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RESEARCH ARTICLE

Towards environmentally friendly finfish farming: A potential for mussel farms to compensate fish farm effluents

Jonne Kotta[1] | **Brecht Stechele**[2] | **Francisco R. Barboza**[1] | **Ants Kaasik**[1] | **Romain Lavaud**[3]

[1]Estonian Marine Institute, University of Tartu, Tallinn, Estonia

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

[3]School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, Louisiana, USA

Correspondence
Jonne Kotta
Email: jonne@sea.ee

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Abstract

1. Aquaculture is seen as a possible solution to meet the rising demand for fish but only if the sector reduces its use of wild fish in feed as well as its environmental impacts. The cultivation of extractive species along with fish farming (the integrated multi-trophic aquaculture system) has a potential to mitigate the adverse environmental effects of fish farming. The dynamic energy budget (DEB) modelling is a powerful tool to be used in different aquaculture settings to achieve the Blue Growth goals set by the commission.
2. This study explored the potential of mussel for bioremediation at finfish farms to develop environmentally sustainable finfish farming solutions in the eutrophic Baltic Sea region.
3. The study integrated the DEB models of blue mussels *Mytilus edulis/trossulus* and rainbow trout *Oncorhynchus mykiss* and a regional hydrodynamic-biogeochemical model to explore the potential of mussel farming to fully compensate nutrient discharges from finfish farms.
4. The DEB models demonstrated that despite suboptimal mussel growth conditions (low salinity), mussel farming has a potential to fully compensate for the discharge of nutrients from fish farms and thereby provide a solution for sustainable fish farming in the Baltic Sea region.
5. *Synthesis and applications*. As such fish farming may become a necessary enabler of economically sustainable mussel farming in the region. Mussel farming facilitates finfish farming licensing whereas finfish farming covers some costs of mussel farming thereby increasing the economic feasibility of this activity in the region.

KEYWORDS
aquaculture, Baltic Sea, DEB modelling, fish farming, IMTA, mussel farming, sustainable development

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1 | INTRODUCTION

The global demand for fish has increased tremendously in the past decades and is expected to increase by 16.3% in the coming 10 years (OECD/FAO, 2020). Due to such rising demand, overfishing has become one of the most serious conservation concerns in marine ecosystems as the depletion of fish stocks has strong and often irreversible ecosystem-wide impacts (Pinsky et al., 2011). Although management reforms have aimed to reduce fishing to exploitation rates that allow for maximum sustainable yield, conservative estimates suggest that 40% of global stocks are exploited over sustainable levels and 46% show decreasing trends in biomass (Britten et al., 2021).

Finfish aquaculture is seen as a possible solution to reverse the trend, but only if the sector reduces both its use of wild fish in feed and its environmental impacts (Naylor et al., 2000). During the last 20 years, pressure on the aquaculture industry to adopt comprehensive sustainability measures has resulted in improved governance, technology, siting, and management, including significant improvements in aquaculture feed (Naylor et al., 2021). Nevertheless, surplus nutrient emissions by finfish farms and largely unpredictable impacts on biogeochemical cycles remain obstacles to sustainable finfish farming (Holmer, 2010).

Enclosed seas and basins are particularly vulnerable to nutrient emission as slow and limited dispersal of dissolved substances leads to high retention rates resulting in the accumulation of excess nutrients and severe eutrophication (Sarà et al., 2018). To attain the targets of environmental sustainability in these ecosystems, management should aim for zero emissions. In this context, the integrated multi-trophic aquaculture (IMTA) concept may offer solutions to reduce considerably the environmental effects of intensive finfish aquaculture systems. By applying a circular economy approach (i.e. the co-production of aquaculture species), energy losses and/or nutrient leaking to the environment are minimized (Chopin et al., 2012). The IMTA system reduces environmental impacts directly through the active uptake of dissolved and particulate nutrients released from finfish farms by low trophic level organisms (e.g. macroalgae and bivalves). Harvesting these organisms removes the assimilated nutrients from the ecosystem (Duarte et al., 2009). Although macroalgal and mussel farming is increasingly recognized for its ecosystem services, assessment of these services is lacking and their potential is generally underexploited (Naylor et al., 2021; Smaal et al., 2019). This is especially true for temperate coastal regions where only a few countries have IMTA systems operating at a near commercial scale. Consequently, the potential of low trophic aquaculture to mitigate the environmental impacts of finfish farming remains largely unexplored (Barrington et al., 2009; Duarte et al., 2009). To ensure the expansion of IMTA in these regions, the environmental benefits of IMTA systems should be quantified and stakeholders educated about these practices.

The Baltic Sea is one of the most data-rich regions in the world (Reusch et al., 2018) and, thus, constitutes a good example to demonstrate the potential of the IMTA solution to mitigate the adverse environmental effects of finfish farming. Finfish farming is not yet considered sustainable in the Baltic Sea region due to the degree of eutrophication maintained by significant internal release of legacy phosphorus (P) and biological fixation of nitrogen (N) (Conley et al., 2009, 2011; Vahtera et al., 2007). Therefore, traditional finfish aquaculture is forced to implement comprehensive environmental measures to minimize nutrient emissions. Farming and harvesting of the native blue mussel species is an emerging sector in the Baltic Sea region and, importantly, is recognized as a promising internal measure for eutrophication control in the brackish Baltic Sea (Buer et al., 2020; Holbach et al., 2020; Kotta et al., 2020). However, due to the low salinity of the Baltic Sea (and lower production yield), mussel farming is not yet considered economically viable (Gren, 2019). Nevertheless, when combined with finfish farming, mutual gains can be expected. Mussel farming facilitates finfish farming licensing and finfish farming covers some costs of mussel farming, thereby increasing the economic feasibility of mussel farming in the region.

Quantifying the fluxes of energy and matter from various IMTA settings to the environment requires precise tools. A promising approach to quantify the rates of nutrient emission or sequestration at aquaculture sites is dynamic energy budget (DEB) modelling. Based on thermodynamic principles (Sousa et al., 2006), the DEB theory enables mechanistically linking biology to the abiotic environment, ensuring that energy-based trade-offs are incorporated into fitness measures and thereby predicting physiological responses of organisms to environmental drivers (Kooijman & Kooijman, 2010). When DEB models are combined with hydrodynamic-biogeochemical models, the effects of aquaculture on nutrient cycles in coastal areas can be realistically estimated (Holbach et al., 2020). DEB models have been previously used to quantify nutrient fluxes at finfish (e.g. Stavrakidis-Zachou et al., 2019) and mussel farms (Filgueira et al., 2016; Holbach et al., 2020) but not in IMTA settings to assess the potential of mussel for bioremediation at finfish farms.

