Potential and Feasibility of *Mytilus* spp. Farming Along a Salinity Gradient

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Mussel farming, compared to marine finfish aquaculture, represents an environmentally friendly alternative for a high quality protein source and can at the same time be a measure to remove excess nutrients in eutrophic areas. As such, it is considered as a promising "blue growth" potential and promoted within the European Union. To expand mussel aquaculture, new regions have to be considered because there are multiple marine usages, and spatial limitations occur in coastal areas. The brackish Baltic Sea might be considered for expansion of mussel aquaculture. This study focusses on estimated production potential, economic profitability and nutrient remediation potential of mussel farming at different salinities. Four experimental mussel farms were set up along the German Baltic coast at salinities ranging from 7 to 17 psu. Collected growth data was used to calibrate and validate a Dynamic Energy Budget model and to predict the potential mussel production at 12 sites along the German coast. The estimated production and nutrient removal was used to assess economic profitability, assuming two usages of the harvest: human consumption and mussel meal production. Measured mussel specific growth rates increased with salinity from 0.05 mm d^{-1} in Greifswald Bay to 0.11 mm d^{-1} in Kiel Fjord. Within 6 months, a 1-ha farm could produce from 1 t (Darss-Zingst-Bodden-Chain) to 51 t (Flensburg) fresh mussels and remove 1.1 to 27.7 kg P and 24.7 to 612.7 kg N, respectively. Mussel farms at sites west of Rostock at salinities >10 psu could produce 5 cm mussels within 18 months, but only farms at Flensburg, Eckernförde and Kiel Fjord became profitable at a farm size of 4 ha (160,000 m^3) at current market prices of 2.2 € kg^{-1}. Regardless of the farm size, none of the farm sites could operate profitable if fresh mussels were sold for animal feeding at sales price of 0.06 € kg^{-1}. Yearly nutrient removal costs at a small-scale farm (1 ha) ranged between 162 € (Flensburg) and 4,018 € (Darss-Zingst-Bodden-Chain) kg^{-1} nitrogen, and 3,580 € and 88,750 € kg^{-1} phosphorus, respectively.

Keywords: Baltic Sea, mussel cultivation, growth rates, DEB-model, profitability

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Abbreviations: CI, (mussel) condition index; DZBC, Darss-Zingst-Bodden-Chain; GWB, Greifswald Bay; RMSD, root-mean-square difference; WB, Wieker Bay.

INTRODUCTION

Mollusk aquaculture plays an important role across the globe. Its production in Asia rose up to 16,000,000 t in 2017, while European production stagnated at 630,000 t. *Mytilus edulis* is the main species in European mollusks production (22%), followed by *M. galloprovincialis* (16%). Nonetheless, the total production quantity of *M. edulis* decreased from 190,000 t in 2,000 to 140,000 t in 2017 (FAO Database, 2019[1]). As a consequence, the European Union (EU) has developed strategies to support mussel cultivation, which include cultivation in regions with sub-optimal growing conditions, like the brackish Baltic Sea (Blue Growth Strategy; European Comission [EC] 2013, 2014, 2017; Beyer et al., 2017). So far, low salinities, ice occurrence, little or no legislation and a lack of tradition in mussel cultivation (EUMOFA, 2019) have limited the expansion of blue mussel aquaculture in the Baltic Sea.

In the Baltic Sea, two species of blue mussels, *M. edulis* and *M. trossulus*, as well as hybrids of these, occur naturally (Peine et al., 2005; Klamt and Schernewski, 2013; Darr et al., 2014; Schiele et al., 2014, 2015; Larsson et al., 2017). As the species distribution boarders within the Baltic Sea are not clearly defined and study sites are located within a mixture zone of *Mytilus* species (Väinölä and Hvilsom, 1991; Larsson et al., 2017; Stuckas et al., 2017), it will further be referred to as *Mytilus* spp. or blue mussels as common name, combining *M. edulis*, *M. trossulus*, and potential hybrids.

Mytilus spp. are osmo-conformers and short-term osmo-regulators (Davenport, 1979). Numerous studies have found that low salinity bears the largest impact on mussel growth rates (Bøhle, 1972; Westerbom et al., 2002; Wing and Leichter, 2011; Riisgård et al., 2012, 2014; Landes et al., 2015; Maar et al., 2015). Growth rates reduce with lower salinity due to the hypo-osmotic stress with high metabolic cost, which leaves less energy for growth (Hawkins and Hilbish, 1992; Neufeld and Wright, 1996). Optimal growth is considered around 20–32 psu (Almada-Villela, 1984; Riisgård et al., 2014) and below 8 psu, mussels become dwarfed (Kautsky, 1982; Kautsky et al., 1990; Riisgård et al., 2013a). However, little is known about mussel larvae occurrences and settling densities, mussel growth rates in suspended cultures and potential mussel farm production at lower salinities in the Baltic Sea. As a result, there is a need to further explore the potential of mussel farming in the Baltic Sea, taking into account environmental and economic aspects.

