of the variation in the production yield of *S. latissima*. Salinity was the most important predictor in the model explaining 98% of total variability, followed by the marginal contribution of wave height. At salinities >23 the production yields were high and stable. Algal production was significantly lower in less saline environments with virtually no production at salinity <15. The elevated local exposure to waves reduced production but this effect was orders of magnitude weaker compared to the effect of salinity (Fig. S1).

As predicted by the environment-production relationships, the highest production yields can be expected in the westernmost areas of the Baltic Sea where salinity is constantly >23. The environmental conditions suitable for the cultivation of *S. latissima* abruptly deteriorate further south with the southernmost plausible farming region predicted in southern Denmark and northern Germany (Fig. 1).

3.1.2. *Ulva intestinalis*

The BRT model accounted for 72.5% of the variance in the production yield of *U. intestinalis*. Solar irradiance, temperature and nitrate concentration were the most important variables accounting for 80% of the model variability (58% of total variability explained). The remaining variability was explained by water phosphate, salinity and wave height. In general, the production yield was higher at elevated values of all these

environmental variables exhibiting a saturation behaviour above particular light, nutrient and salinity threshold values (Fig. S2). Moreover, salinity interacted strongly with nitrate and irradiance. At salinities >4, the response of algal production to changes in irradiance and nitrate were stronger (Fig. S3).

Due to its broad environmental tolerance, *U. intestinalis* had a wide spatial distribution of production hotspots, covering all Danish Straits, the coasts of southern Sweden, Germany, Poland, Lithuania, Latvia and Estonia (Fig. 2). The expected farm yields at these hotspots are in all cases >0.75 kg ww m⁻¹. Low production zones were limited to the northernmost parts of the Baltic Sea (e.g. Bothnian Bay) and the easternmost parts of the Gulf of Finland where the expected production yields were almost zero.

3.1.3. *Fucus vesiculosus*

The BRT model fitted on the production yield of *F. vesiculosus* accounted for 84.7% of the variance. Solar irradiance, water nitrate, temperature and salinity were the most important variables, accounting for more than 90% of the model variability (78% of total variability explained). The remaining 10% was attributed to water phosphate and wave height. Algal production increased monotonically in response to most of the studied environmental variables, attaining a plateau at high ranges of environmental variables. However, increasing concentrations of water phosphate resulted in an abrupt reduction in production (Fig. S4). The BRT modelling also unveiled strong interactive effects between temperature, irradiance and salinity. Specifically, at high irradiances the production yields were high regardless of temperature and salinity values. In addition, elevated nitrate values triggered stronger response of production yields to changes in temperature (Fig. S5).

Clear hotspots of *F. vesiculosus* production were identified in the western Baltic Sea. However, high production values were also predicted across the southern Baltic and along the Polish, Lithuanian and Estonian coastlines (Fig. 3). The expected production yield at these hotspots attained as much as 1.5 kg algae per m³ cage. The production potential gradually decreased to zero in the marginal habitats of the Baltic Sea (e.g. in Bothnian Bay,

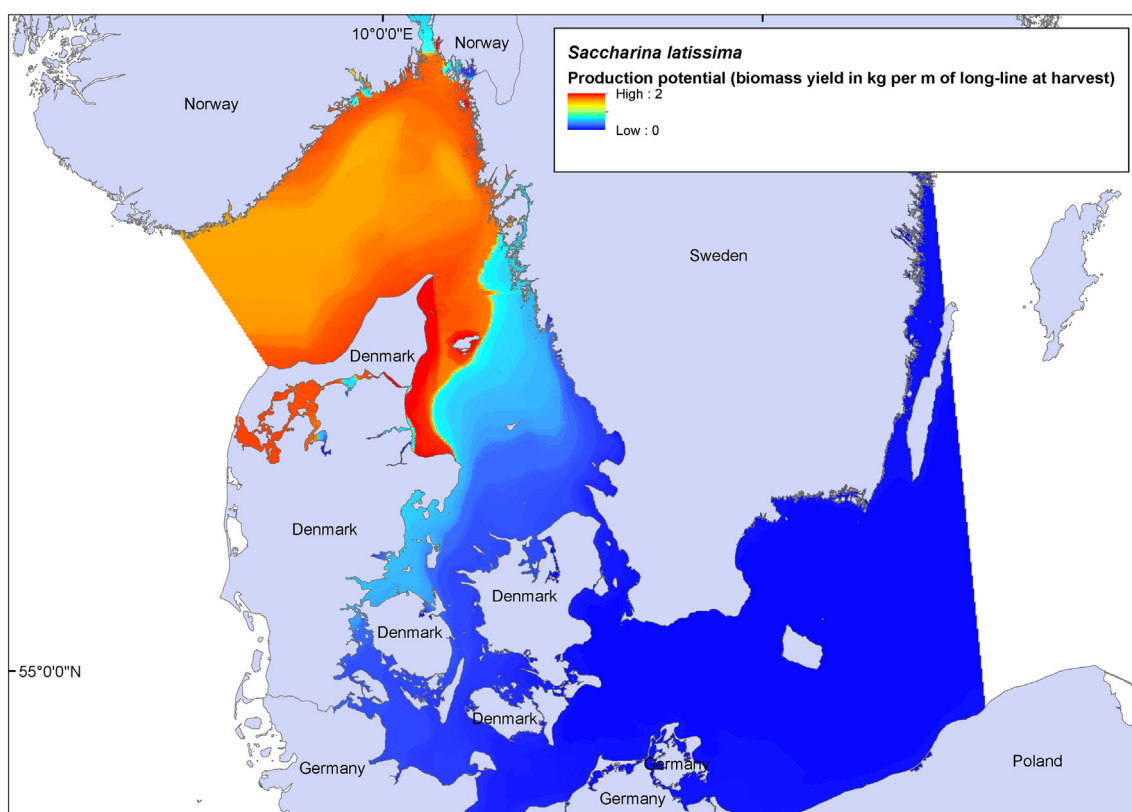


Fig. 1. The production potential of *Saccharina latissima* per harvest in the Baltic Sea area (kg algae per m of long-line at harvest).