Within a DEB modelling framework, physiological processes including feeding, growth, and metabolism of farmed finfish and mussels can be quantified. Individual fish release nutrients through excretion (dissolved inorganic NH_4 and PO_4) and defecation (particulate organic nitrogen [PON] and phosphorus [POP] and dissolved organic nitrogen [DON] and phosphorous [DOP] in case the particulate fraction is resuspended). Moreover, there are direct nutrient losses in the form of uneaten feed. These different emission fractions affect different parts of marine ecosystems. The larger faeces sink to the sediment and affect benthic communities, while dissolved inorganic and organic nutrients can trigger microalgal blooms in the pelagic environment (Dalsgaard & Krause-Jensen, 2006). Importantly, these separate fractions can be modelled in the DEB framework. Farmed suspension-feeding mussels remove phytoplankton from the water column (Kotta et al., 2020), and in this process, some phytoplankton nutrients are incorporated into tissues, some are released back into the sea as inorganic nutrients and some are deposited to the seafloor as faeces (Griffiths et al., 2017). Such mussel-derived organic input to the sediment can be locally important (Kautsky & Evans, 1987) and significantly modify benthic habitats (Kotta et al., 2009).

In this study we integrated the DEB models of blue mussels *Mytilus edulis/trossulus* and rainbow trout *Oncorhynchus mykiss* and a regional hydrodynamic-biogeochemical model to explore the potential of mussel farming to compensate finfish farm effluents in the low-salinity areas of the Baltic Sea. To quantify the potential of mussel farming to mitigate the nutrient emission of finfish farming, separate DEB models were run both for rainbow trout and mussel in each model grid cell. The DEB models incorporated the expected responses of these species to ambient salinity, temperature and food availability. By linking the results of the DEB models to a regional hydrodynamic-biogeochemical modelling framework capable of replicating natural and farm-induced nutrient fluxes, we were able to provide a spatially explicit representation of the extent of mussel farms needed to attain net zero-emissions from finfish farms in the highly eutrophicated and brackish Baltic Sea.

2 | MATERIALS AND METHODS

This study was not subject to any ethical approval requirements.

2.1 | Study area

The study area is located in the north-eastern Baltic Sea adjoining Latvia, Estonia, Finland and Russia (the study area extended from 56° to 61°N and from 19° to 28°E). The sea area is brackish with salinities varying from 10 in the west to almost 0 in the easternmost embayments. Wave energy is lower on the coasts than in the open sea, but may still be considerably in shallow exposed sites, especially during autumn and winter storms. The study area is characterized by strong seasonality in temperature. Near-zero temperatures prevail in winter and ice cover, especially near the coast, can last for several months (e.g. usually from December to April) (Kotta et al., 2008; Sooäär & Jaagus, 2007). In summer, water temperatures usually fluctuate around 20°C, but in extreme years, temperatures may reach 30°C in near-coastal areas. Seasonal stratification occurs in summer when the uppermost 10–20 m thick layer of water warms to 20–25°C. The water beneath this layer remains close to 4–5°C (Kotta et al., 2008; Suursaar, 2020). Some areas are subjected to irregular upwelling events induced by wind conditions and such events may change temperature conditions greatly, especially in summer (Suursaar, 2020). Eutrophication is one of the biggest environmental problems in the Baltic Sea, resulting from the accumulation of nutrients (mostly N and P compounds) in the marine environment (HELCOM, 2018).

Finland currently has several coastal finfish farms whereas Estonia has only one. However, the Estonian Maritime Spatial Planning recommends that aquaculture should be further developed and combined with more sustainable/extractive farming activities (e.g. macroalgal and mussel farms) (Hendrikson, 2020). Nevertheless, due to environmental issues, permits to operate open-net finfish farms are limited and the overall production volumes are extremely low. Estonia currently has one mussel farm while Finland and Latvia had a pilot mussel farm some years ago (Kotta et al., 2020).

2.2 | Studied species

Blue mussels consist of a group of three closely related taxa known as the *Mytilus edulis* complex that can hybridize with each other (Wenne et al., 2020). The brackish nontidal Baltic Sea is colonized by *M. edulis* and *M. trossulus*; the species inhabit various hard and mixed bottom subtidal habitats. Due to its wider salinity tolerance, *M. trossulus* is distributed almost throughout the Baltic Sea, while *M. edulis* occupies the westernmost higher salinity sub-basins (Kijewski et al., 2019; Knöbel et al., 2021; Stuckas et al., 2017). Nevertheless, there exists no pure *M. trossulus* in the Baltic Sea with all mytilids having various fractions of *M. edulis* alleles in their genomes (Kijewski et al., 2019). Salinity drives the large-scale distribution of *M. edulis/trossulus* in the region. Locally water temperature and food availability are expected to interactively shape the growth in mussels (Kotta et al., 2015, 2020; Maar et al., 2015).

The rainbow trout *O. mykiss* is a salmonid species native to cold-water tributaries of the Pacific Ocean in Asia and North America. The rainbow trout is commercially farmed in many countries throughout the world and is one of the most suitable finfish species for aquaculture in the brackish Baltic Sea. The rainbow trout is an omnivorous predator with a not very selective diet. Its growth varies with habitat characteristics, life history and quality and quantity of food (Blair et al., 2013).

2.3 | Test farms

2.3.1 | Mussel farm

A test mussel farm is located in Tagalaht Bay (58.46°N, 22.05°E). This blue mussel farm is self-regulating since the farming relies on the recruitment of free-swimming larvae from wild populations that disperse passively from natural mussel reefs. After dispersal, larvae attach themselves to farm substrates. Our test farm uses a smart farm system, that is, mussels are grown on nets placed at 1–5 m depth and attached to long buoyancy lines. Mussels are cleaned and harvested by specialized machines, which run along the nets. The mussel farm has an area of 0.25 ha and consists of six 100 m long farm lines. The stocking density of such a mussel farm is approximately 40 million individuals (Kotta et al., 2020; Kraufvelin & Díaz, 2015). The cultivation period is from 1 June to 31 October of the following year, that is, the biomass is harvested 1.5 years after the establishment of the farm.