To serve this need, several mussel farm trials throughout the Baltic Sea (Sweden, Denmark, Germany, Poland, Latvia, Estonia, and Finland) have been carried out within various research projects. Results of these studies are mainly published in reports, rather than scientific, peer-reviewed publications (e.g., Tørring et al., 2008; CRM, 2011; Diaz and Kraufvelin, 2013; Palm et al., 2015; Minnhagen, 2017; Lyngsgaard et al., 2019; Kotta et al., 2020). The different usages of mussel yield, besides human consumption, are under constant debate. They focus especially on mussel meal production for husbandry, poultry or aquaculture feeding (Berge and Austreng, 1989; Lindahl, 2013; McLaughlan

et al., 2014). The calcareous mussel shells, commonly known as waste product, have recently been evaluated as part of the carbon trading system (Filgueira et al., 2015; Morris et al., 2018). Furthermore, mussel farming is highly discussed as nutrient remediation measure to combat eutrophication (Lindahl and Kollberg, 2008; Petersen et al., 2014, 2016, 2019; Gren and Elofsson, 2017; Hedberg et al., 2018; Taylor et al., 2019; Holbach et al., 2020; Kotta et al., 2020), to improve water transparency (Lindahl et al., 2005; Schröder et al., 2014; Timmermann et al., 2019), and to provide ecosystem services (e.g., habitat provision for other species) (Nielsen et al., 2016; van der Schatte Olivier et al., 2018; Petersen et al., 2019). Combined with other trophic levels, such as finfish and macro- or micro-algae, mussels can be part of a so-called multi-trophic aquaculture (MTA). Hereby, particulate organic matter, such as fish feed waste, fish faces and an increased phytoplankton production, will serve as feed for the filtering organisms (Holdt and Edwards, 2014).

The present study evaluates the feasibility and profitability of implementing mussel aquaculture along the German Baltic Sea coast. Therefore, four mussel farm trials were set up under differing environmental conditions, to compare mussel densities and growth. Further, a calibrated eco-physiological model was used to predict mussel growth under different environmental conditions of salinity, temperature and chlorophyll-*a* provided by monitoring data. Predicted mussel growth was used to determine farm harvest yields at selected sites and profit according to two harvest products (mussels for human consumption and mussels for animal feeds). In addition, the nutrient remediation potential at each site was assessed, based on known nitrogen and phosphorus contents and predicted mussel biomass. The obtained results were finally used to compare the feasibility between different sites and to make recommendations for future mussel aquaculture activities in the region.

STUDY SITES AND METHODS

Environmental Data

Long term (2007–2017) monitoring data were collected by the Federal State Agency for the Environment in Schleswig-Holstein (LLUR) and Mecklenburg Western-Pomerania (LUNG). Coastal stations (**Figure 1**) were sampled on a monthly basis, including measurements for salinity, water temperature, and chlorophyll a (chl-*a*). Water samples were taken near the surface form 0.5 to 1 m depth. Chl-*a* was determined fluorometric (665 nm) after filtration (GF/F, 0.7 μm), extraction with ethanol and acidification (ISO 10260:1992[2]). Monitoring sites closest to the mussel farms (**Figure 1**) were chosen to compare long-term environmental conditions (salinity, chl-*a*, and water temperature) between sites and to force the mussel growth model.
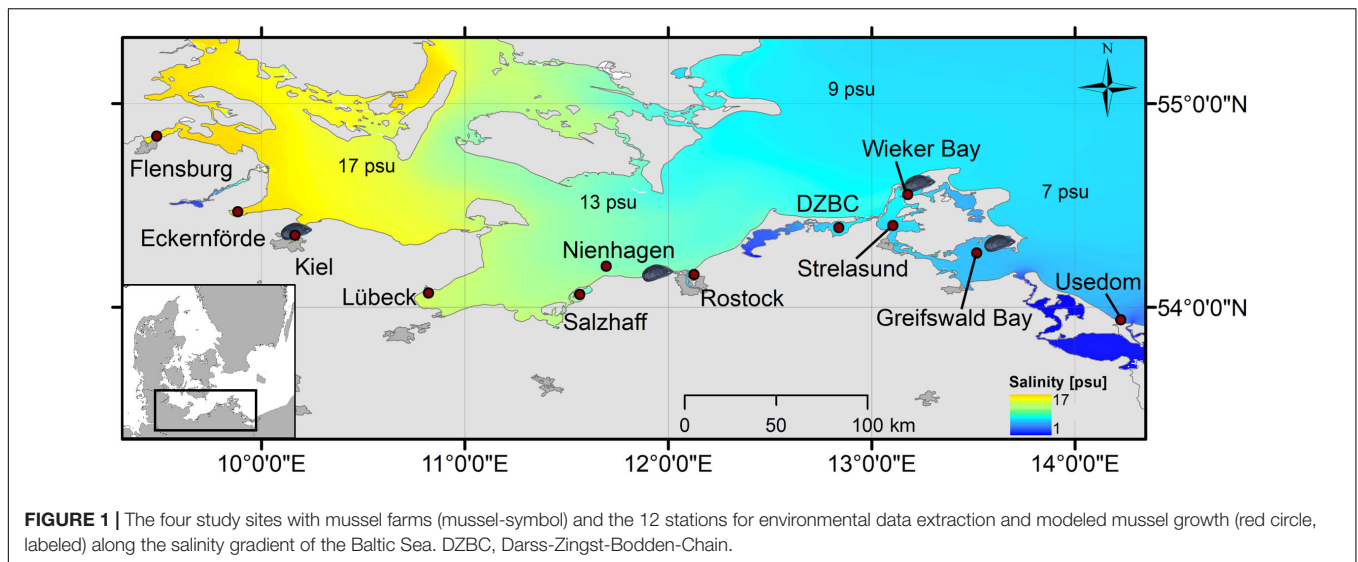