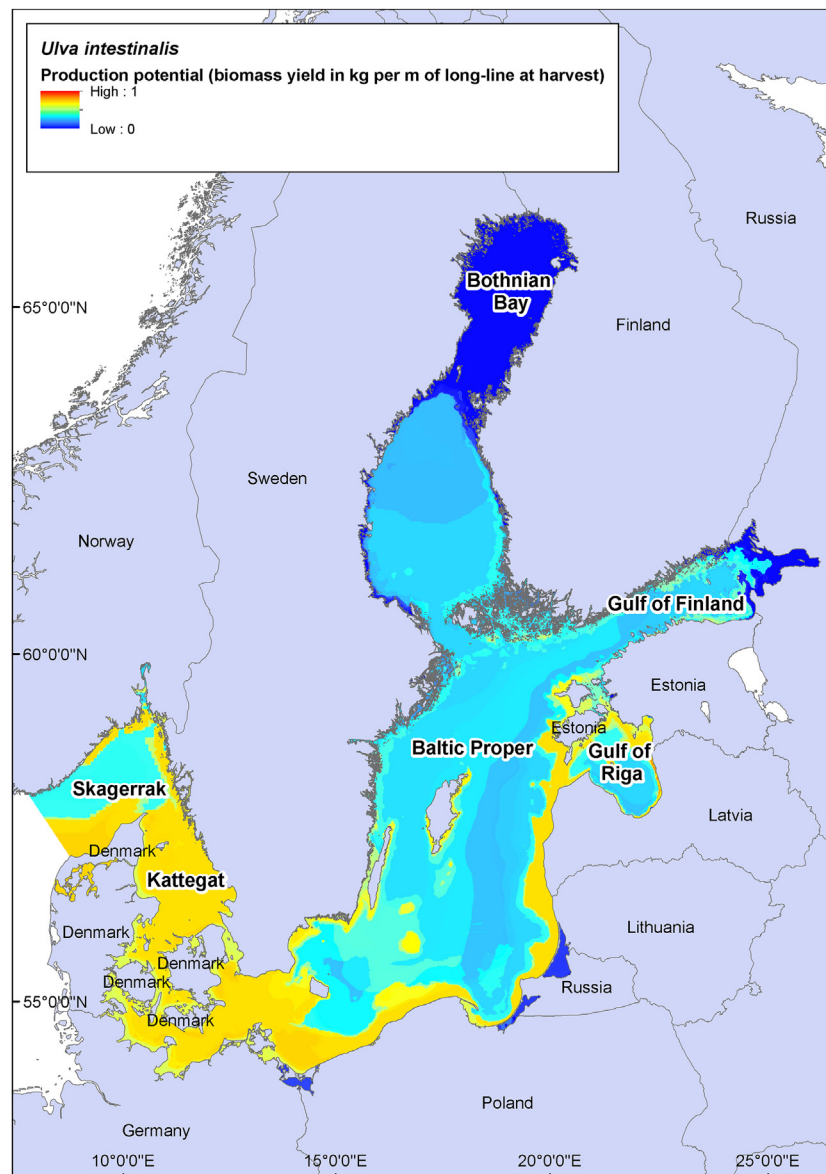


Fig. 2. The production potential of *Ulva intestinalis* per harvest in the Baltic Sea area (kg algae per m of long-line at harvest).

the Gulf of Riga and the eastern parts of the Gulf of Finland). In these regions salinity is below the lower threshold for the algal species.

3.2. Nutrient removal at farms

Saccharina latissima was most efficient in nutrient removal in the Skagerrak area (Fig. 4A, B). The amount of N and P removed at the farm scale during the deployment period was a few tens of kg. The farm efficiency to extract nutrients drops down several orders of magnitude in an abrupt transition zone between Skagerrak and Kattegat. This transition zone closely matches the location of the salinity front between the Skagerrak (salinities ca 30) and the Kattegat (salinities 18–26). The Skagerrak area is suitable for the farming of *S. latissima* owing to the high current speeds that bring nutrient-rich waters from adjacent areas to the farms, while displacing nutrient-depleted waters from the farms to the adjacent region (Fig. 5A). Over a cultivation cycle, one *S. latissima* farm can remove up to 0.07% of available nitrogen and phosphorus from a 1 km² sea area (Fig. 6A, B). Consequently, in terms of nitrogen the critical minimum distance between two *S. latissima* farms without inducing nutrient limitation on macroalgal production yields is 100 m. However, in terms of phosphorus this distance is often only 30 m (Fig. 7A, B).