2.3.2 | Finfish farm

The rainbow trout farm is located adjacent to the mussel farm in Tagalaht Bay. The fish farm deploys robust and flexible plastic rings and net cages. A farm is made up of seven net cages, each with a diameter of 38 m and containing tens of thousands of individual fish. The fish are produced in a hatchery and then released into the cages at a size of 0.85 kg wet weight. The feed is loaded onto boats in the harbour and delivered to the cages. However, the feed cannot be delivered to the fish during storms (wave height >2 m), which can affect growth rates. The cultivation period is 6 months from the 1st of May to the 31st of October. In our scenario analyses, we used the BioMar products Blue Impact 9024 6 mm and Blue Impact 9024 8 mm as feed (https://www.biomar.com/globalassets/.global/pdf-files/datasheets/-denmark/trout/en-dk-blue-impact-aqua-9024-45-8-mm-trout.pdf). Smaller fish are fed with 6-mm pellets and larger fish with 8-mm pellets. Because the 8-mm feed contains less P and N, nutrient emissions also decrease with increasing fish size with the average N and P content (dry matter) of feed over the entire incubation cycle being 5.87% and 0.69%, respectively. Importantly, most of the P settles to the seabed as hydroxyapatite ($Ca_5(PO_4)_3OH$) particles. As the hydroxyapatite deposited to the seabed is not bioavailable, this fraction is not considered a P emission.

2.4 | Physical and biogeochemical conditions

Model inputs for the physical and biogeochemical conditions (salinity, temperature, wave conditions, chlorophyll *a*) in the entire study region 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-h 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). Our analyses used daily averages of environmental variables.

2.5 | Dynamic energy budget modelling

The individual bioenergetic models used in this study are based on the DEB theory established by Kooijman and Kooijman (2010). General principles of the theory and the detailed model description and DEB parameters for both species are provided in Supporting Information S1.

The standardized Add-my-Pet procedure (Lika, Kearney, & Kooijman, 2011) was used to re-estimate some of the model parameters (Supporting Information S2). This method allows for simultaneous estimation of the parameters from empirical data (Lika, Kearney, Freitas, et al., 2011). In this study, parameter estimations, validations and simulations were run using Matlab version R2019b. The standardized AmP scripts used for the parameter estimation and data used for model calibration and validation were added to Supporting Information S3. The detailed model simulation procedures with DEB model calibration and validation results are provided in Supporting Information S4. DEB models for mussels were parameterised using univariate (18) and multivariate (13) datasets. Validation was performed using six datasets. Model estimates for 32 of these datasets were acceptable (MRE <0.2). DEB models for trout were parameterised using univariate (24) and multivariate (17) datasets. Validation was performed using two datasets. Model estimates from 34 of these datasets were acceptable (MRE <0.2).

2.6 | Spatial predictions at farm scale

To scale up the biomass growth of individual blue mussel and rainbow trout to the farm scale, we used realistic densities at the test mussel (40 million individuals) and fish farm (70,000 individuals) in Tagalaht Bay. Farmed mussels can extract large quantities of phytoplankton from seawater. If the uptake of phytoplankton by the mussel farm exceeds the import of phytoplankton from neighbouring areas, the food supply within the farm will be lower than in neighbouring areas. The actual chlorophyll *a* concentration at the farm is linearly related to the hydrodynamics and was modelled following the approach described in Holbach et al. (2020) and using the daily mean current velocity at each location (obtained from the NEMO model BALTICSEA_ANALYSISFORECAST_PHY_003_006). The resulting adjusted phytoplankton density was used in the DEB model to provide realistic farm-scale nutrient discharge and phytoplankton uptake and biomass at harvest. To provide spatial prediction of nutrient fluxes and growth of farmed mussels and fish in the entire study area, the mussel and fish DEB models were run independently for each grid cell of 1 km^2 size. These models assume the absence of mussel and fish farms in the neighbourhood grid cells.

3 | RESULTS

The DEB model predicted that across the entire study area and over the cultivation period a standard mussel farm has the capacity to produce, on average, 24 tons of mussels and a standard finfish farm to produce 265 tons (net production of 195 tons) of fish (wet weight) (Figure 1). The mussel farm removes on average 210 kg N and 25 kg P from the water column with 130.0 and 7.8 kg of these nutrients incorporated into mussels (Figure 2). The finfish farm was predicted to emit 5500 kg N and 20 kg P to the water column as dissolved inorganic nutrients and 1500 kg N and 500 kg P as particulate organic fraction (Figure 3).

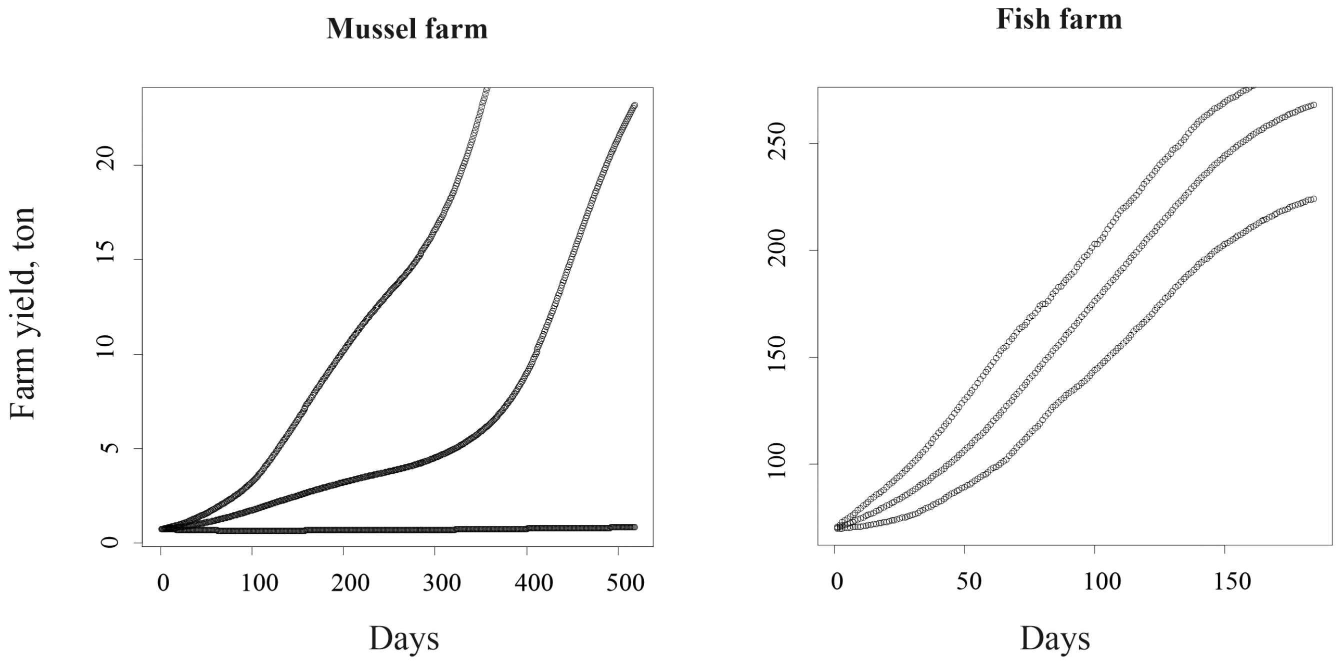

FIGURE 1 Cumulative increase in the biomass yield of mussel and fish farms during one cultivation cycle (wet weight in tonnes). Three lines represent predicted minimum, mean and maximum values in the entire study area.

