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Cleaning up seas using blue growth initiatives: Mussel farming for eutrophication control in the Baltic Sea

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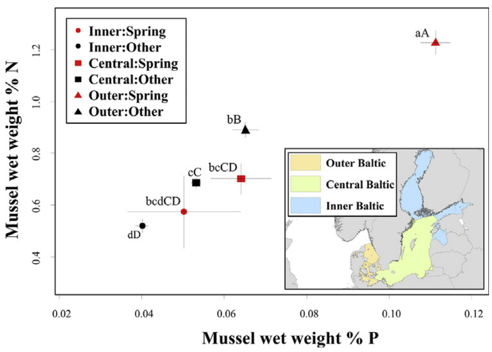
HIGHLIGHTS

- Mussel farming is a viable internal measure to address Baltic Sea eutrophication.
- Rates of nutrient removal depend on salinity at the regional scale and food availability at the local scale.
- Cost effectiveness of nutrient removal by mussel farming depends also on farm type.
- Total farm area needed for achieving HELCOM nutrient reduction targets is realistic.

GRAPHICAL ABSTRACT



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ABSTRACT

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Eutrophication is a serious threat to aquatic ecosystems globally with pronounced negative effects in the Baltic and other semi-enclosed estuaries and regional seas, where algal growth associated with excess nutrients causes widespread oxygen free "dead zones" and other threats to sustainability. Decades of policy initiatives to reduce external (land-based and atmospheric) nutrient loads have so far failed to control Baltic Sea eutrophication, which is compounded by significant internal release of legacy phosphorus (P) and biological nitrogen (N) fixation. Farming and harvesting of the native mussel species (*Mytilus edulis*/*trossulus*) is a promising internal measure for eutrophication control in the brackish Baltic Sea. Mussels from the more saline outer Baltic had higher N and P content than those from either the inner or central Baltic. Despite their relatively low nutrient content, harvesting farmed mussels from the central Baltic can be a cost-effective complement to land-based measures needed to reach eutrophication status targets and is an important contributor to circularity. Cost effectiveness of nutrient removal is more dependent on farm type than mussel nutrient content, suggesting the need for additional development of farm technology. Furthermore, current regulations are not sufficiently conducive to implementation of internal measures, and may constitute a bottleneck for reaching eutrophication status targets in the Baltic Sea and elsewhere.

1. Introduction

Eutrophication is a global threat to many aquatic ecosystems and its negative effects are particularly pronounced in semi-enclosed estuaries and regional seas (Diaz and Rosenberg, 1995; Conley et al., 2009a; Rabalais et al., 2009). Excessive amounts of nitrogen (N) and phosphorus (P) from present-day and legacy sources support massive algal blooms which results in widespread and increasing oxygen free "dead zones" (Breitburg et al., 2018), increasing susceptibility to ocean acidification (Cai et al., 2011), reduced biodiversity and loss of ecosystem functions and services (Smith, 2003; Riedel et al., 2016). In the Baltic Sea, a multi-jurisdictional water body, >40 years of international efforts to reduce external nutrient (N and P) inputs have failed to solve the eutrophication problem (Fleming-Lehtinen et al., 2015; Andersen et al., 2017). Today, 97% of the marine area is considered as degraded due to eutrophication (HELCOM, 2018, Fig. 1) and despite significant reduction in external loads, the total P pool in Baltic Sea waters continues to increase (Savchuk, 2018) and internationally agreed upon water quality targets are still not met. To date, management actions have primarily focused on minimizing external loads, i.e., terrestrial point sources and diffuse nutrient inputs. Agriculture is targeted in many cases (Larsson and Granstedt, 2010) but the internal loads of legacy P released from marine sediments (Vahtera et al., 2007; Conley et al., 2009a) and atmospherically fixed N are often neglected (Vahtera et al., 2007), as are non-food nutrient sources (Hamilton et al., 2018).

Aquaculture is a key component of the EU Blue Growth strategy (EC, 2012) and can have significant positive and negative effects on water quality. Aquaculture is the fastest growing food-producing sector and currently represents nearly 50% of global fish, crustacean and mollusc production (FAO, 2018). Marine bivalves, e.g., mussels, oysters, clams and other shellfish, are often referred to as extractive species as these filter feeding species act as nutrient sinks by ingesting particles suspended in the water column. Importantly, harvesting of cultivated mussels removes both N and P, thereby improving water quality in affected areas (Carlsson et al., 2012; Kraufvelin and Díaz, 2015).

Aquaculture can also make a positive contribution to circularity and nutrient recycling. Most internal eutrophication control measures make P unavailable for re-use through, e.g., bottom water oxygenation to change sediment redox status and the binding of P to iron (Stigebrandt et al., 2015) or aluminium treatment to effectively immobilize P in the sediment (Rydin et al., 2017). Unlike the aforementioned measures, harvesting of internally produced biomass, (i.e. farmed mussels) offers the potential for efficient recirculation of nutrients from sea to land. Harvested mussels can be used to produce feed for chickens (McLaughlan et al., 2014) or fish (Vidakovic et al., 2015), as well as for human consumption (Gren et al., 2009). Harvested mussels can also be used for bioenergy production (Hu et al., 2011; Nkemka and Murto, 2013), or as a soil amendment.

The failure to control Baltic Sea eutrophication through external nutrient load reduction measures has highlighted the need for in-situ (internal) methods to lower nutrient concentrations in the water column, e.g. through geoengineering (Stigebrandt et al., 2015; Rydin et al., 2017) or biomass harvesting (Gren et al., 2009). Intensive fishing of commercial or non-commercial fishes (e.g., three-spined stickleback, round goby) has been proposed as an alternative means for removing nutrients from the Baltic Sea. However, this could have unknown and potentially catastrophic consequences for marine biodiversity due to the role as top or intermediate predators that these species have in littoral habitats. While internal measures for nutrient regulation are not a universal means of controlling eutrophication, they should be considered when feasible external measures have been tried and found to be inadequate (Savchuk, 2018). It should be noted, however, that many internal measures have been associated with high costs for nutrient removal (Lurling et al., 2016) as well as undesirable secondary effects such as damage to benthic habitats (Stadmark and Conley, 2011), potentially harmful shifts in thermal regime (Conley, 2012) and/or food web impacts (Naylor et al., 2001). The Baltic Sea region is an important test case highlighting the opportunities and challenges of farming native bivalve species as an internal measure to mitigate the adverse effects of coastal eutrophication. The region has a long, well-documented history of ecosystem deterioration, high data density and multiple cross-border environmental management actions to counter marine eutrophication (Reusch et al., 2018).

Farming of the ubiquitous blue mussel species complex (*Mytilus edulis*/*trossulus*, Stuckas et al., 2009) has been proposed as an internal measure for eutrophication control in the brackish Baltic Sea (Lindahl et al., 2005; Gren et al., 2009; Petersen et al., 2014; Schröder et al., 2014; Ozoliņa, 2017; Kiessling et al., 2019). Mussel farming has also been criticized as being not cost effective (Hedberg et al., 2018) and harmful to the environment (Stadmark and Conley, 2011).

Blue mussels are marine species and form hybrid zones within the Baltic Sea (Stuckas et al., 2009). While individuals are able to survive down to salinities of 4–5 practical salinity units (PSU), they grow better in high salinity conditions where they do not need to expend as much energy on osmoregulation (Maar et al., 2015). Blue mussels are primary consumers and usually the dominant species (i.e. main contributor to abundance and biomass) in the environments where they occur, and consequently their sustainable harvest is not expected to produce cascading effects or other impacts on the stability of the food web.

Blue mussel farming relies on recruitment of free-swimming larvae (veligers) from wild populations that are entrained into the water column and passively dispersed from natural mussel reefs. After dispersal,