Ulva intestinalis and *Fucus vesiculosus* showed similar nutrient removal patterns. The highest removal hotspots were located adjacent to river estuaries of the western and southern Baltic Sea and in the Gulf of Riga and in the Bothnian Sea. While *U. intestinalis* had a higher nutrient removal potential in coastal areas, the nutrient removal potential of *F. vesiculosus* was higher in offshore areas. In high productivity areas, a single farm of *U. intestinalis* can remove up to tens of kg of nutrients, and a *F. vesiculosus* farm can remove up to a few kg of nutrients. In the estuaries of large rivers of the southern Baltic Sea, the removal of nutrients can be an order of magnitude greater (Fig. 4C–F). The daily mean distance over which the influence of *U. intestinalis* and *F. vesiculosus* can potentially spread exceeds 5 km in the offshore areas of the Gulf of Bothnia, the Gulf of Finland, the Gulf of Riga and the Baltic Proper. In coastal areas of the Bothnian Sea, the Gulf of Finland and the Baltic Proper the distance is three times longer (Fig. 5B). Over a cultivation cycle, a farm of *U. intestinalis* or *F. vesiculosus* can remove up to 0.30% or 0.15% of the available nutrient stocks from a 1 km² sea area, respectively (Fig. 6C,D). The critical minimum distance between two farms without inducing nutrient limitation is 150 m for *U. intestinalis* and 250 m for *F. vesiculosus*. However, the critical distance can be <100 m for *U. intestinalis* and <150 m for *F. vesiculosus* in many regions (Fig. 7C–F). Importantly, the expected spatial propagation of nutrient

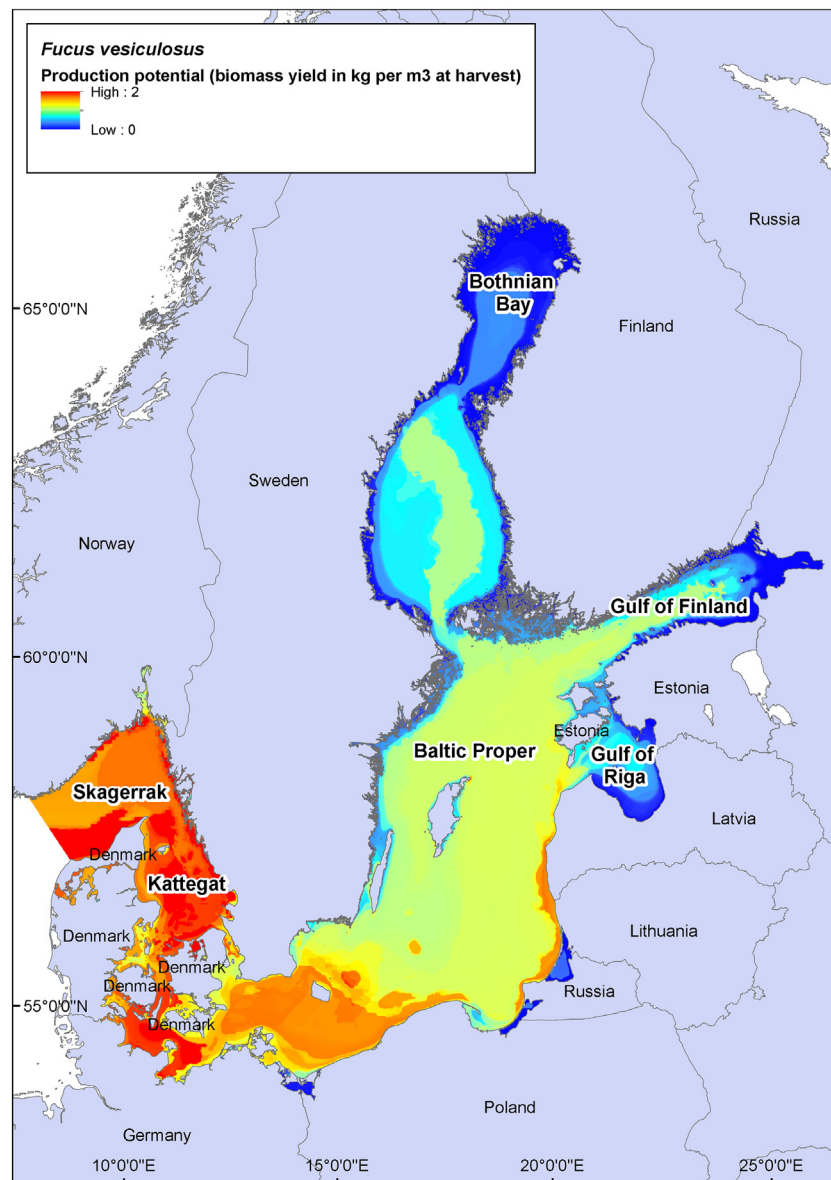


Fig. 3. The production potential of *Fucus vesiculosus* per harvest in the Baltic Sea area (kg algae per m³ of incubation cage at harvest).

limitation due to macroalgal farming is always greater for nitrogen than for phosphorus.

4. Discussion

4.1. Species-specific production potential in the Baltic Sea

The models and derived spatially explicit predictions of production potential for *S. latissima*, *U. intestinalis* and *F. vesiculosus* presented provide the first region-wide assessment of the environmental suitability for the development of macroalgal farming in the Baltic Sea. The large-scale, empirical and integrative nature of the generated evidence revealed the opportunities the heterogeneous environmental mosaic of the Baltic Sea offers for the development of sea-based macroalgal aquaculture. Beyond the intuitive production hotspots predicted in the more saline western Baltic Sea for all analysed species, promising areas to cultivate *U. intestinalis* and *F. vesiculosus* were also identified in the less saline eastern sub-basins. Predicted biomass yields and the estimated distances required to prevent nutrient limitations in farms suggest that viable macroalgal farming initiatives relying on different species are possible across the region. This finding —

along with the spatially defined estimates for nutrient removal at farms — provides the required input for an informed and coordinated consideration of sea-based macroalgal aquaculture as a viable internal measure for mitigating eutrophication at the Baltic Sea scale.