The mussel growth yield and hence their ability to sequester nutrients from the environment was a function of ambient salinity, temperature and food availability (i.e. chlorophyll *a* concentration). Because environmental conditions varied extensively, there was high spatial variability in mussel-driven nutrient removal with higher values predicted in the most saline regions of the south-western parts of the study area and negligible values predicted in low-saline regions of the easternmost parts of basins (Figure 4). On the other hand, the finfish farming potential and hence their contribution to nutrient emission was more constant across the study area with differences being mostly due to spatial differences in temperature regimes and partly due to wave conditions (Figure 5).

Consequently, the potential of mussel farms to fully sequester finfish farming effluents is highest in the south-western parts of the study area and lowest in the easternmost areas. Mussel farms were more efficient in sequestering emitted N than P. In these suitable locations for mussel production, only an 8-ha mussel farm would be needed to totally compensate N and P emissions from a fish farm (Figure 6).

4 | DISCUSSION

The development of sustainable finfish farming in the Baltic Sea region is possible if pressures on the environment are significantly reduced. One way of achieving this is through on-land fish production. However, this often involves higher energy expenditure than sea-based farming, making it difficult to meet sustainability criteria related to reducing carbon footprints (Bjørndal et al., 2018). Alternatively, in-situ measures can be developed (Barquet et al., 2020; Haman et al., 2021) to capture and/or remove emitted nutrients directly from the waterbody. These methods have been rarely used in the Baltic Sea region, but these measures can have desirable effects as they offer greater possibilities for circularity and nutrient reuse. Here, we evaluated how mussel farms can serve as an effective mitigation measure to compensate the discharge of nutrients from finfish farms. The native blue mussel *M. edulis/trossulus* is a common filter-feeding bivalve that consumes phytoplankton and detritus in the water column. Mussels provide several ecosystem services, such as increasing water transparency and light penetration, reducing nutrient concentrations and providing habitat to local biological communities supporting biodiversity restoration (Hedberg et al., 2018; Petersen et al., 2014). Our DEB models showed that mussel farming can help to promote sustainable finfish farming in the Baltic Sea region. Results suggest that to fully compensate the nutrient emissions of a medium-sized finfish farm would require an 8-ha mussel farm in areas favourable for mussel growth. This size corresponds to the size of the first operational mussel farms in the Baltic Sea region (Kotta et al., 2020).

Another important aspect of sustainability is innovation related to the development of finfish feeds to significantly decrease nutrient emissions. In this study, we employed the recently developed BioMar feed. Most P in this product is bound to hydroxyapatite, which exits the nutrient cycle once deposited on the seabed. Thus, only a 0.8-ha mussel farm is needed to fully compensate P emissions at finfish farms. Large P input from land has severely disrupted the nutrient balance in the Baltic Sea region and to date, the legacy P accounts for about 45% of the P entering the sea (Gustafsson et al., 2017; McCrackin et al., 2018). Thus, from a sustainability perspective, it is of utmost importance that P emissions are limited at

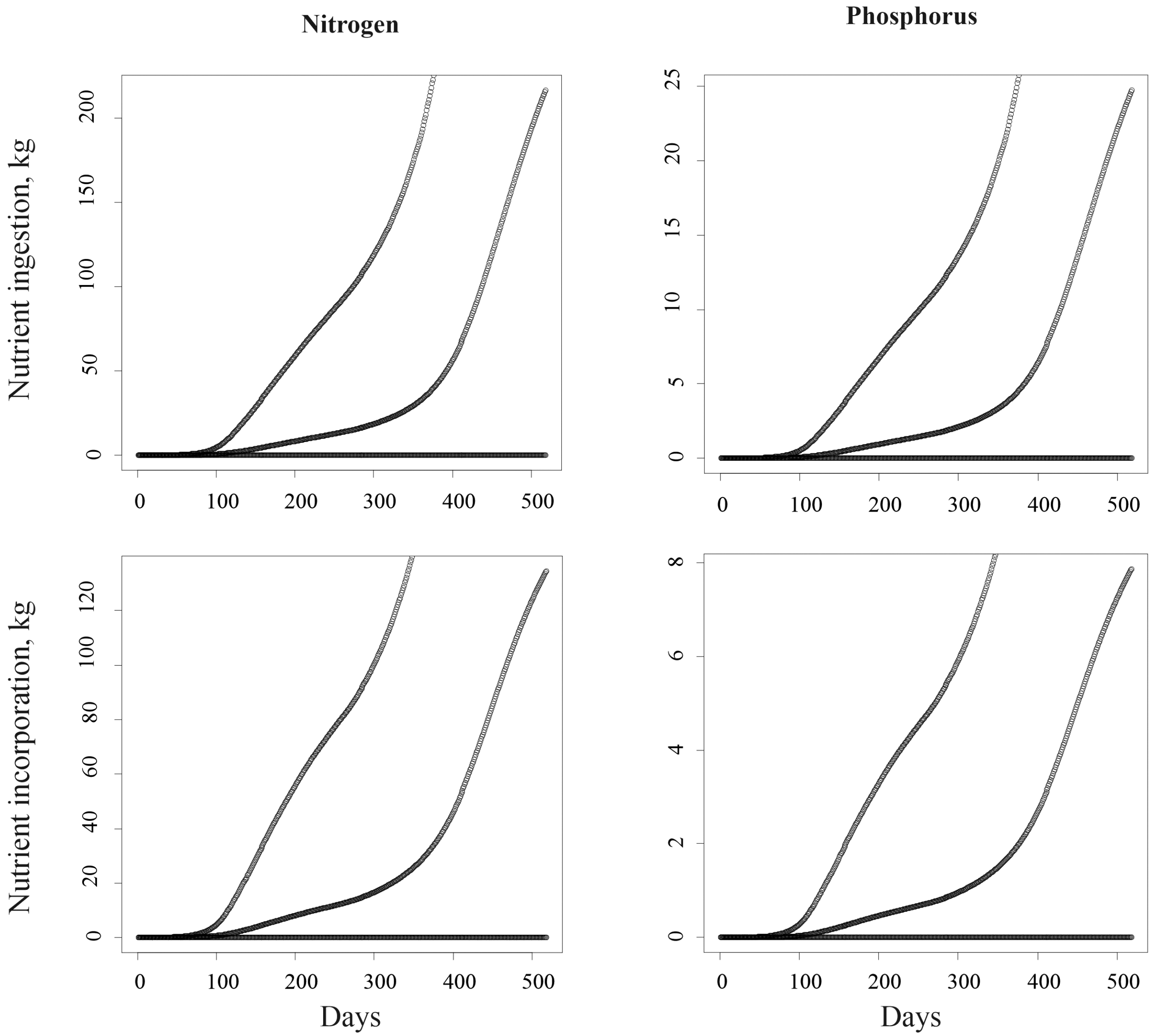

FIGURE 2 Cumulative increase in the nutrient ingestion and incorporation (kg) by a mussel farm during one cultivation cycle. The lines represent predicted minimum, mean and maximum values in the entire study area.