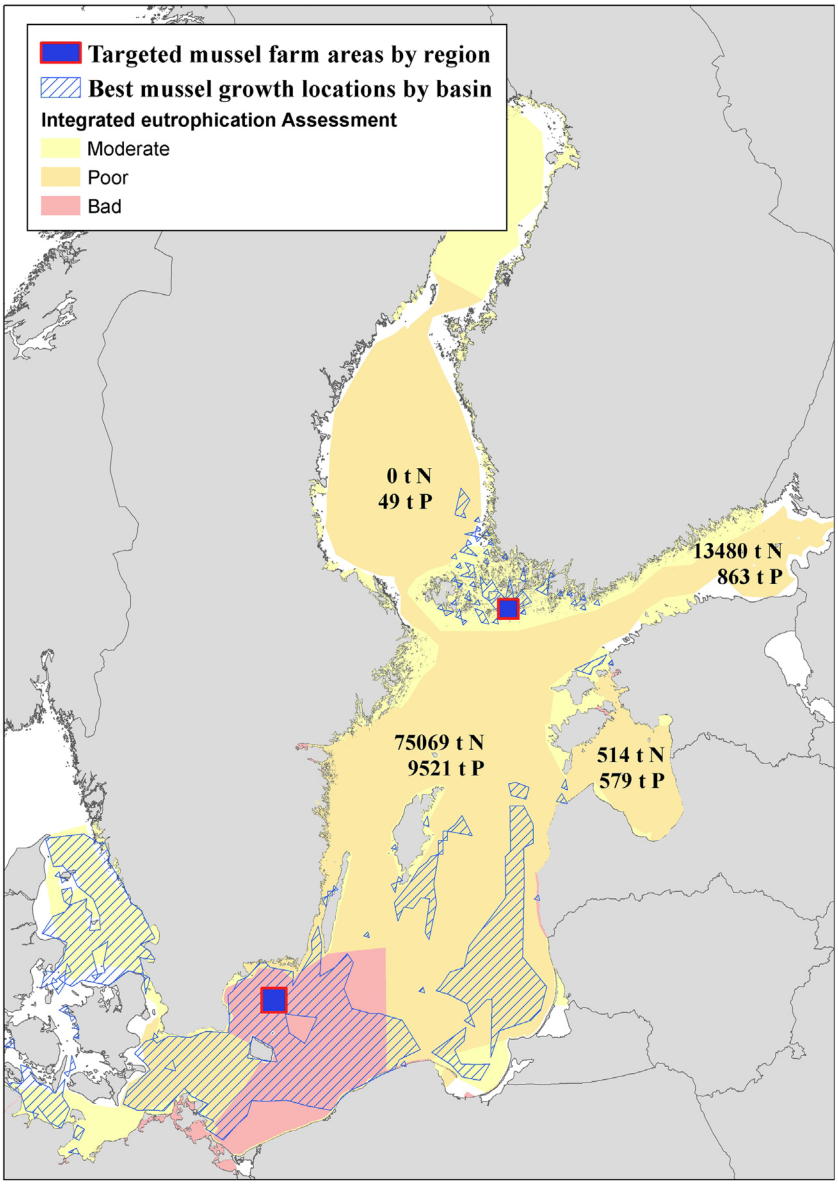

Fig. 1. Areas of the Baltic Sea (coloured; 97% of its total surface area) that currently have unacceptable water quality with respect to eutrophication. Different colours indicate different water quality classes. The 2013 HELCOM Ministerial Meeting agreed on the amount of reduction in emissions for nitrogen (N) and phosphorus (P) in different sub-basins of the Baltic Sea in order to meet goals of the Baltic Sea Action Plan. However, trend-based estimates demonstrate that the maximum allowable nutrient inputs are still exceeded in the Central and Inner Baltic Sea. The excesses are shown as numbers in the different sub-basins. Blue hatched areas show the best mussel growth location separately for Outer, Central and Inner regions predicted by the model. Within these regions, blue rectangles show the surface area of future mussel farms that are needed to meet the basin-specific goals of nutrient load reduction defined in the Baltic Sea Action Plan. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

veligers attach themselves to available substrates, including objects in the water column, e.g., mussel farms. Thus, determining how to best allocate areas suitable for mussel farming requires consideration of the connectivity between candidate farm sites and natural mussel reefs in order to define areas that do not require artificial mussel seeding.

Farms using ropes with high surface area per unit length, i.e. ribbons, Swedish bands or so-called “fuzzy ropes” promote higher rates of larval settlement. After settlement, it is necessary to account for the way in which salinity, food availability and wave action affect growth rates and to select sites with the highest harvest potential. A typical Baltic Sea mussel farm has an area of a <5 ha and consists of 10–100 km of rope suspended at different depths (Holmer et al., 2015; Kraufvelin and Díaz, 2015). Cost effectiveness of the farms is dependent on nutrient and salinity levels as well as the type of equipment for culturing mussels, with specialized ropes that optimize veliger recruitment being the most effective for culturing the small mussels found in the Baltic. Harvest rates are usually expressed in units of mass of mussels per metre of rope. Mussels are harvested one to two years after recruitment, depending on site productivity. As farmed mussels spend their entire life suspended in the water column, they are less affected by contaminated sediments than benthic dwelling organisms but can be susceptible to contamination by algal toxins (Sipiä et al., 2001).

A synthesis of a large number of recent measurements of farmed mussel growth in the Baltic Sea and a new model chain for predicting growth and nutrient removal potential across key environmental gradients are presented. The relationship between wild mussel production and predicted nutrient removal through harvest of farmed mussels was quantified by modelling occurrence of wild mussels throughout the whole Baltic Sea. A biophysical dispersal model was used to analyse direction and distance of larval drift from each natural mussel reef. Next, spatially explicit and empirically modelled growth rates of farmed mussels were combined with measured N and P concentrations in mussels harvested from production-scale farms to quantify nutrient removal potential. Finally, farm-scale nutrient removal estimates were upscaled to predict the total area of mussel farms needed to make a meaningful contribution to reducing Baltic Sea eutrophication.

2. Material and methods

2.1. Study area

The Baltic Sea is shallow, brackish and has almost no tide but experiences intense seasonality in temperature and inflow. It is heavily affected by eutrophication with N and P concentrations showing decreasing and increasing trends, respectively (HELCOM, 2018; Savchuk, 2018).

For most of the analyses presented here, the Baltic Sea was divided into Outer (Kattegat and Belt Sea), Central (Northern Baltic Proper, Western and Eastern Gotland Basins, Gdansk Basin and Bornholm Basin) and Inner regions (Bothnian Bay, Bothnian Sea, Archipelago Sea, Åland Sea, Gulf of Finland and Gulf of Riga), representing the gradient from the near-oceanic (Outer) to brackish-water conditions (Fig. 2).

Despite salinity constraints, several characteristics of the Baltic Sea favour mussel farming for eutrophication control. First, the Baltic Sea is very eutrophic and food is only rarely a limiting factor for mussels (Kotta et al., 2015). Thus, within suitable habitat ranges, elevated resource availability can compensate for growth limitation associated with reduced salinity (Kotta et al., 2015). Second, high nutrient concentrations in the water require in-situ removal actions for which mussel farming is promising. Finally, more than forty years of international agreements and land-based measures have failed to solve the problem of Baltic Sea eutrophication; large amounts of money have been allocated to reduce inputs from land with variable, often minimal, effects (Helin, 2013).

2.2. Mussel farms

Harvest data are reported from three farms, one each in the Outer, Central and Inner Baltic (Table 1 and Fig. 1). The Kumlinge farm (Inner Baltic) is located in the Åland archipelago. It was established in spring 2010 and harvested in November 2012. The farm technology consisted of four 120 × 3 m nets with a mesh size of 15 cm fastened to floating

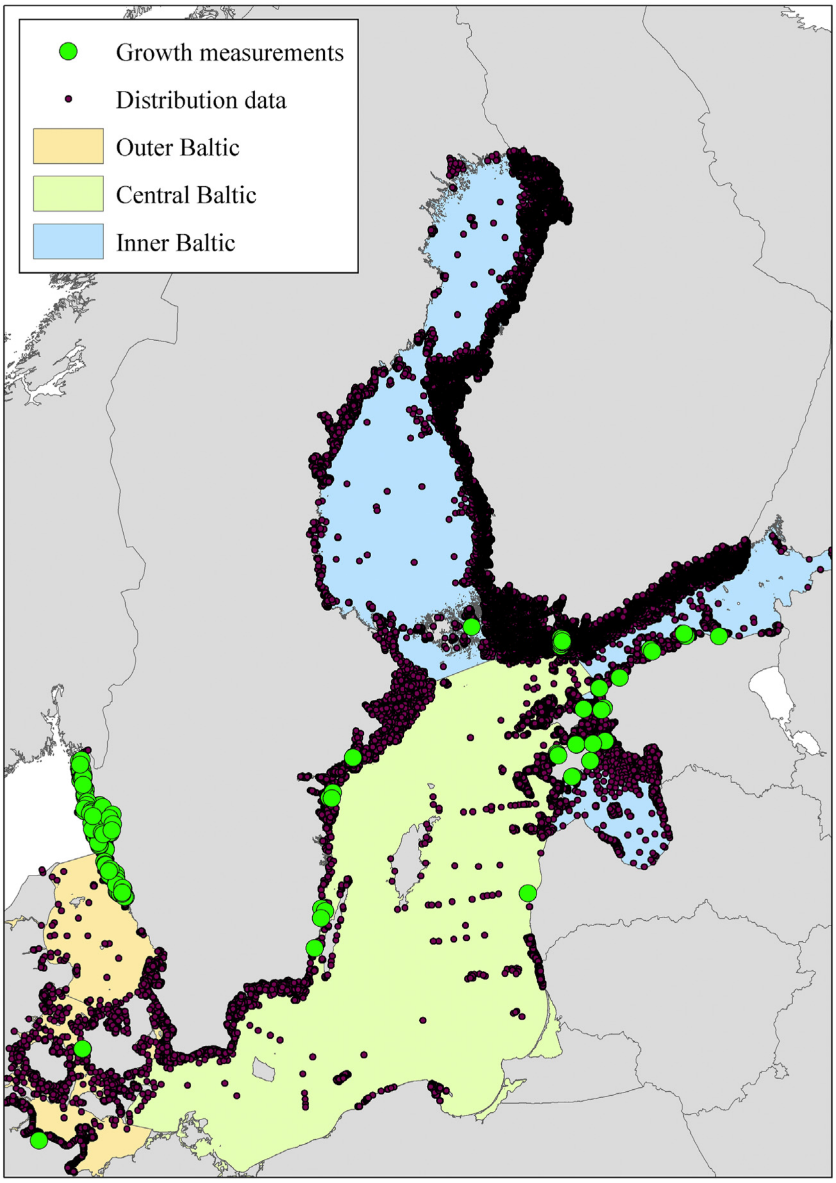

Fig. 2. Location of sampling points for the distribution and growth of blue mussels. Colours depict different sub-regions of the Baltic Sea. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Summary of environmental conditions, nutrient removal and economic factors for three blue mussel farms in the Baltic Sea.