4.1.1. *Saccharina latissima*

The predicted changes in production yields for *S. latissima* closely followed the steep salinity gradient in the western Baltic Sea, being the main limiting factor for the development of *S. latissima* farms in the region. Consequently, the viability of *S. latissima* farming is expected to be greatest in the Skagerrak area and northern Danish Kattegat, where the species finds favourable salinity conditions (>23, Snoeijis-Leijonmalm and André, 2017) in which to grow and produce biomass (*S. latissima* shows its photosynthesis and growth optima in salinities between 23 and 35; Gerard et al., 1987; Karsten, 2007; Peteiro and Sánchez, 2012). Interestingly, even if *S. latissima* attains much greater production under field conditions along adjacent oceanic areas, predicted production yields for northern Denmark did not differ greatly from those reported, for example, for the Norwegian west coast (Göran Nylund, pers. comm.). The final biomass of *S. latissima* yield at farms depends strongly on cultivation practices and technologies

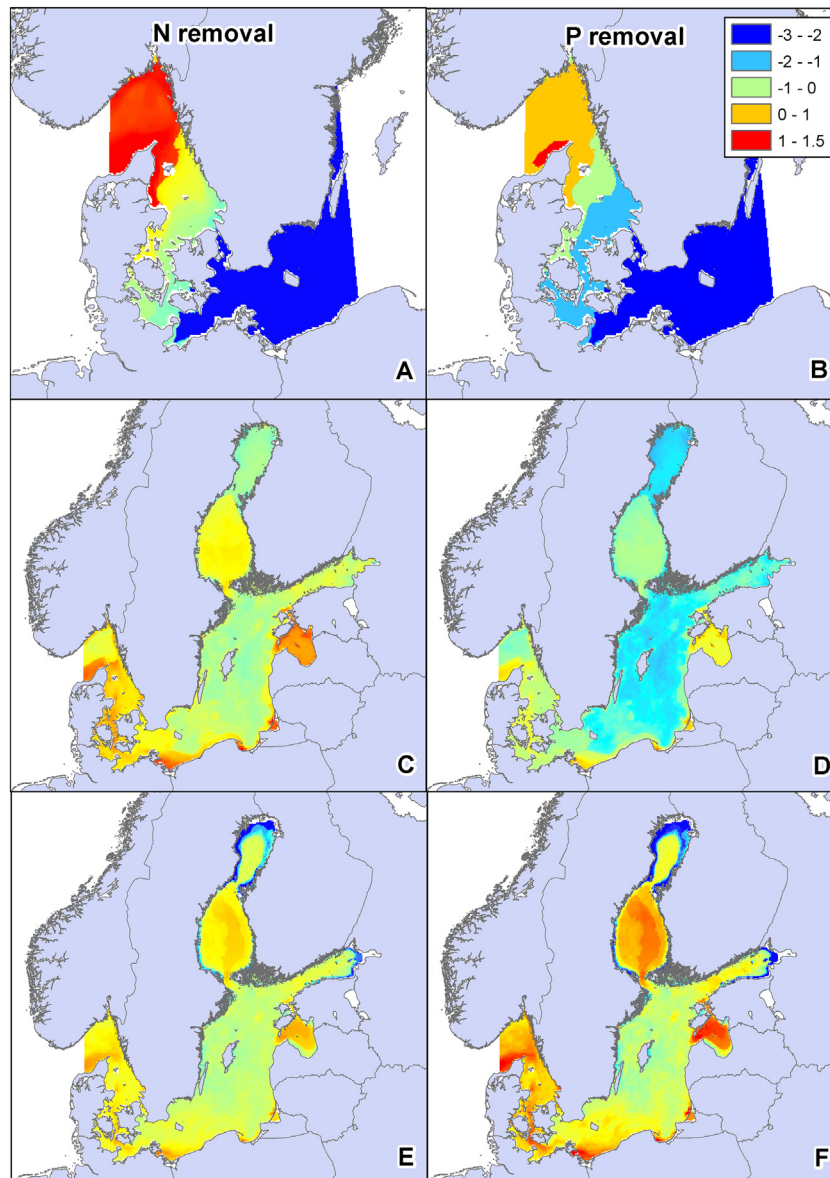


Fig. 4. The amount of N and P removal (kg per harvest) by farms of *Saccharina latissima* (A, B), *Ulva Intestinalis* (C, D) and *Fucus vesiculosus* (E, F). Note that the predicted amounts on colour bars are given in log₁₀ scale.

applied (such as the design of the cultivation system or deployment timing), which help to compensate the effects of biotic and abiotic factors with consequences on production (e.g., salinity, exposure or fouling, Boderskov

et al., 2021 and references therein). The growth of *S. latissima* decreases southward with the decrease in salinity along the western Baltic Sea (Nielsen et al., 2014, 2016) and with it, the possibility of attaining viable

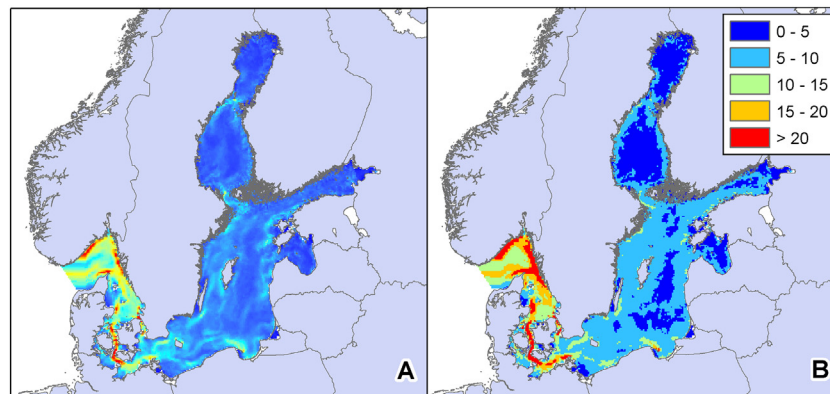


Fig. 5. The daily average travelling distance of surface water (km) during the deployment period of *Saccharina latissima* (A), *Ulva Intestinalis* and *Fucus vesiculosus* farms (B).