finfish farms as much as possible; the development of sustainable feed is an effective way to reach this goal. When using feed pellets in which P is bound in hydroxyapatite, emissions do not easily enter into the nutrient cycle and mussel farming in combination with fish farming can actually remove legacy P from the marine ecosystem. Nevertheless, it is practically impossible to directly capture the N released due to finfish excretion; mussel farming provides a promising internal measure to mitigate these emissions (Petersen et al., 2016; Žilinskaitė et al., 2021).

Elevated salinities combined with higher food availability resulted in a high production potential of mussels in the south-western parts of the study area. These areas are also expected to be the most rewarding in terms of co-production of mussels and finfish as an areal efficiency of mussel farm to mitigate emissions from finfish farms are the highest. Moreover, the relatively high biomass yields at mussel farms in the south-west region should ensure the economic feasibility of these farms beyond the compensation bargain. Currently, blue mussel farming is considered economically unsustainable in the Baltic Sea (Žilinskaitė et al., 2021), due mostly to the low number of mussel farms in the region. Once a sufficient and reliable quantity of mussel biomass is produced, greater incomes can be expected. Moreover, to date mussels are mostly sold on the non-food market (e.g. as fertilizer, biogas or feed resource), thus the costs for farmers are still too high to generate adequate profit. However, when mussels are valorised as food, economic sustainability of mussel farming can be significantly improved (Adler et al., 2022). In fact, such intensive mussel production has been tested in eutrophic estuary systems in the westernmost Baltic Sea. These bays are the heart of

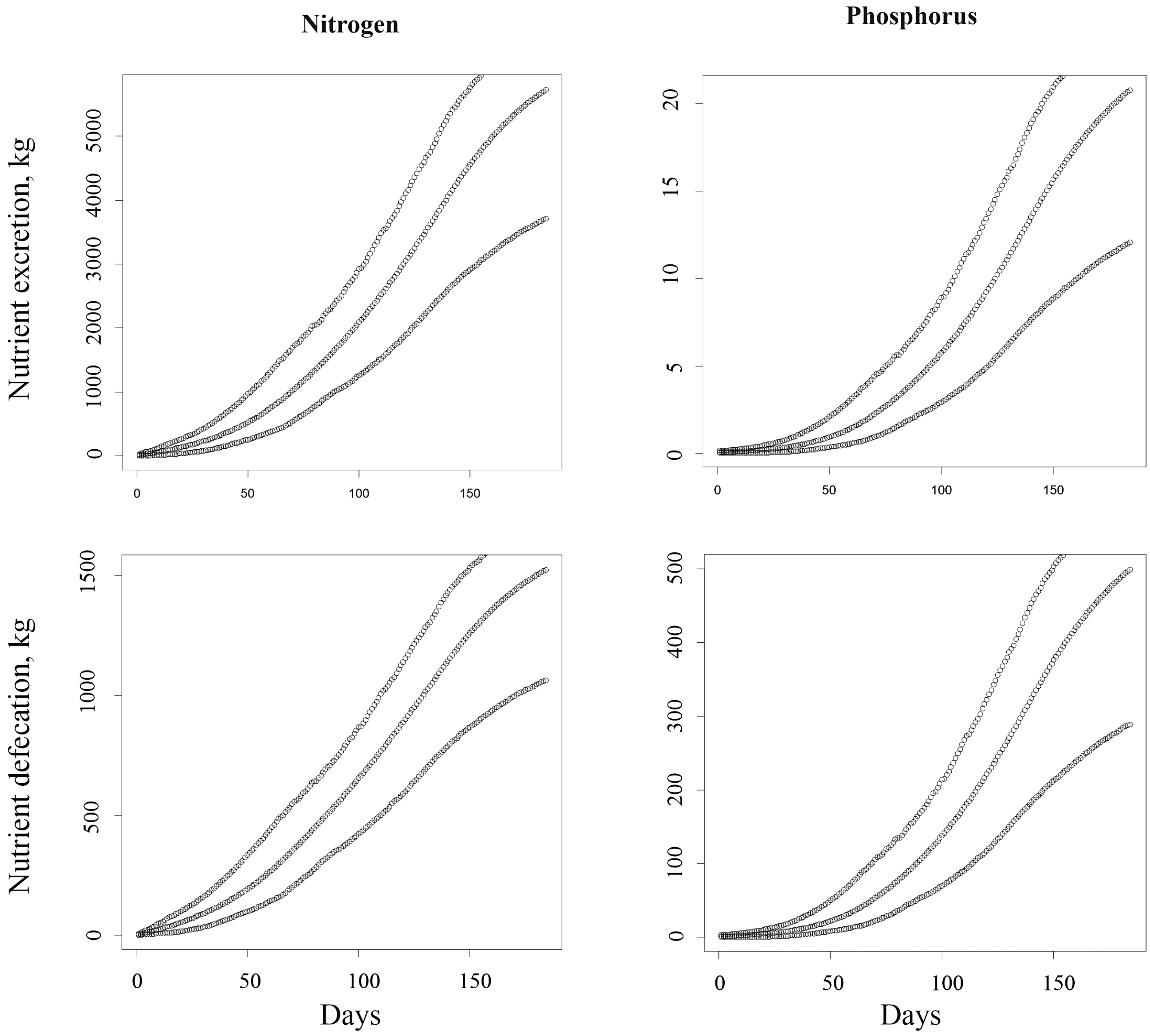

FIGURE 3 Cumulative increase in the nutrient excretion and defecation by a finfish farm during one cultivation cycle (kg). The lines represent predicted minimum, mean and maximum values in the entire study area.

the Danish shellfish industry, where mussel farming is seen as both an important means of supplying seafood and combating the negative effects of eutrophication (Petersen et al., 2014; Taylor, 2020). Pending the development of shellfish valorisation methods for the low salinity regions of the Baltic Sea, mussel farms can serve as a mitigation tool, allowing new finfish farms to be established in selected areas of the Baltic Sea. As such, finfish farms may become a necessary economic enabler for the expansion of mussel farming in the region.