Variable	Unit	Kumlinge	Sankt Anna	Kiel
Latitude		60.2147° N	58.3564° N	54.3755° N
Longitude		20.7524° E	16.9368° E	10.1634° E
Region of the Baltic Sea		Inner	Central	Outer
Average salinity		6	6	15
Chlorophyll *a* (mean/max/min)	mg m^{-3}	2.0	2.0/3.5/1.0	2.3/4.5/0.9
Farm technology		Nets	"Spat catching" rope	Ropes with collector bands
Nitrogen removal at harvest	kg ha^{-1}	83	140	148
	g m^{-1}	3.74	23.26	22.25
Phosphorus removal at harvest	kg ha^{-1}	6.4	10.8	10.8
	g m^{-1}	0.29	1.80	1.63
Farm size	ha	0.90	4.0	0.30
Long line length	km	20	24	2
Long line density	km ha^{-1}	22.2	6.0	6.7
Observed biomass	tonnes	14.4	81.50	5.00
yield	kg m^{-1}	0.72	3.40	2.50
Modelled biomass yield	kg m^{-1}	0.75	1.3	14.7
Investments	€ kg^{-1}	5.45	0.35	0.36
Operational expenses	€ kg^{-1}	3.08	0.17	1.49
Total costs	€ kg^{-1}	8.52	0.52	1.85
N removal cost	€ kg^{-1}	1638	76	208
P removal cost	€ kg^{-1}	21,300	981	2846

plastic pipes. The average water depth was 8 m and average bottom water current speeds were 3–4 cm s^{-1} (Kraufvelin and Díaz, 2015). The Sankt Anna farm (Central Baltic) is located on a sheltered site in the Swedish Östergötland archipelago. The farm was established in spring 2016 and harvested in October 2018. The farm technology consisted of "spat catching" rope developed by Quality Equipment Ltd. and optimised for settling of small mussels. Ropes were hung at a depth of 2–12 m. Average water depth at the site was 20 m and bottom water current speeds were low. The Kiel farm (Outer Baltic) is located near Kiel, Germany. The farm technology consists of ropes with collector bands and socks optimised for the production of large mussels. Ropes were suspended at depths of 1–3.5 m and average water depths ranged between 7 and 11 m (Schröder et al., 2014). The farm was established in 2011 and the first harvest took place in September 2012.

2.3. Spatial mapping

The blue mussel distribution data were combined from different sources: benthos database of the Estonian Marine Institute, University of Tartu (http://loch.ness.sea.ee/gisservices2/liikideinfoportaal/); the VELMU database, Finnish Environment Institute (http://www.ymparisto.fi/en-US/VELMU); the database of the Swedish National Monitoring Programme (http://sharkdata.se/), benthic inventory data collected by AquaBiota (http://www.aquabiota.se/en/researchservices/inventories-using-underwater-video/), the database of Marine Research Institute, Klaipeda University; EurOBIS (http://www.eurobis.org/) and EMODnet (http://www.emodnet-biology.eu/portal/) (Fig. 2). Altogether, data from 226,031 stations from coastal hard and soft bottom habitats of the Baltic Sea were included in this study. This dataset was based on a regional sampling and sample processing protocol developed for the HELCOM COMBINE programme (HELCOM, 2015). The stations included were sampled at least once in summer (June to August) between 2005 and 2015. On hard bottoms, blue mussels were collected by divers using a standard bottom frame (0.04 m^2) and/or a hand-held drop camera operated from small motorboats with recording devices operated on the surface. On soft bottoms, samples were collected using different benthos grabs (sampling area 0.02–0.1 m^2). Quantitative samples were sieved in the field using 0.25 mm mesh screens. The residues were stored at −20 °C and subsequent sorting, counting, weighing and measuring of blue mussels were performed in the laboratory.

Oxygen measurements under the farms were made with a JFE Advantech optical DO sensor (https://www.jfe-advantech.co.jp/eng/ocean/rinko/rinko3.html).

The majority of existing experimental measurements of mussel growth in the Baltic Sea ($n = 14{,}944$) were used to model the potential growth and yields across the key environmental gradients. This includes the original data of the INTERREG Baltic EcoMussel and Baltic Blue Growth projects as well as data from different national research initiatives from Estonia, Finland, Sweden, Denmark and Germany (Fig. 2).

2.4. Mussel tissue analysis

Nutrient content was analysed for 124 samples of blue mussel tissue. In each case, 100–150 g of fresh material (shells, soft tissue and associated water) were analysed in the following manner. Whole frozen mussels were removed from the freezer and thawed. A portion of the thawed mussels (shells, soft tissues and associated water) were manually crushed using a mortar and pestle. Between 100 and 150 g of the crushed mussels were weighed. This weight is reported as the sample wet weight. The samples were then freeze-dried at −80 °C and weighed. They were then oven dried at 105 °C (to remove any residual moisture) and weighed again to determine dry mass and dry matter fractions.

Prior to the nutrient analysis, dried material was filtered through a 1 mm sieve. Total N measurements were performed by the laboratories of Swedish University of Agricultural Sciences using the total Kjeldahl nitrogen (TKN) method. Total phosphorus (P) concentrations were analysed by Agrilab AB. Samples were acidified using sulfuric acid. P concentrations were obtained using ICP-AES.

2.5. Statistical analysis of nutrient concentrations

In order to account for regional variability in the nutrient content of mussels, samples were classified into those obtained in the Outer, Central or Inner Baltic Sea. These three functionally different regions were used to account for the regional-specific nutrient accumulation in mussels when assessing the potential of nutrient removal through harvesting.

Because the sampling design was unbalanced, i.e., the same number of samples were not available for the different months across regions, only the samples collected from the Outer Baltic were used to define the best way of grouping the samples obtained in the different seasons for subsequent analyses. A Tukey's Honest Significant Difference (HSD) post-hoc test of an ANOVA predicting wet weight P concentrations as a function of month indicated that samples from March, April, May and June belonged to the same group (spring) and had no overlap with the group of samples collected in other months (other). This grouping was corroborated by the analysis of wet weight N concentrations.

To facilitate the comparison with mussel harvest values, which are typically reported as total mass of mussels (i.e. shells, soft tissue and associated water), ANOVA analyses were performed on wet weight concentrations. Pairwise differences were assessed using the Tukey's HSD test. The ANOVAs tested for the fixed effects of region (Outer, Central and Inner), season (spring or other) and their interaction.

2.6. Modelled environmental variables

Care was taken to select the most relevant ecological variables in order to reach the most robust predictions about the role of the environment for blue mussel occurrence and growth. When the variable selection is inadequate, a model may include irrelevant variables and its predictive power is low (MacNally, 2000). Earlier studies have shown that water salinity, temperature conditions, and food availability (a product of phytoplankton concentration and water flow) mostly shape the distribution and growth of blue mussels at the Baltic Sea scale (Kotta et al., 2015).

Model inputs for the physical and biogeochemical conditions in the Baltic Sea were obtained from the products BALTICSEA_ANALYSIS_FORECAST_PHY_003_006 and BALTICSEA_ANALYSIS_FORECAST_BIO_003_007 at the Copernicus open access data portal (http://marine.copernicus.eu/services-portfolio/access-to-products/). These physical products covering the whole Baltic Sea area contain data with hourly resolution and 25 vertical levels. The biogeochemical data are served with 6-h resolution and 25 vertical levels. For both products, the horizontal grid step is regular in latitude and longitude and is approximately 1 nautical mile. The physical product is based on simulations with the HBM ocean model code (HIROMB-BOOS-Model). The biogeochemical product is based on simulations with the BALMFC-ERGOM version of the biogeochemical model ERGOM, originally developed at IOW, Germany. The BALMFC-ERGOM version has been further developed at 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 the analyses presented here, annual averages of salinity and current velocity and summer averages (June to August) of temperature and chlorophyll *a* concentration were used.

In addition to the aforementioned data layers, depth data acquired from the Baltic Sea Bathymetry Database (Baltic Sea Hydrographic Commission, 2013) were used as a modelling input variable for predicting blue mussel presence and growth. The locations of hard bottom areas were obtained from the EMODnet portal (http://www.emodnet.eu/) and unpublished sediment data were collated from Finnish Environment Institute, Geological Survey of Sweden, and the Bundesamt für Seeschifffahrt und Hydrographie. Wave exposure data were produced by Aquabiota, using the Simplified Wave Model method (SWM; Wijkmark and Isæus, 2010). The SWM method calculates the wave exposure for mean wind conditions using a nested-grids technique to take into account long distance wind effects on the local wave exposure regime. This method results in a pattern where the fetch values are smoothed out to the sides, and around islands in a similar way that refraction and diffraction make waves deflect around islands. Then a depth-attenuation correction was applied to the SWM in order to estimate depth-attenuated wave exposure (Bekkby et al., 2008). For maps of environmental variables, see Supplementary Fig. 1.

2.7. Modelling the occurrence of blue mussel reefs along environmental gradients of the Baltic Sea

In the case of distribution data, all samples having positive coverage or biomass were considered as indicative of mussel presence and all other samples were considered as absences. The occurrence probability of wild blue mussels on seafloor was modelled as a function of depth, salinity, temperature, wave exposure and the presence of hard or mixed substrate with sand, boulders and bedrock. These substrate types are known to be good habitats for blue mussels in the Baltic Sea area (e.g. Westerbom, 2006). A binomial Generalized Additive Model (GAM) with logit link function was used for modelling occurrence. Possible over-fitting was limited by constraining the degrees of freedom of model covariates.