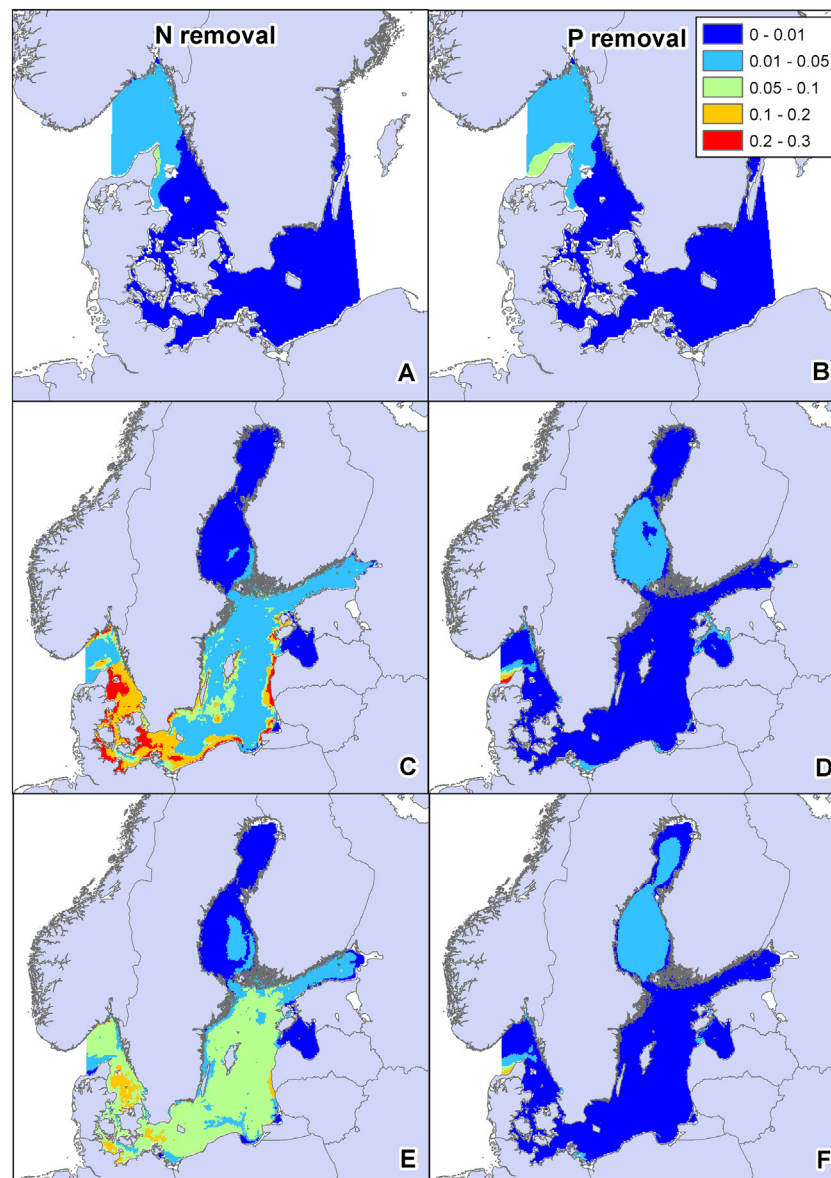


Fig. 6. Mean N and P daily removal by farms of *Saccharina latissima* (A, B), *Ulva Intestinalis* (C, D) and *Fucus vesiculosus* (E, F) relative to N and P stocks in percentage. This is calculated as N (P) uptake by a farm in a day divided by the mass of total N (P) in a grid cell of 1 km² and 10 m depth. Daily values are averaged over the period of farm deployment.

production levels for farms to function at a fully commercial scale. Although sea-based cultivation has been developed as far south as in the Kiel Fjord (Wang et al., 2019; Weinberger et al., 2020), ecophysiological studies have reported lower growth rates for *S. latissima* at the prevailing salinities of the area (i.e., 16, Bartsch et al., 2008 and references therein). This situation is expected to worsen further east. Salinity conditions beyond those prevailing in the Danish straits (<10) are expected to constrain severely the physiological performance of the species, compromising its photosynthetic machinery, dampening its growth and dramatically increasing mortality rates (Bartsch et al., 2008; Spurkland and Iken, 2011), rendering commercial sea-based production of *S. latissima* unfeasible.