The feasibility of mussel farming is defined largely by salinity in the Baltic Sea area (Holbach et al., 2020; Kotta et al., 2020). Low salinity reduces maximum size and increases the probability that mussels are dislodged from the substrate where they are growing. This largely explains why the south-west region of the study appeared as the most promising area for nutrient mitigation by mussels. Nevertheless, these limiting factors do not prevent the successful farming of mussels in the Baltic Sea region, as farming solutions are still being optimized (Žilinskaitė et al., 2021). Importantly, the appropriate site selection for the co-farming of mussel and finfish can result in reducing both expenses and impacts.

To quantify nutrient fluxes at mussel and finfish farms we used DEB modelling. DEB applications to shellfish or finfish production are numerous, but have been focussed on growth and reproduction; few studies have analysed nutrient dynamics between the cultivated species and their environment (Filgueira et al., 2015; Galasso et al., 2020; Lavaud et al., 2020; Mangano et al., 2019; Sarà et al., 2018). DEB applications in the IMTA context (Reid et al., 2020) or the quantification of ecosystem services (Lavaud et al., 2021) have

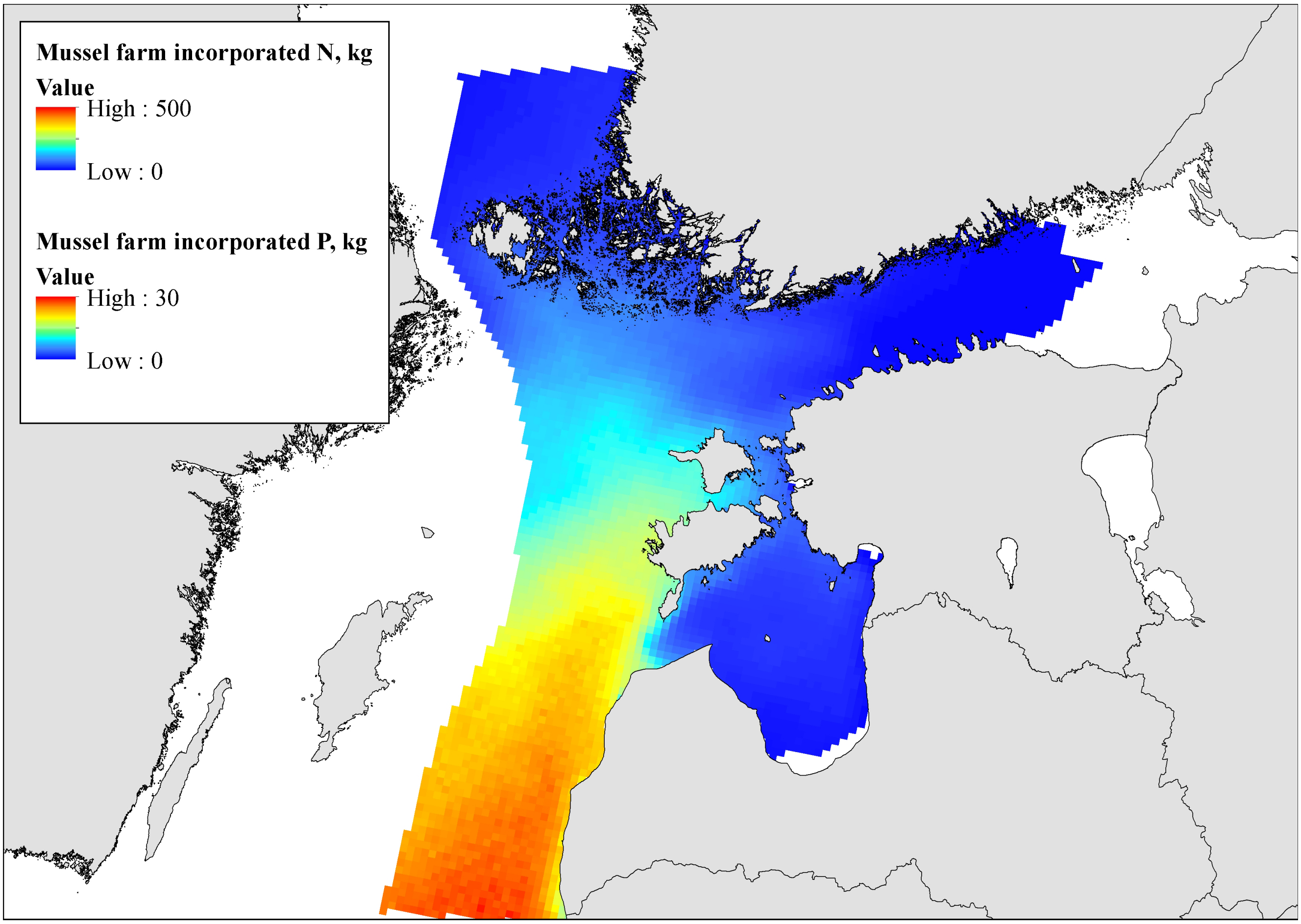

FIGURE 4 Spatial variability in the total nitrogen (N) and phosphorus (P) (kg) incorporated by a mussel farm per cultivation cycle. As the spatial patterns of N and P incorporation were exactly the same, we have used a single figure to show the values for N and P. Please refer to the specific legends for the actual values of the incorporated nutrients.

been described, but surprisingly, only a few studies have used DEB models to evaluate mitigation and bioremediation strategies (e.g. shellfish farms; Dong et al., 2022) or quantifying nutrient emissions (e.g. at finfish farms). Nevertheless, the fact that a single framework combined with hydrodynamic-biogeochemical models can be used to model aspects of site suitability for cultivation and/or emission mitigation potential proves the value of using the DEB framework in these kinds of studies (Holbach et al., 2020; Lavaud et al., 2021).

The transferability potential of the DEB modelling is great as the core principles, assumptions and set of parameters do not vary, only values. Thus, the current work can be applied to other aquaculture species without much additional effort (for species present in the Add-my-Pet collection). The DEB models are already used in standardized ecotoxicological tests by the EU (EFSA, 2018) and the methodology is very promising for use in other aquaculture settings to achieve the Blue Growth goals set by the commission (European Commission, 2012).