2.8. Hydrodynamic connectivity model

The connectivity structure among all mussel reefs in the Baltic Sea area was estimated with a biophysical model of larval dispersal. Blue mussel larvae may drift in the water column for up to 30 days (Bayne, 1965). The biophysical model combined flow fields from an ocean circulation model with a Lagrangian particle-tracking model simulating transport of individual larvae from spawning to settling locations. The ocean current velocity fields were produced with the three-dimensional NEMO-Nordic model (Hordoir et al., 2013, 2015), a regional configuration of the NEMO ocean engine (Madec, 2010) covering the Baltic Sea, the Kattegat, the Skagerrak, and most of the North Sea. The model has a horizontal spatial resolution of 3.7 km and 84 vertical levels with depth intervals of 3 m at the surface and 23 m for the deepest layers. The model has open boundaries between Cornwall and Brittany, and between the Hebrides Islands and Norway with tidal harmonics defining sea surface height (SSH) and velocities, and Levitus climatology defining temperature and salinity (Levitus and Boyer, 1984). The applied model had a free surface and the atmospheric forcing was based on the re-analysis dataset ERA40 (Uppala et al., 2005). Runoff was based on climatological data from several databases for the Baltic Sea and the North Sea. Validation of the NEMO-Nordic showed that the model correctly represents both tidally induced and wind driven SSH anomalies (Hordoir et al., 2015).

To simulate larval drift trajectories, the Lagrangian particle-tracking model TRACMASS (De Vries and Döös, 2001), that calculates transport of particles using stored flow field data from the ocean model, was used. The velocity, temperature and salinity were updated with a regular interval for all grid boxes in the model domain (in this study - every three hours), and the trajectory calculations were performed with a 15-min time step. Particles simulating larvae of blue mussels were released from the model grid cells (3.7×3.7 km^2) that overlapped with the mussel reef areas. From each grid cell, 294 particles were released on three occasions between June to July as this time corresponds to a planktonic larval phase of blue mussels in the Baltic Sea region (Kautsky, 1982). Each larva was forced to drift in one of three depth intervals: 25% of larvae between 0 and 10 m, 50% of larvae between 10 and 15, and 25% of larvae between 15 and 30 m (Corell et al., 2012). The pelagic larval duration (PLD) was set to either 20 or 30 days with equal probability, and settlement was assumed at the location when the PLD was completed. All these simulations were repeated for 8 years (1995–2002), representing a range of North Atlantic oscillation index values (NAO; Hurrel and Deser, 2009), which is known to correlate well with the variability in circulation pattern, making a total of 670,000 released particles. A grid cell was considered to receive recruits if larvae spawned at any of the reefs in the Baltic Sea range settled at the specified grid cell (Supplementary Fig. 2).

2.9. Modelling the growth of blue mussels along environmental gradients of the Baltic Sea

Blue mussel growth was modelled as statistical relationships between environmental variables and mussel growth yield experimentally evaluated all over the Baltic Sea region. Only the environmental variables known to affect regional patterns of Baltic Sea mussel growth (salinity, temperature, chlorophyll *a*, exposure to waves) were included in the model. It was assumed that new larvae can settle from 1st to 30th of June and only in the grid cells that are connected to mussel reefs (see previous subsection). The growth simulations were based on dry weight of mussels as opposed to length (this allowed for negative growth during periods of resource limitation and for greater flexibility when dealing with gamete production). The model assumed that the new larvae appeared in June. Yields were normalized with the total incubation time (to produce data for yield per day) but a linear pattern was observed within a year, thus allowing to extrapolate the predictions to 365 days. Two year predictions were calculated from one-year predictions using a coefficient obtained from individual growth patterns.

Gaussian GAMs with an identity link function were used for modelling. Possible over-fitting was reduced by constraining the degrees of freedom of model covariates. Final growth model included salinity and interaction between wave exposure and chlorophyll *a*. Two random factors were used to model the dependence inherent in the growth data. First, for a combination of farm area and year to allow for yearly variation in different farming areas. Second, for a combination of place

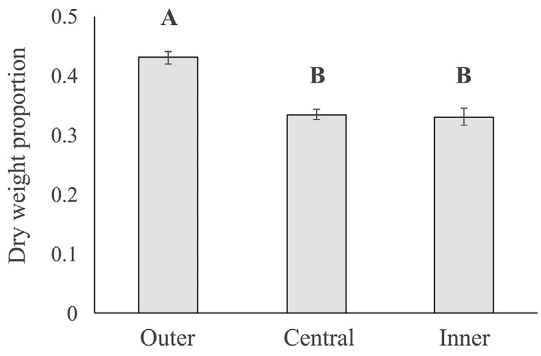

Fig. 3. Mean and standard errors (bars) of the mean dry weight proportion in the Outer, Central and Inner Baltic Sea. Letters depict statistically significant differences between groups (Tukey's HSD test results at $p < 0.05$) and levels are statistically significantly different if they do not have any letters in common.

(within area) and year to allow for yearly variation within areas. Thus it was assumed that yields for two farms from the same area or place from the same year are more similar than yields for two farms from different areas or places from the same year. To normalize the residual distribution, the yield per day was fourth-root transformed.

For prediction, it was assumed (based on empirical knowledge) that no further gain can be obtained from wave exposure values above 200,000 which represents a transition from moderately exposed to exposed areas (Kotta et al., 2015). Blue mussel growth was deemed impossible at salinity values below 3.5 (Riisgård et al., 2014). The available growth data was more evenly spread along the north-eastern and south-western coasts as compared to central coasts of the Baltic Sea. Hence, in these sparsely sampled areas, growth for locations far from any growth assessment was estimated by spatial extrapolation. However, with respect to salinity, the main factor explaining mussel growth in our model, extrapolations are not extensive, since the growth data spans the salinity gradient.

To quantify meaningful effect sizes of the two components (salinity vs chlorophyll *a* and exposure to waves) in the study area, predictions of two-year yield were obtained for six different combinations of predictor values, as follows. First, for each predictor the 2.5% quantile (low), the median and the 97.5% quantile (high) were determined. To assess the interaction effect of chlorophyll *a* and wave exposure, salinity was kept at its median value while four different value combinations (low-low, low-high, high-low, high-high) were assigned to the other two predictors. To assess the effect of salinity, the other two predictors were kept at their respective medians while two different value combinations (low and high) were assigned to salinity.

2.10. Nutrient removal at harvest

The mass of N and P removed during harvest at the three farms was estimated by multiplying reported wet weight harvest values and least squares mean estimates for “other season” wet weight nutrient percentages for the three regions of the Baltic. These estimated percentages were obtained from analyses of variance (ANOVA) of N and P tissue concentrations from 124 composite samples (Supplementary Tables 2 and 3).

3. Results

3.1. Analyses of farmed mussels

A total of 9478, 1516 and 4912 mussel samples were harvested and measured from farms in the Outer, Central and Inner Baltic Sea (three major analysis regions, Fig. 2). Average densities and individual wet weights (±SE) of harvested mussels were 2654 ± 77 individuals m^{-1} (individuals per metre of rope) and 0.50 ± 0.02 g ww (wet weight) in the Outer Baltic; 4998 ± 329 individuals m^{-1} and 0.20 ± 0.01 g ww in the Central Baltic and 2326 ± 24 individuals m^{-1} and 0.16 ± 0.001 g ww in the Inner Baltic, respectively.

In total, 124 composite samples of whole mussels (shell and soft tissue) were available for dry matter and nutrient analysis. Samples of blue mussels from the Outer Baltic had significantly higher dry matter content (42.5%) than mussels from the Central (34.0%) or Inner (32.6%) Baltic (Supplementary Table 1, Fig. 3). Region, season and their interaction accounted for 62.3% and 67.7% of the total observed variation in mussel tissue N and P percentages (Supplementary Tables 2 and 3). Nitrogen concentrations were highest in Outer Baltic samples from spring (1.23%), followed by those obtained for the same region in other seasons (0.89%). There were no significant differences among spring Central Baltic samples (0.70%), Central Baltic samples from other seasons

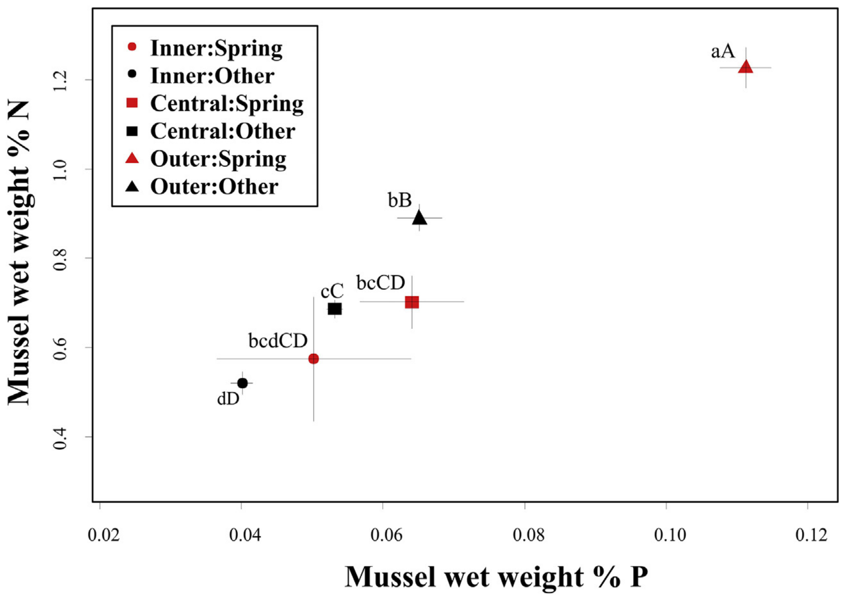

Fig. 4. Mean (filled shapes) and standard errors (bars) of nitrogen (N) and phosphorus (P) content in farmed mussels expressed as a percentage of wet weight in spring vs other seasons in the Outer, Central and Inner Baltic Sea. Letters depict statistically significant differences between groups (Tukey's HSD test results at $p < 0.05$) with capital letters denoting N and lowercase letters P groups. N and P levels are statistically significantly different if they do not have any letters in common.