4.1.2. *Ulva Intestinalis*

The high production levels predicted for both *U. intestinalis* and *F. vesiculosus* farms along the southern and eastern coasts of the Baltic Proper, and for *U. intestinalis* in the Gulf of Riga, provide auspicious estimates for the development of farming projects utilizing these species in less saline areas of the Baltic Sea. The wide salinity tolerance breadth of *U. intestinalis* allows the species to transiently endure salinities near 0

(Kamer and Fong, 2000) and to grow actively in salinities between 5 and 10 (e.g., Martins et al., 1999; Ruangchuay et al., 2012), making this species an ideal candidate for farming initiatives in low salinity waters that other commonly farmed macroalgae cannot osmotically withstand. As evidenced by the main and interactive effects estimated in our fitted models, light and nitrate availability as well as temperature outweigh the role of salinity in conditioning the capacity of *U. intestinalis* to produce biomass under farming conditions. Previous experiments indicate that nitrogen enrichment mitigates the negative impacts that lower salinities might have on *U. intestinalis*, allowing the species to proliferate in brackish systems (e.g., Kamer and Fong, 2001; McAvoy and Klug, 2005). Additional evidence has shown that light >90 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ and temperatures >15 °C strongly stimulate the growth of germlings of this green alga and might help to compensate the effects of low salinities at this life stage (Kim and Lee, 1996; Kim et al., 2021). Thus, under the favourable nutrient conditions of the eutrophic waters of the Baltic Sea and with abundant light levels, the standard farms received by the surface layers, *U. intestinalis* can maintain high production levels in spite of osmotic constraints (provided that salinities do not attain steady lethal levels). Moreover, if these conditions

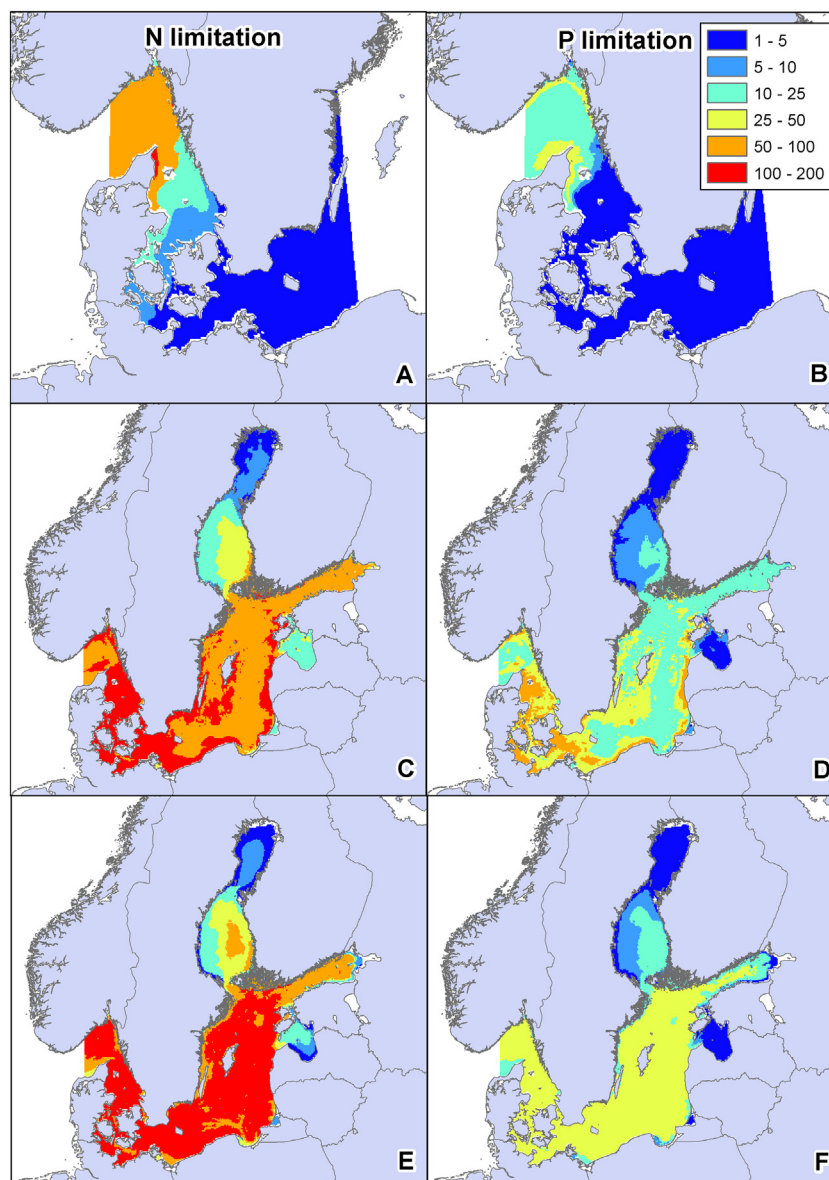


Fig. 7. Critical minimum distance between two farms (m) of *Saccharina latissima* (A - nitrogen, B - phosphorus), *Ulva Intestinalis* (C - nitrogen, D - phosphorus) and *Fucus vesiculosus* (E - nitrogen, F - phosphorus) to avoid nutrient limitation impacts on algal production yields.

couple with prolonged warm seasons, even higher production yields may be expected (e.g. as in the Gulf of Riga, which is a shallow, warm and nutrient rich environment). Therefore, it can be expected that farms producing *U. intestinalis* located on the coasts of Poland, Lithuania, Latvia and Estonia could be as productive as those established in the western Baltic Sea.