Nevertheless, DEB models are complex and numerous parameters are involved in simulating nutrient balances and fluxes through the individual. Although many DEB models are described in the AmP database, local adaptation and parameter variability through populations call for the re-parameterization of established parameter sets, and validation with local datasets. In addition, many of the published DEB parameters are not 'complete', which is expressed from 0 (low) to 10 (high), and higher levels can be achieved only by including datasets related to feeding, faeces production and elementary composition of organic compounds. These datasets, especially in an open-sea IMTA setting, are difficult to collect and are often characterized by high variability. This calls for the systematic collection of basic autecology data to fill the generic gap of knowledge of species ecology.

The assumptions of the DEB model are well described in Kooijman and Kooijman (2010, p. 77). These assumptions are very theoretical and relate to the physiology of organisms and are, therefore, beyond the scope of this work, which is primarily focused on an application of DEB models. Nevertheless, one of the main limitations of DEB is its complexity and the large number of parameter values. Despite this, there is no plausible alternative to the DEB model, and the complexity is necessary to link an entropy balance to an energy balance to a mass balance to a nutrient balance. All these balances are needed to dynamically specify an individual organism. Simpler forms of the DEB model are available

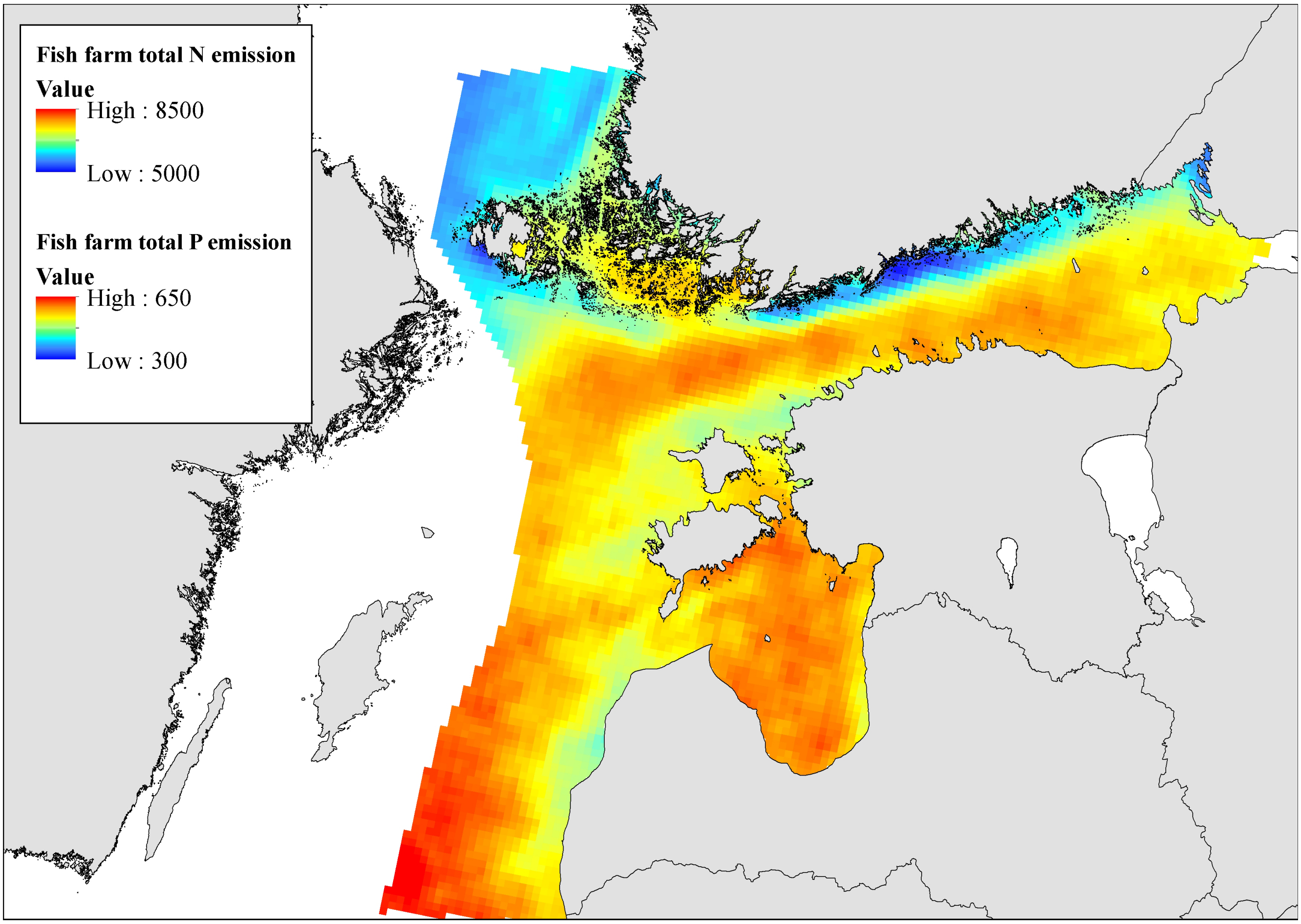

FIGURE 5 Spatial variability in the total nitrogen (N) and phosphorus (P) emission (kg) (excretion + defecation) of a finfish farm per cultivation cycle. As the spatial patterns of N and P emissions were exactly the same, we have used a single figure to show the values for N and P. Please refer to the specific legends for the actual values of the emitted nutrients.

(such as the von Bertalanffy model), but these models apply to specific constrained conditions (such as constant feeding conditions in the case of the von Bertalanffy model) (Kooijman, 2020). Another limitation of the DEB model we used is that it is only constrained by temperature, salinity and chlorophyll *a*. Other environmental factors such as oxygen consumption, current speed, suspended solids and food quality can affect the physiological response of mussels to the environment. We have assumed that these conditions do not severely affect the animals as previous observations have shown that mussels are not strongly food limited in the study area (Kotta et al., 2015), especially aquaculture organisms living in the water column (Kotta et al., 2020, 2022). The majority of the study area is relatively exposed (no hypoxia is expected) and away from sedimentation areas. In addition, mussel farms are located high in the water column. Therefore, resuspended solids are not expected to affect their feeding conditions and ultimately their growth. Furthermore, there are not enough observations in the literature to include the functional response of these factors on the metabolism of the organism.