(0.69%), and spring Inner Baltic samples (0.57%). Inner Baltic samples from other seasons (0.52%) were significantly lower compared to all other contexts except Inner Baltic spring samples (Supplementary Table 2). Observed phosphorous concentrations followed similar trends to those of N (Supplementary Table 3). The highest P concentrations were measured in spring Outer Baltic samples (0.111%) and the lowest in mussels from the Inner Baltic in other seasons (0.040%). Phosphorous concentrations in spring Central (0.060%) and Inner Baltic (0.050%) samples were significantly lower than in spring Outer Baltic samples and did not differ from Outer Baltic samples obtained in other seasons (0.065%). As for N, P concentrations did not statistically differ between seasons in mussels from the Central (spring: 0.060%, other: 0.053) and Inner (spring: 0.050%, other: 0.040%) Baltic (Fig. 4).

Biomass yield and economic information were available for three production farms: Kumlinge (Inner Baltic), Sankt Anna (Central Baltic) and Kiel (Outer Baltic) (Table 1). Although the higher salinity and chlorophyll *a* levels at Kiel may suggest a greater potential for mussel biomass production and hence nutrient removal, this difference was not manifested. In fact, nutrient removal was higher in Sankt Anna (23.3 g N m^{-1} and 1.8 g P m^{-1} line) than either Kiel (22.2 g N m^{-1} and 1.6 g P m^{-1} line) or Kumlinge (3.7 g N m^{-1} and 0.3 g P m^{-1} line). Production costs were approximately four times higher at Kiel (1.85 € kg biomass harvested^{-1}) than at Sankt Anna (0.52 € kg biomass harvested^{-1}). Costs were much higher at Kumlinge (8.52 € kg biomass harvested^{-1}). Differences in production costs were the main driver of the large difference in nutrient removal costs which were lowest at Sankt Anna (76 € kg N)$^{-1}$ and 981 € kg P^{-1}) and higher at the other two farms.

3.2. Modelling of biomass yield and regional nutrient removal

Spatially explicit estimates of farm biomass yield were predicted as a function of site salinity, exposure to waves and food availability (i.e. chlorophyll *a* concentration) (Fig. 5). The model explained 82.3% of the variation in the data. Modelled patterns of biomass yield were driven by salinity at the regional scale and food availability at the

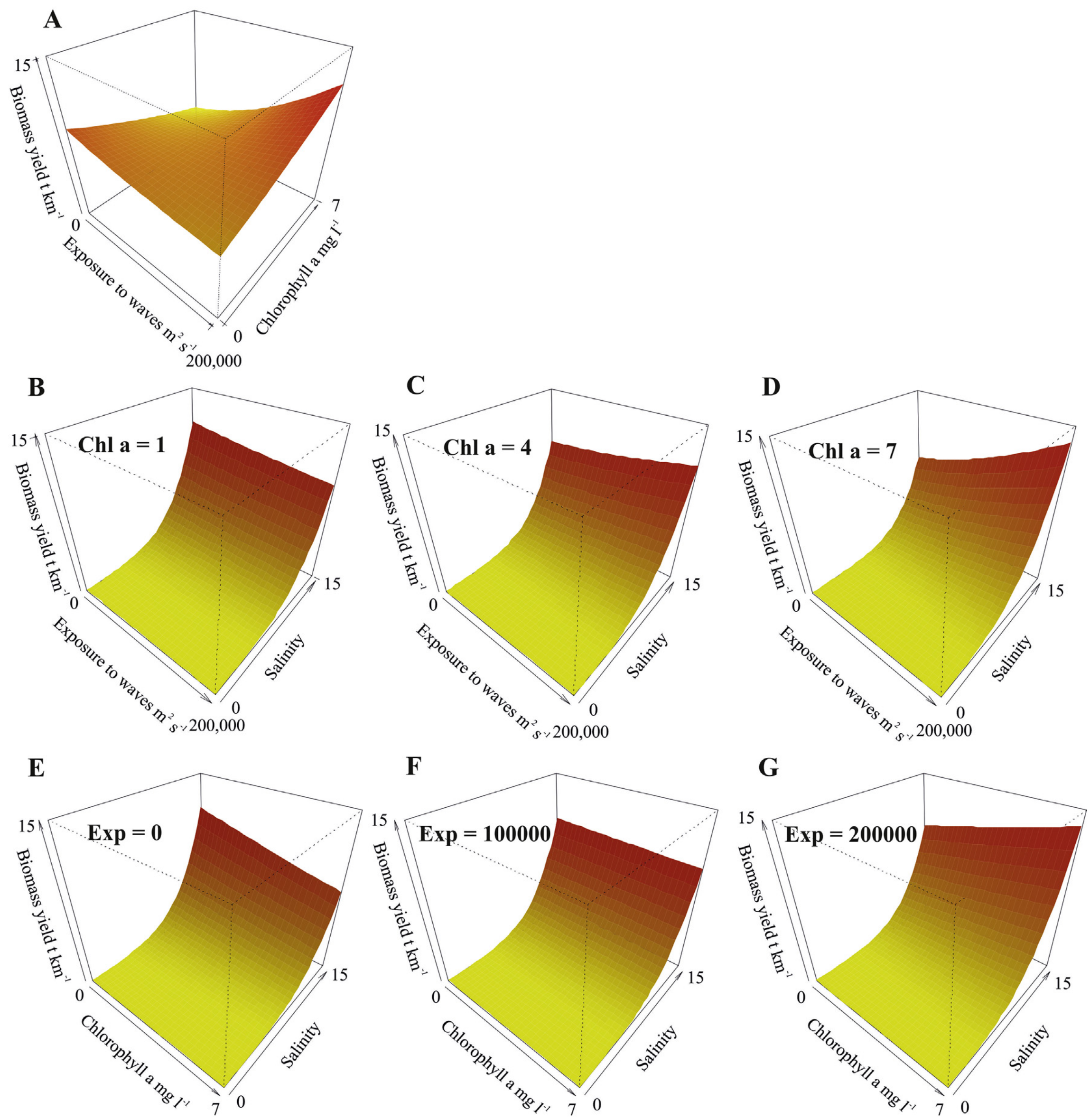

Fig. 5. Overview of the blue mussel biomass yield model and obtained response curves. Estimations refer to biomass yields obtained two years after the establishment of the farms. Panel A shows the interactive effects of exposure to waves and chlorophyll *a* concentration (i.e. food availability) at a salinity of 7.5 psu. Panels B-D show the interactive effects of exposure to waves and salinity at low, medium and high chlorophyll *a* concentrations. Panels E-G show the interactive effects of salinity and chlorophyll *a* at low, medium and high exposure levels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

local scale. On the model scale, the effect of salinity was estimated to be linear (and positive) which translated to a quartic effect on the response scale. The interaction between food concentration and exposure to waves (a good proxy of water movement and exchange) was more complex. At low water movement, elevated chlorophyll *a* concentrations were associated with low biomass yield of mussels, whereas at moderate to good water exchange, increasing chlorophyll *a* resulted in the raised biomass yield. The overall effect size of salinity was about 13 times as large as the effect size of the aforementioned interaction. The random effects, accounting for the inter-annual and spatial variation not explained by the mean trends in salinity and the interaction between wave exposure and food availability, explained approximately 50% of the total variance. The model does not simulate disastrous loss of harvestable mussel biomass associated with severe storms or harmful algal blooms.

Response curves predicting mussel yield as a function of environmental conditions (Fig. 5) were combined with spatial data on salinity, wave exposure and surface chlorophyll *a* concentrations to produce pan-Baltic estimates of potential rates of biomass removal that can be obtained using farmed blue mussels (Supplementary Fig. 3). The model extrapolation power was assessed by predicting the average yield in the Kiel mussel farm that was not used for model fitting. On the model scale, the average yield was predicted to be only 10% smaller than what was actually measured. Higher growth was predicted at higher salinities and/or better food regimes, i.e. the Outer and Central Baltic. Predicted biomass yield was highest in high-salinity areas of the