4.1.3. *Fucus vesiculosus*

The models suggest that *F. vesiculosus* also qualifies as an attractive species for farming in the eastern Baltic Sea. Despite exhibiting drops in productivity earlier in the salinity gradient than *U. intestinalis*, our predictions indicate that this species is still capable of considerable biomass production in the southern and eastern coasts of the Baltic Proper. In this context, previously described Baltic populations of *F. vesiculosus* locally adapted to the low salinity conditions (e.g. Kautsky et al., 2019) represent ideal primary sources for effective farming. Similar to *U. intestinalis*, light and nitrate availability were key determinants of the production potential of *F. vesiculosus*, partly offsetting the impacts of decreasing salinities. High nutrient concentrations have been proved experimentally to help *F. vesiculosus* tolerate reduced salinities (Nygård and Dring, 2008) and earlier studies

have also shown that discharges of nutrient enriched sewage can stimulate the growth of the species under critical salinities (Waern, 1952; Pekkari, 1973). Large rivers in the southern Baltic Sea and in the Gulf of Riga transport significant amount of nutrients to the sea. The currents are not overly strong, thereby maintaining high nutrient concentrations in these coastal areas all year round with limited dilution to offshore waters (e.g. Soosaar et al., 2016). These conditions suggest that the nutrient rich waters of the Baltic Sea might help to boost the productivity of *F. vesiculosus* farms beyond the limits imposed by the prevailing brackish conditions.

4.2. Macroalgal farming: practical considerations for eutrophication mitigation

Farming of macroalgae in the Baltic Sea is today regarded as a promising approach both to increase and diversify the sea-based production of food and raw material and as an internal measure to mitigate the pervasive impacts of eutrophication. Attaining this goal requires the identification of species-specific suitable areas for farming and the development of cognizant strategies to expand macroalgal farming in the region. These strategies should consider both the constraints that might arise from increasing the density of farms and the capacity of farms to reduce nutrient loads in

different waterbodies. Careful consideration should be given to the spatial configuration of farms in order to avoid exceeding the carrying capacity of the environment and assure sufficient distances between farms to prevent nutrient limitations on production yields (Campbell et al., 2019). Furthermore, the selection of farm sites must consider not only areas of optimal growth but also waterbodies suffering most from eutrophication, such as shallow coastal areas. Consequently, by modelling the dynamic of nutrients as a function of concentrations in the water, hydrodynamics and the rate of nutrient assimilation of macroalgae cultivated at defined standard farms, reductions in nutrient loads at species-specific farms and their effects on surrounding areas could be estimated.

Surprisingly, the propagation of nutrient reduction effects around standard farms was not extensive, indicating that the prevailing hydrodynamics and the availability of nutrients in the Baltic Sea allows the placement of farms in relatively close proximity (in the range of 100–250 m, and even less in some sub-basins). Higher propagation distances were found in areas of low nutrient and low water exchange (e.g., offshore areas in the Baltic Proper), while shorter distances were predicted in areas of high nutrient and high water exchange (e.g., western Baltic Sea, Gulf of Riga). Nutrient limitation between standard macroalgal farms in the Gulf of Riga is only expected at distances less than 10–20 m. Together with the already described species-specific environmental suitability for biomass production, the general estimated minimum placement distances for farms embolden the scaling-up of cultivation projects and the overall expansion of the industry.

U. intestinalis and *F. vesiculosus* farms offer an effective remedy to ease the burden of excessive nutrient loads in the Baltic Sea. The models indicate similar ability of these two species to sequester nutrients. A single farm can remove a few tens of kg of N or several kg of P per harvest, especially in coastal areas and sheltered bays that are phosphorus limited i.e. characterized by elevated ratio of nitrogen to phosphorus (Kõuts et al., 2021). Elevated removal is expected in the Gulf of Riga, the Bothnian Sea, and in the southern coastal areas of the Baltic Proper as well as in the Skagerrak-Kattegat area. Of note, even if the Gulf of Riga stands out as an area of particularly high nutrient removal capacity, the predicted sequestration can be somewhat overestimated as the coupled NEMO-ERGOM model reproduces nutrient fields of low quality in this area (e.g. Kõuts et al., 2021). Additionally, an important impact on available nutrient budget is also expected in open areas of the Gulf of Finland for both *U. intestinalis* and *F. vesiculosus*, but only for *U. intestinalis* along the coastlines. The width of this coastal zone, as depicted in the maps, matches the described area of high spring phytoplankton production in the Gulf of Finland (Lessin et al., 2009), giving rise to potential negative competitive effects for *F. vesiculosus*. The ability of *F. vesiculosus* to store nutrients in their thallus might be insufficient to cope with the accelerated depletion of nutrients caused by blooming phytoplankton, leading to lower growth and nutrient removal performance in this area. By contrast, *U. intestinalis* is a faster growing species (Wallentinus, 1984) that can better compete with phytoplankton for nutrients, thereby outperforming *F. vesiculosus* in the coastal areas of the Gulf of Finland.

Nutrient removal at macroalgal farms is a co-product of site-specific macroalgal productivity and nutrient availability. Thus, spatial differences in the growth pattern of macroalgae would lead to macroalgal farms having differing potential for eutrophication mitigation within the Baltic Sea. As *S. latissima* finds favourable growth conditions in the western Baltic Sea, only *U. intestinalis* and *F. vesiculosus* can be farmed in other subbasins to mitigate the pervasive impacts of eutrophication. Here, *U. intestinalis* shows greater potential as it thrives in highly eutrophicated less saline embayments where *F. vesiculosus* cannot grow. Moreover, given its shorter cultivation cycle, the annual nutrient removal potential of *U. intestinalis* is several times greater than that of *F. vesiculosus*. It is important to stress though that practical applications may differ from our modelled scenario, especially if farm configurations are significantly different than our standard farms (as different initial standing stocks and productivity result in different nutrient sequestration).