In the DEB modelling, we explored the potential of mussel farms to mitigate nutrient emissions at finfish farms, but an assessment of the ecosystem-level effects of the IMTA farms was beyond the scope of this study. Future studies are expected to quantify the ecological interactions between IMTA farms and the environment. Nevertheless, considering that eutrophication is one of the main environmental threats to the Baltic Sea and our study delivered solutions to design zero-emission IMTA farms, the potential environmental effects can be avoided with careful site and technological planning of the IMTA farms (e.g. Lavaud et al., 2020; Zhang et al., 2019). The suitable IMTA sites should have sufficient current velocity to support healthy conditions at fish farms (Timmerhaus et al., 2020) as well as to ensure the highest mitigation potential at mussel farms (Kotta et al., 2020). Moreover, under low current regime, the sedimentation of faeces may cause anaerobic conditions beneath the farms (Olsen et al., 2008; Zhang et al., 2019). Importantly, different environments are characterized by different nutrient recycling capacity, which is a function of nutrient dilution by hydrodynamics, nutrient uptake by phytoplankton and nutrient transfer to higher trophic levels, but the former is the key process in defining the realized impacts of fish farms at the ecosystem level (Olsen et al., 2008). After establishing IMTA farms it is, however, important to establish an extensive environmental monitoring program

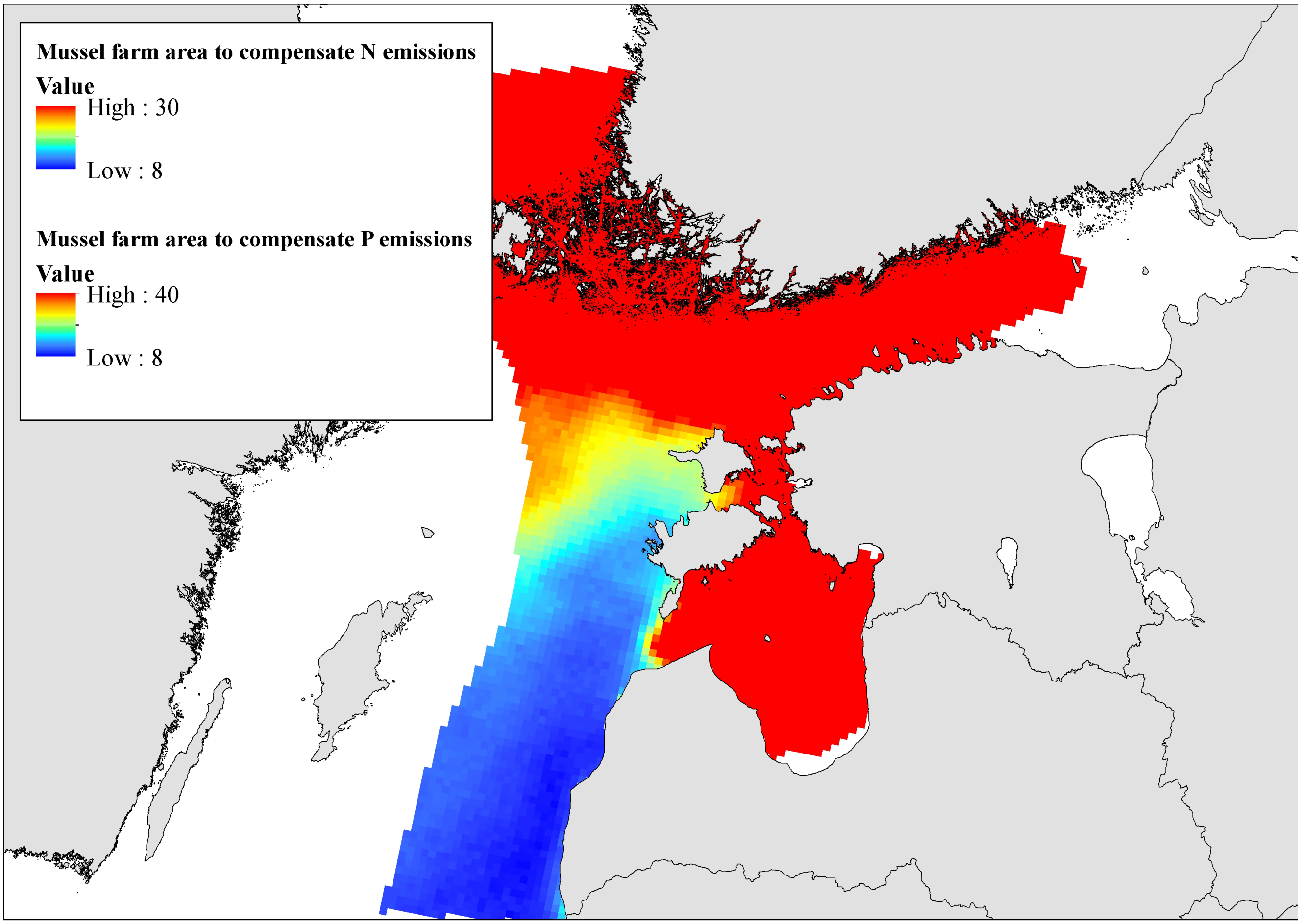

FIGURE 6 Spatial variability in the required surface area of a mussel farm (ha) to fully compensate nutrient emissions at a finfish farm. As the spatial patterns of nitrogen (N) and phosphorus (P) compensation potential were exactly the same, we have used a single figure to show the values for N and P. For the actual compensation values, please refer to the legend for the specific nutrient.

to assure that bottom conditions, for example, oxygen levels and benthic flora and fauna, do not deteriorate.

5 | CONCLUSIONS

This paper quantified the nutrient fluxes within finfish and mussel farms using a DEB modelling framework. Simulations demonstrated that despite suboptimal mussel growth conditions, mussel farming has the potential to fully compensate for the discharge of nutrients from finfish farms and may thus represent a solution to sustainable finfish farming in the Baltic Sea region. The models also demonstrated that in the most rewarding areas for the co-production of mussels, relatively high biomass yields at mussel farms may ensure the economic feasibility of these farms beyond the compensation bargain. The mechanistic approach developed in this study constitutes a concrete application that provides valuable information for the Baltic Sea stakeholders. This tool could be used to explore the effects of future conditions on aquaculture (Sarà et al., 2018) and can be transferred to other aquaculture systems. Ultimately, such an approach may be essential to inform marine planning and ensure sustainable aquaculture operations.

AUTHOR CONTRIBUTIONS

Jonne Kotta, Brecht Stechele, Ants Kaasik and Romain Lavaud conceived the ideas and designed methodology. Jonne Kotta and Brecht Stechele built the databases. Jonne Kotta, Brecht Stechele, Ants Kaasik and Romain Lavaud analysed the data. Jonne Kotta, Brecht Stechele, Romain Lavaud, Francisco R. Barboza and Ants Kaasik wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

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.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.3ffbg79pd (Kotta et al., 2023).

ORCID

Jonne Kotta https://orcid.org/0000-0002-4970-6755

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SUPPORTING INFORMATION

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

Supporting Information S1: DEB formulation.

Supporting Information S2: DEB model calibration and validation.

Supporting Information S3: Parameter estimation files.

Supporting Information S4: DEB model simulation, calibration and validation results.

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