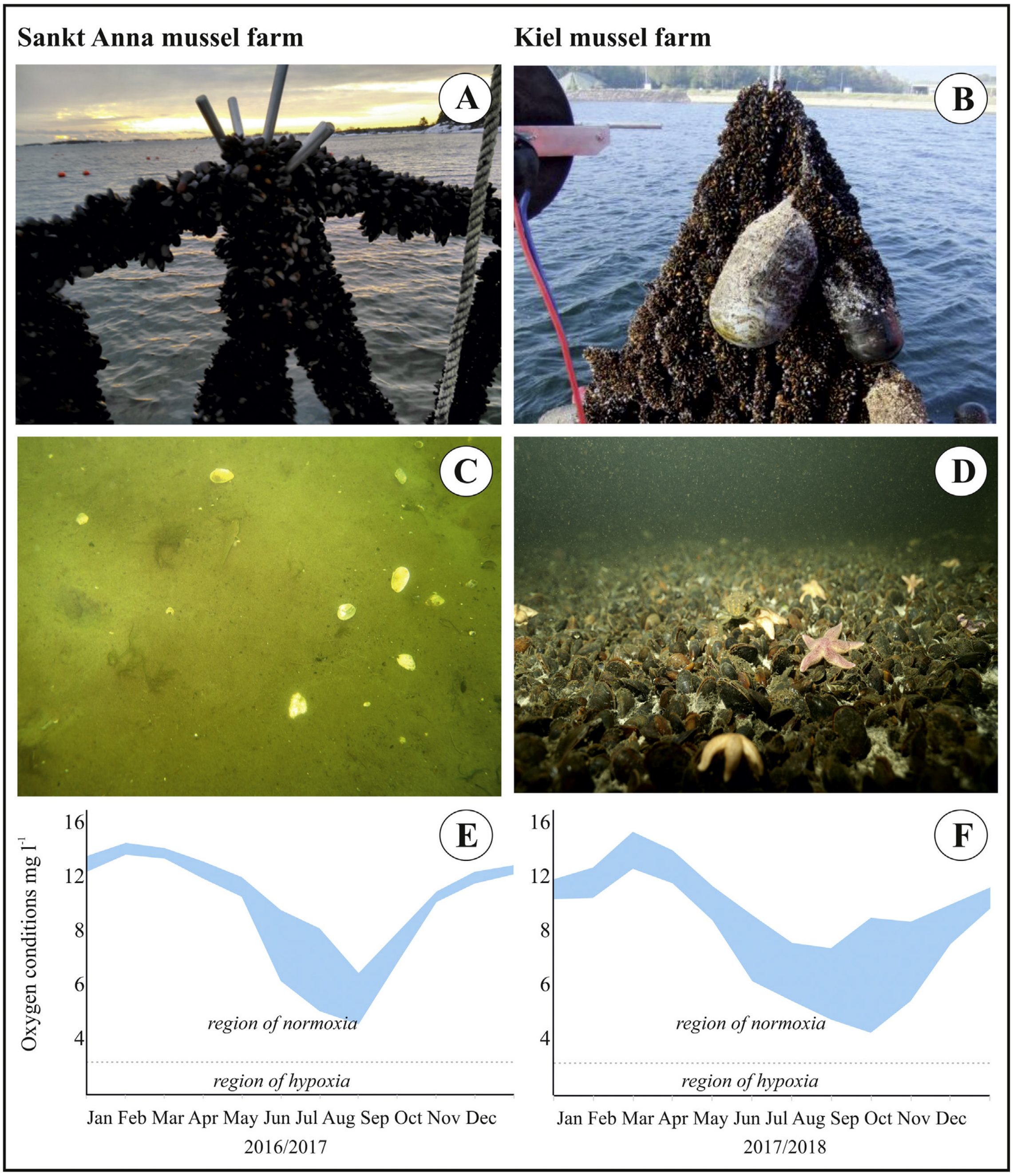

Fig. 6. Long line removed from the water at Sankt Anna (A) showing mussel growth. View of mussel farm at Kiel showing floats on which lines are suspended (B). Panels (C) and (D) show the environment underneath the same farms. Blue surfaces of panels (E) and (F) show variability in oxygen conditions (mg l^{-1}) measured at the sediment-water interface underneath the farms and dotted lines indicate the region of hypoxia and normoxia (for further data see http://www.sea.ee/bbg-odss/Ocean/OceanMain). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Outer Baltic where it was estimated at 15 kg m^{-1} per harvest. With declining salinity, predicted biomass yields varied between 1 and 3 kg m^{-1} in the Central Baltic. In marginal (Inner Baltic) regions, predicted biomass yields never exceeded 1 kg m^{-1}. Patterns in modelled rates of biomass removal are similar to the observed patterns of N and P content (Fig. 4), which are higher in the Outer Baltic than in either the Central or Inner Baltic.

The harvest data from the three example farms (Table 1) can be put into a regional context by comparing them to regional modelled rates of biomass removal (Supplementary Fig. 3). The observed harvest at Kumlinge is similar to model projections while the actual harvest at Sankt Anna is 2.5 times larger than model projections and the Kiel harvest is 5 times smaller (Table 1). Mussels grow larger in waters that are more saline and therefore their substrate (i.e., the settlement rope) becomes quickly saturated and competition between mussels for space is high. A multi-layered structure of large mussels is very unstable and even moderate storms can remove outer layers from suspended ropes. Many detached mussels were observed underneath the Kiel farm, whereas no such losses were recorded in Sankt Anna (Fig. 6). Nevertheless, the full potential of high-salinity areas is demonstrated based on harvest data from experimental fuzzy ropes deployed in Kiel farm over a year and such substrates hosted nearly 10 kg mussels m^{-1} (Supplementary Fig. 4).

When evaluating the potential of mussel cultivation as a mitigation tool to reach regional nutrient reduction targets, a surprisingly small marine area would need to be used for mussel farms in order to close the remaining nutrient reduction gaps, i.e., 900 km^2 for the Central Baltic and 600 km^2 for the Inner Baltic (Fig. 1). When farms are established at optimal growth locations and optimal density, then nutrient removal during mussel harvest can compensate up to 100% of the local and a large part of the regional nutrient loading. Although the modelling results presented here suggest a higher efficiency of mussel farms at high salinity, the factual evidence suggests that Outer Baltic farms are not necessarily more efficient in nutrient removal as compared to Central Baltic farms. Importantly, the predicted total area of farms needed for achieving HELCOM nutrient reduction targets could be achievable under the current marine spatial planning regime in the Baltic Sea.

4. Discussion

Marine eutrophication is a pervasive and growing threat to global sustainability (Conley et al., 2009b). While all reasonable efforts to reduce nutrient inputs from land to sea must continue, internal measures are also needed to ensure the timely recovery of eutrophicated systems (Savchuk, 2018). Extractive harvesting of farmed native bivalve species, including *M. edulis/trossulus*, is a sustainable, low-impact (Petersen et al., 2014, 2019), circular (Spångberg et al., 2013) and potentially cost-effective (Gren et al., 2009) internal measure for eutrophication control (Suplicy, 2018). While arguments have been made against the use of internal measures such as mussel farming (Stadmark and Conley, 2011) or geo-engineering (Conley, 2012), there can be little doubt that internal measures must be considered when all feasible external measures for nutrient load reduction have been explored, applied and found to be inadequate or insufficient.

The Baltic Sea is a plausible representation of the likely future state of other coastal seas globally (Reusch et al., 2018) and the accumulated knowledge for this region may serve as a useful future management model for other internationally managed seas. Mitigation has already been largely successful for recovery of Baltic Sea top predators (Reusch et al., 2018) and some fish stocks (Eero et al., 2012). External loads of both N and P from the surrounding catchment have declined (Reusch et al., 2018; Savchuk, 2018) but average N concentrations are decreasing slowly, if at all, while P concentrations continue to increase (Savchuk, 2018). This mismatch between the successful reduction of terrestrial nutrient inputs and failure to observe corresponding improvements in water column nutrient concentrations is due in part to the ongoing release of nutrients accumulated in marine sediments (Vahtera et al., 2007).

The predicted nutrient removal by mussel harvesting largely follows the spatial patterns of mussel growth, i.e., farms in the Outer Baltic are expected to have higher yields than in other Baltic Sea regions. Harvest weight (kg m^{-1}) is linearly related to mussel size (Nielsen et al., 2016) and blue mussels do not grow as rapidly in brackish waters as they do in fully marine environments. While the small size of harvested mussels poses challenges for feed or food production, the data presented here suggest that the overall potential for nutrient removal does not diminish along the salinity gradient, except for the innermost parts of the Baltic Sea (Table 1, Supplementary Fig. 3). While it is important to prioritize high salinity sites in order to enhance the yield, even at reduced salinities in the central Baltic Sea, a one hectare mussel farm with a density of appropriate ropes may yield hundreds of tons of biomass per harvest cycle. Furthermore, the harvest strategy can be optimised as smaller mussels may be more efficient at nutrient removal due to lower detachment rates as density dependent losses can reach 50% in oceanic regions with high biomass production (Haamer, 1996).

Unlike earlier studies (Dahlbäck and Gunnarsson, 1981; Hartstein and Stevens, 2005), the monitoring of all existing mussel farms in the Baltic Sea region offers no evidence to suggest that blue mussel farms in the Baltic Sea have any negative effects on the local oxygen conditions at the sediment–water interface (Aigars et al., 2019). While others have suggested that mussel farms can cause promote lower sediment oxygen concentrations associated with a reduction in bioturbation or excessive accumulation of organic matter (Stadmark and Conley, 2011), the opposite phenomenon was observed at the Kiel mussel farm where an increase in bioturbation led to higher sediment oxygen concentration (Aigars et al., 2019). When sediments remain oxygenated, there is unlikely to be any additional internal loading of P. However, oxygenated conditions in the sediment under farms can suppress denitrification (Carlsson et al., 2012).

Shellfish farming generally has lower environmental impacts than other forms of aquaculture (Forrest et al., 2009; Kraufvelin and Díaz, 2015). Farmed blue mussels do not require any nutrient external inputs. This means that unlike other forms of aquaculture, all of the nutrients removed during harvest make a positive contribution to regional eutrophication reduction and a valuable regulative ecosystem service in eutrophic waters (Suplicy, 2018; Petersen et al., 2019). However, the potential for localised nutrient enrichment in the immediate vicinity of mussel farms does exist in very sheltered areas (e.g., Stadmark and Conley, 2011; Holmer et al., 2015) and in such areas the possibility of undesirable local eutrophication must be recognised and addressed.