4.3. Macroalgal farming: application and future perspectives

The maps and underlying models offer essential input for the direct inclusion of sea-based macroalgae aquaculture in national strategies and maritime spatial planning across the Baltic Sea, which to date has been neglected (Camarena Gómez and Lähteenmäki-Uutela, 2021). These models explicitly incorporated experimental evidence on the effects of relevant environmental drivers on macroalgal growth and of production measurements obtained at actual farms, allowing to better represent cause-effects relationships in models of correlational nature (given the regional scale of the analysis), to increase the realism of obtained predictions on biomass production and to facilitate their extrapolation to real farms. Furthermore, the generated products helped to define suitable areas for the placement of macroalgal farms and to evaluate their effects on nutrient budgets of different water masses.

The latter aspect is very important as the sustainable expansion of macroalgal farming supports not only food security, sustainable agriculture and responsibly managed living aquatic resources, but also contributes to the regional targets of nutrient emission reduction in the Baltic Sea region (HELCOM, 2013). Moreover, farmed macroalgae are also recognized as sites of intense carbon sequestration and storage, thereby representing eco-industrial production systems that mitigate both marine eutrophication and climate change (Zhang, 2021). Nevertheless, macroalgal farming can realize their role in carbon sequestration only under specific management conditions (Duarte et al., 2013; Trevathan-Tackett et al., 2015). Thus, despite clear evidence that macroalgae contribute to carbon sequestration there is still considerable disagreement as to whether macroalgae and macroalgal farms meet the criteria to be considered within the blue carbon framework (Howard et al., 2017; Smale et al., 2018; Zhang, 2021).

To date, macroalgal farms are limited mostly to the westernmost parts of the Baltic Sea where some commercial scale farming solutions have been recently developed (Thomas et al., 2019). Consequently, the production cost of macroalgae in the Baltic Sea region remains uncertain, which makes it challenging to quantify the economic value of the nutrient removal by macroalgal farming in the Baltic Sea. Nutrient trading alone cannot probably cover the costs of farming in practice. However, as macroalgal farming relates to multiple ecosystem services including climate regulation, storm protection, biogeochemical cycling and provisioning of food and habitat, or refugia to support secondary production for wild capture fisheries (e.g. Corrigan et al., 2022), macroalgal farming significantly improves environmental sustainability and economic viability beyond nutrient mitigation. These aspects need to be investigated jointly in future studies to ensure viable macroalgal farming in the Baltic Sea region.

However, as this new information becomes available, the map layers developed in this paper can be combined with maps of other ecosystem services provided by macroalgal farms, as well as of other human uses in order to find synergies, trade-offs and avoid potential conflict over resources and/or space with other existing maritime sectors. These maps may also point out aspects that prevent macroalgal farming e.g. sites containing high loads of toxicants. When *S. latissima* or *U. intestinalis* is intended for human consumption, farms should be in areas with no chemical pollution to ensure high product quality. To operationalise the modelled data, the map layers of macroalgal farm production were published along with mussel farming potential (Kotta et al., 2020) in the Operational Decision Support System (ODSS) developed to support maritime spatial planning processes in the Baltic Sea. All environmental data from potential macroalgal cultivation sites, the results of the spatial modelling of production potential and effects on nutrients loads is accessible to all through the user-friendly ODSS online platform at <http://www.sea.ee/bbg-odss/Map/MapMain>. Through its analytical capabilities to synthesize and disseminate up-to-date information and knowledge to different end-users, the ODSS is designed to facilitate and improve the quality of decision-making processes of maritime spatial planners, scientists, policy actors and investors. Previously, stakeholders lacked the capacity to address the environmental aspects of macroalgal and mussel production in the Baltic

Sea as no data-driven tools relying on harmonized information were available. The models and maps provided here, and their open-access availability through the fully functional ODSS web application, provide scientific support for public authorities on the opportunities and challenges of farming native macroalgae and bivalve species as an internal measure to remove excess nutrients already present in the Baltic Sea. Just a few small-scale macroalgal and mussel farms can mitigate the adverse effects of coastal eutrophication, by efficiently recirculating nutrients from sea to land while providing valuable marine resources for fuel, food, feed, bioenergy and raw material. While internal measures for nutrient regulation cannot completely eliminate eutrophication, they can complement external measures, which are likewise themselves inadequate (Savchuk, 2018). Lastly, the maps can serve to reveal the potential of sea-based low trophic aquaculture production in the Baltic Sea region and to generate data-driven support for the required legislative framework.

5. Conclusions

The western and southern Baltic Sea exhibited the highest farming potential for the studied macroalgal species, along with a few promising areas being identified in the southern and the eastern Baltic Sea. Farms in these areas also have the highest efficiencies of nutrient removal. The results presented above provide factual data to support political decision making on internal measures for eutrophication control and to promote the sustainability of the Baltic Sea region through macroalgal farming for nutrient management. Eutrophication is a leading cause of impairment of many aquatic ecosystems including the Baltic Sea. While external measures to control nutrient inputs must be pursued, internal measures to restore water quality and enable ecosystem recovery must be implemented in a timely manner. Macroalgal farming is a promising low-impact and native species-based internal method for eutrophication control in the Baltic Sea and beyond.

CRedit authorship contribution statement

Conceived the study and wrote the paper: JK, RSK, FRB, HJ, AK, LL, RA, MF. Collected data: JK, UR, IM, FRB, AA, IB, PB, FG, MH, MJ, PaK, NK, PeK, TK, AK, IK, SL, GN, TP, HP, IP, MR, VS, WV, BY. Obtained funding and analysed data: JK, UR, IM, AK. All authors discussed the results and edited the manuscript.

Data availability

The datasets that were generated and/or analysed during the current study are freely available from the corresponding author on request.

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 data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.156230>.

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