Furthermore, farms can provide additional habitat for colonization to supplement natural mussel reefs lost to anthropogenic impacts, especially human-facilitated invasion impacts of benthic predators. In the Baltic Sea, the most relevant invasive predator is round goby, which causes large-scale losses of benthic blue-mussel populations (Skabeikis et al., 2019), e.g. one case-study location is estimated to have lost 23% of its 230km^2 pre-invasion mussel reef area due to round goby predation (Liversage et al., 2019). Suspended mussels will attract negligible predation from such benthic predators, thus mussel farming will help restore overall population levels. If a switch does occur from natural mussel reefs to suspended farm mussels, this may involve a reduced local-scale per-capita impact on eutrophication because material excreted from suspended mussels will have greater dispersal and dilution by water movements (Hartstein and Stevens, 2005) rather than direct benthic retention. In addition, aquaculture activities often produce benthic shell debris deposits (Sanchez-Jerez et al., 2019) which increase sediment porosity and oxidised sediment layer depth, as well as infaunal bioturbation (Zaiko et al., 2010). These benefits may be expected following extended establishment of mussel farms.

Using mussel farming as an internal measure to mitigate eutrophication in the Baltic requires the development of appropriate legislative instruments (Ozoliņa, 2017) and resolution of sea-use conflicts along maritime spatial planning process (Kannen, 2014). The model-predicted locations of mussel farms for achieving eutrophication reduction targets do not take multiple sea-use conflicts into account, especially tourism and fisheries (Lindahl et al., 2005). While maritime spatial planning tools for optimizing interests of various stakeholders are well developed, the tools do not yet incorporate the implementation of mussel farming. Careful planning of large-scale mussel farming could avoid unacceptable environmental impacts or conflicts with other uses. Farms should be located in semi-exposed or exposed areas with good water circulation where negative local effects to benthic habitat quality are unlikely. Additionally, predation can compromise the production of bivalves in otherwise suitable areas. Therefore, the risk of losing biomass to, e.g., the eider ducks (*Somateria mollissima*) in the Outer Baltic must be assessed before initiating a full-scale mussel production. Other technical challenges including storms, epiphytes, and in some regions ice, will also need to be considered and lessons learnt from previous mussel farming programmes need to be applied (National Research Council, 2010). Furthermore, farm technology adapted to the culturing of small mussels should be used whenever possible to maximize yields. Blue mussel farming as a mitigation measure is particularly efficient to counteract diffuse nutrient emissions as to date there are few other effective options to remove nutrients that have already reached the sea. Commercial mussel farming can also contribute to rural sustainability by providing jobs in economically depressed areas. It may also contribute to a clean-up of the local marine environment with benefits for local tourism, recreation and other cultural ecosystem services.

5. Conclusions

Eutrophication is a leading cause of impairment of many aquatic ecosystems globally. While external measures to control nutrient inputs must be pursued, there is also a need for internal measures in order to restore water quality and enable ecosystem recovery in a timely manner. Blue mussel farming is a promising low-impact and native species-based internal method for eutrophication control in the Baltic Sea and beyond. Mussels filter the water for phytoplankton and trap nutrients which are then removed from the aquatic environment through harvest, allowing nutrient reuse as part of the circular economy. Blue mussel farming in the Baltic Sea not only provides a tool for nutrient mitigation, but also contributes to the social and economic sustainability of rural areas. These results presented here provide factual data to support political decisions on internal measures for eutrophication control and promote the sustainability of the Baltic Sea region through mussel farming for nutrient management.

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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Author contributions

Conceived the study and wrote the paper: JK, MF, AK, KL, LB, PRJ. Collected data: MR, FRB, PB, IB, ED, SK, PaK, PeK, OL, ML, MML, MM, ANS, HOK, MO, SK, JR, AŠ, EV, HS. Obtained funding and analysed data: JK, MF, AK, KH, PRJ, AV. 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 a request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.136144.

References

Aigars, J., et al., 2019. Ecological impacts at the small-scale commercial mussel farms in the Baltic Sea. Interreg Baltic Sea Region Baltic Blue Growth Project. Final Report.
Andersen, J.H., et al., 2017. Long-term temporal and spatial trends in eutrophication status of the Baltic Sea. Biol. Rev. 92, 135–149.
Baltic Sea Hydrographic Commission. Baltic Sea Bathymetry Database Version 0.9.3. Downloaded from http://data.bshc.pro/ on 13.04.2016 (2013).
Bayne, B.L., 1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis*. Ophelia 2, 1–47.
Bekkby, T., Isachsen, P.E., Isaeus, M., Bakkestuen, V., 2008. GIS modeling of wave exposure at the seabed: a depth-attenuated wave exposure model. Mar. Geod. 31, 117–127.
Breitburg, D., et al., 2018. Declining oxygen in the global ocean and coastal waters. Science 359, eaam7240.
Cai, W.J., et al., 2011. Acidification of subsurface coastal waters enhanced by eutrophication. Nat. Geosci. 4, 766.
Carlsson, M.S., Engström, P., Lindahl, O., Ljungqvist, L., Petersen, J.K., Svanberg, L., Holmer, M., 2012. Effects of mussel farms on the benthic nitrogen cycle on the Swedish west coast. Aquaculture Environment Interactions 2 (2), 177–191 (2012).
Conley, D.J., 2012. Save the Baltic Sea: geoengineering efforts to bring oxygen into the deep Baltic should be abandoned. Nature 486, 463–465.
Conley, D.J., et al., 2009a. Controlling eutrophication: nitrogen and phosphorus. Science 323, 1014–1015.
Conley, D.J., et al., 2009b. Hypoxia-related processes in the Baltic Sea. Environ. Sci. Technol. 43, 3412–3420.
Corell, H., Moksnes, P.O., Engqvist, A., Döös, K., Jonsson, P.R., 2012. Larval depth distribution critically affects dispersal and the efficiency of marine protected areas. Mar. Ecol. Prog. Ser. 467, 29–46.
Dahlbäck, B., Gunnarsson, L., 1981. Sedimentation and sulfate reduction under a mussel culture. Mar. Biol. 63, 269–275.
De Vries, P., Döös, K., 2001. Calculating Lagrangian trajectories using time-dependent velocity fields. J. Atmos. Sci. 18, 1092–1101.
Diaz, R.J., Rosenberg, R., 1995. Marine benthic hypoxia. A review of its ecological effects and the behavioral responses of benthic macrofauna. Oceanogr. Mar. Biol. Ann. Rev. 33, 245–303.
EC. European Commission, 2012. Blue Growth Opportunities for Marine and Maritime Sustainable Growth COM/2012/0494 Final.
Eero, M., Köster, F.W., Vinther, M., 2012. Why is the eastern Baltic cod recovering? Mar. Pol. 36, 235–240.
FAO, 2018. The State of World Fisheries and Aquaculture. Available at. http://www.fao.org/3/i9540en/I9540EN.pdf.
Fleming-Lehtinen, V., et al., 2015. Recent developments in assessment methodology reveal that the Baltic Sea eutrophication problem is expanding. Ecol. Indic. 48, 380–388.
Forrest, B.M., Keeley, N.B., Hopkins, G.A., Webb, S.C., Clement, D.M., 2009. Bivalve aquaculture in estuaries: review and synthesis of oyster cultivation effects. Aquaculture 298, 1–15.
Gren, M., Lindahl, O., Lindqvist, M., 2009. Values of mussel farming for combating eutrophication: an application to the Baltic Sea. Ecol. Eng. 35, 935–945.
Haamer, J., 1996. Improving water quality in a eutrophied fjord system with mussel farming. Ambio 25, 356–362.
Hamilton, H.A., et al., 2018. Trade and the role of non-food commodities for global eutrophication. Nature Sustainability 1, 314.
Hartstein, N.D., Stevens, C.L., 2005. Deposition beneath long-line mussel farms. Aquacultural Engineering 33, 192–213.
Hedberg, N., Kautsky, N., Kumblad, L. & Wikström, S. A. Limitations of using blue mussel farms as a nutrient reduction measure in the Baltic Sea. Report from Baltic Sea Centre 2/2018. Stockholm: Stockholm University. Available at: https://www.su.se/polopoly_

fs/1.406424.1539853328!/menu/standard/file/BSC_Mussels_report_2_2 018_lowres.pdf (2018).
HELCOM, 2015. Manual for Marine Monitoring in the COMBINE Programme of HELCOM.
HELCOM, 2018. HELCOM thematic assessment of eutrophication 2011-2016. Available at. http://www.helcom.fi/baltic-sea-trends/holistic-assessments/state-of-the-baltic-sea-2018/reports-and-materials/.
Helin, J., 2013. Cost-efficient Nutrient Load Reduction in Agriculture: A Short-term Perspective on Reducing Nitrogen and Phosphorus in Finland Doctoral Dissertation. University of Helsinki Available at. http://jukuri.luke.fi/handle/10024/481612.
Holmer, M., Thorsen, S.W., Carlsson, M.S., Kjerulf, P.J., 2015. Pelagic and benthic nutrient regeneration processes in mussel cultures (*Mytilus edulis*) in a eutrophic coastal area (Skive Fjord, Denmark). Estuar. Coasts 38, 1629–1641 (2015).
Hordoir, R., Dieterich, C., Basu, B., Dietze, H., Meier, H.E.M., 2013. Freshwater outflow of the Baltic Sea and transport in the Norwegian current: a statistical correlation analysis based on a numerical experiment. Cont. Shelf Res. 64, 1–9.
Hordoir, R., Axell, L., Löptien, U., Dietze, H., Kuznetsov, I., 2015. Influence of sea level rise on the dynamics of salt inflows in the Baltic Sea. J. Geophys. Res. - Oceans 120, 6653–6668.
Hu, S., Wang, Y., Han, H., 2011. Utilization of waste freshwater mussel shell as an economic catalyst for biodiesel production. Biomass Bioenergy 35, 3627–3635.
Hurrel, J.W., Deser, C., 2009. North Atlantic climate variability: the role of the North Atlantic oscillation. J. Mar. Syst. 78, 28–41.
Kannen, A., 2014. Challenges for marine spatial planning in the context of multiple sea uses, policy arenas and actors based on experiences from the German North Sea. Reg. Environ. Chang. 14, 2139–2150.
Kautsky, N., 1982. Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in a Baltic *Mytilus edulis* population. Mar. Biol. 68, 143–160.
Kiessling, A., Futter, M.N., Elofsson, K., Vidakovic, A., 2019. Mussel farming in the Baltic Sea as an environmental measure. Availabe at. https://www.slu.se/globalassets/ew/org/centrb/aquaculture/dokument/policy-brief-new-data-on-musselfarming-as-environmental-service-in-baltic-proper-eng.pdf.
Kotta, J., et al., 2015. Establishing functional relationships between abiotic environment, macrophyte coverage, resource gradients and the distribution of *Mytilus trossulus* in a brackish non-tidal environment. PLoS One 10, e0136949.
Kraufvelin, P., Díaz, E.R., 2015. Sediment macrofauna communities at a small mussel farm in the northern Baltic proper. Bor. Environ. Res. 20, 378–390.
Larsson, M., Granstedt, A., 2010. Sustainable governance of the agriculture and the Baltic Sea—agricultural reforms, food production and curbed eutrophication. Ecol. Econ. 69, 1943–1951.
Levitus, S., Boyer, T.P., 1984. World Ocean atlas. Salinity. Volume 5. NOAA atlas.
Lindahl, O., et al., 2005. Improving marine water quality by mussel farming: a profitable solution for Swedish society. Ambio 34, 131–138.
Liversage, K., Kotta, J., Aps, R., Fetissov, M., Nurkse, K., Orav-Kotta, H., Rätsep, M., Forsström, T., Fowler, A., Lehtiniemi, M., Normant-Saremba, M., Puntila-Dodd, R., Arula, T., Hubel, K., Ojaveer, H., 2019. Knowledge to decision in dynamic seas: methods to incorporate non-indigenous species into cumulative impact assessments for maritime spatial planning. Sci. Total Environ. 658, 1452–1464.
Lurling, M., Mackay, E.B., Reitzel, K., Spears, B.M., 2016. A critical perspective on geo-engineering for eutrophication management in lakes. Water Res. 97, 1–10.
Maar, M., Saurel, C., Landes, A., Dolmer, P., Petersen, J.K., 2015. Growth potential of blue mussels (*M. edulis*) exposed to different salinities evaluated by a dynamic energy budget model. J. Mar. Syst. 148, 48–55.
MacNally, R., 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between — and reconciliation of — 'predictive' and 'explanatory' models. Biodivers. Conserv. 9, 655–671.
Madec, G., 2010. Nemo Ocean Engine, Version 3.3, Tech. Rep. IPSL.
McLaughlan, C., Rose, P., Aldridge, D.C., 2014. Making the best of a pest: the potential for using invasive zebra mussel (*Dreissena polymorpha*) biomass as a supplement to commercial chicken feed. Environ. Manag. 54, 1102–1109.
National Research Council, 2010. Ecosystem Concepts for Sustainable Bivalve Mariculture. The National Academies Press, Washington, DC https://doi.org/10.17226/12802.
Naylor, R.L., Williams, S.L., Strong, D.R., 2001. Aquaculture – a gateway for exotic species. Science 294, 1655–1656.
Nielsen, P., Cranford, P.J., Maar, M., Petersen, J.K., 2016. Magnitude, spatial scale and optimization of ecosystem services from a nutrient extraction mussel farm in the eutrophic Skive Fjord, Denmark. Aquacult. Env. Interac. 8, 311–329.
Nkemka, V.N., Murto, M., 2013. Two-stage anaerobic dry digestion of blue mussel and reed. Renew. Energ. 50, 359–364.
Ozoliņa, Z., 2017. Mussel farming and its potential in the Baltic Sea. Econ. Business 30, 40–50.
Petersen, J.K., et al., 2014. Mussels as a tool for mitigation of nutrients in the marine environment. Mar. Pollut. Bull. 82, 137–143.
Petersen, J.K., Holmer, M., Termansen, M., Hasler, B., 2019. Nutrient extraction through bivalves. In: Smaal, A.C., Ferreira, J.G., Grant, J., Petersen, J.K., Strand, Ø. (Eds.), Goods and Services of Marine Bivalves. Springer, Cham, pp. 179–208.
Rabalais, N.N., Turner, R.E., Diaz, R.J., Justić, D., 2009. Global change and eutrophication of coastal waters. ICES J. Mar. Sci. 66, 1528–1537.
Reusch, T.B., et al., 2018. The Baltic Sea as a time machine for the future coastal ocean. Sci. Adv. 4, eaar8195.
Riedel, B., Diaz, R., Rosenberg, R., Stachowitsch, M., 2016. The ecological consequences of marine hypoxia: From behavioural to ecosystem responses. In: Solan, M., Whiteley, N.M. (Eds.), Stressors in the Marine Environment: Physiological Responses and Ecological Implication. Oxford University Press, Oxford, pp. 175–194.
Riisgård, H.U., Larsen, P.S., Turja, R., Lundgreen, K., 2014. Dwarfism of blue mussels in the low saline Baltic Sea—growth to the lower salinity limit. Mar. Ecol. Prog. Ser. 517, 181–192.
Rydin, E., Kumblad, L., Wulff, F., Larsson, P., 2017. Remediation of a eutrophic bay in the Baltic Sea. Environ. Sci. Technol. 51, 4559–4566.
Sanchez-Jerez, P., Krüger, L., Casado-Coy, N., Valle, C., Sanz-Lazaro, C., 2019. Mollusk shell debris accumulation in the seabed derived from coastal fish farming. Journal of Marine Science and Engineering 7 (10), 335.
Savchuk, O.P., 2018. Large-scale nutrient dynamics in the Baltic Sea, 1970–2016. Front. Mar. Sci. 5, 95.
Schröder, T., Stank, J., Schernewski, G., Krost, P., 2014. The impact of a mussel farm on water transparency in the Kiel Fjord. Ocean Coast. Manage. 101, 42–52.
Sipiä, V.O., Kankaanpää, H.T., Flinkman, J., Lahti, K., Meriluoto, J.A., 2001. Time-dependent accumulation of cyanobacterial hepatotoxins in flounders (*Platichthys flesus*) and mussels (*Mytilus edulis*) from the northern Baltic Sea. Environ. Toxicol. 16, 330–336.
Skabeikis, A., Morkūnė, R., Bacevičius, E., Lesutienė, J., Morkūnas, J., Poškienė, A., Šiaulys, A., 2019. Effect of round goby (*Neogobius melanostomus*) invasion on blue mussel (*Mytilus edulis trossulus*) population and winter diet of the long-tailed duck (*Clangula hyemalis*). Biol. Invasions 21 (3), 911–923.
Smith, V.H., 2003. Eutrophication of freshwater and coastal marine ecosystems a global problem. Environ. Sci. Pollut. R. 10, 126–139.
Spångberg, J., Jönsson, H., Tidåker, P., 2013. Bringing nutrients from sea to land–mussels as fertiliser from a life cycle perspective. J. Clean. Prod. 51, 234–244.
Stadmark, J., Conley, D.J., 2011. Mussel farming as a nutrient reduction measure in the Baltic Sea: consideration of nutrient biogeochemical cycles. Mar. Pollut. Bull. 62, 1385–1388.
Stigebrandt, A., et al., 2015. An experiment with forced oxygenation of the deepwater of the anoxic By Fjord, western Sweden. Ambio 44, 42–54.
Stuckas, H., Stoof, K., Quesada, H., Tiedemann, R., 2009. Evolutionary implications of discordant clines across the Baltic *Mytilus* hybrid zone (*Mytilus edulis*, *Mytilus trossulus*). Heredity 103, 146–156.
Suplicy, F.M., 2018. A review of the multiple benefits of mussel farming. Rev. Aquacult. https://doi.org/10.1111/raq.12313.
Uppala, S.M., et al., 2005. The ERA-40 re-analysis. Q. J. Roy. Meteor. Soc. 131, 2961–3012.
Vahtera, E., et al., 2007. Internal ecosystem feedbacks enhance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic Sea. Ambio 36, 186–194.
Vidakovic, A., et al., 2015. Evaluation of growth performance and intestinal barrier function in Arctic Charr (*Salvelinus alpinus*) fed yeast (*Saccharomyces cerevisiae*), fungi (*Rhizopus oryzae*) and blue mussel (*Mytilus edulis*). Aquac. Nutr. 22, 1348–1360.
Westerbom, M., 2006. Population Dynamics of Blue Mussels in a Variable Environment at the Edge of Their Range. Doctoral thesis. Faculty of Biosciences, Department of Biological and Environmental Sciences, University of Helsinki, p. 62 (2006).
Wijkmark, N., Isæus, M., 2010. Wave exposure calculations for the Baltic Sea. AquaBiota Water Research AB, Stockholm, Report, 2.
Zaiko, A., Paskauskas, R., Krevs, A., 2010. Biogeochemical alteration of the benthic environment by the zebra mussel *Dreissena polymorpha* (Pallas). Oceanologia 52 (4), 649–667.