FIGURE 1 | The four study sites with mussel farms (mussel-symbol) and the 12 stations for environmental data extraction and modeled mussel growth (red circle, labeled) along the salinity gradient of the Baltic Sea. DZBC, Darss-Zingst-Bodden-Chain.

TABLE 1 | Farm details and respective monitoring station (Mon. station) providing the environmental surface parameters for water temperature, chl-*a* and salinity from 2007 to 2017. Values for the respective study period are indicated in brackets.

Site		Kiel Fjord	Nienhagen	Wieker Bay	Greifswald Bay
N		54.380	54.180	54.610	54.317
E		10.168	11.954	13.232	13.627
Farm size [ha]		0.7	0.03	0.01	0.25
Water depth [m]		10	13	3	6
Farm system		7 × 100 m LL, 5 cm polypropylene belt spat collectors, socking	3 × 10 m LL, 5 cm polypropylene belt spat collectors, socking	3 × 10 m LL,5 cm polypropylene belt spat collectors	5 × 50 m LL, 5 cm polypropylene belt spat collectors
Collector length [m]		4	5	2	2.5
Year		2010–011	2014–2015	2017–2018	2017–2018
Mon. station		225103	O4	RB3	GB2
Water temperature [°C]	Mean	10.2 ± 5.2 (9.4 ± 5.8)	10.2 ± 6.1 (10.5 ± 5.6)	12.2 ± 6.3 (12.8 ± 5.4)	12.1 ± 6.7 (13.1 ± 7.1)
	Max	19.0 (18.5)	21.5 (18.9)	23.3 (19.7)	22.4 (21.4)
	Min	0.4 (0.4)	-0.3 (2.9)	0.5 (1.9)	0.2 (1.3)
Chl-*a* [mg m^{-3}]	Mean	5.7 ± 5.1 (6.6 ± 5.0)	3.0 ± 2.7 (3.7 ± 3.6)	7.2 ± 5.3 (4.6 ± 3.3)	12.6 ± 8.1 (11.3 ± 7.3)
	Max	38.6 (17.4)	16.5 (16.5)	25.2 (11.8)	54.3 (31.0)
	Min	0.7 (0.8)	0.6 (0.9)	1.0 (1.7)	2.3 (2.6)
Salinity [psu]	Mean	16.1 ± 2.1 (16.0 ± 2.0)	11.8 ± 2.3 (12.4 ± 2.6)	8.9 ± 0.8 (9.1 ± 0.6)	7.2 ± 0.6 (7.1 ± 0.6)
	Max	21.2 (20.4)	20.7 (20.7)	12.0 (10.0)	8.2 (7.8)
	Min	11.7 (12.8)	7.6 (8.8)	7.3 (8.1)	5.7 (6.1)

Blue Mussel Farms in the German Baltic Sea

Trials were established at four sites along the German coast: Kiel Fjord, Nienhagen, Wieker Bay (WB) and Greifswald Bay (GWB) (**Figure 1** and **Table 1**). At all sites, polypropylene belt spat collectors were used as a substrate for mussel settlement. In Kiel Fjord and Nienhagen, additional socking took place after 6 months. This means that mussels are stripped off the collectors, graded and transferred into so-called mussel-socks made out of a mixture of plastic and biodegradable cotton allowing mussels to grow out of the socks over time. To avoid ice damages during the winter season (November to March), farms in GWB and WB were submerged 0.5 m below the water surface.

In order to compare growth data of Baltic Sea mussels with that of North Sea mussels, data from Walter and De Leeuw (2007) was used and illustrated in the results, but not further considered, as focus lies on Baltic Sea mussels.

Growth Measurements

During each study period, mussel-sampling took place monthly except during winter for all sites and late summer 2015 for Nienhagen as well as gaps for WB samples. The amount of mussel individuals per given collector substrate was counted for density calculations. Shell lengths (SL) were measured using a digital caliper. Wet weights (WW) of mussel shells and tissue were measured using an electronic micro-scale at

a minimum sample size of 10. After drying for a minimum of 24 h at 60°C, dry weights (DW) were weighted. Growth (G) was calculated from the SL increase (ΔSL, mm) divided by the number of days (Δt, d) between sampling events:

$$G = \frac{\Delta SL}{\Delta t}$$

The specific growth rate (μ, % d^{-1}) was calculated from the difference in tissue DW between number of sampling days (t) assuming exponential growth (Landes et al., 2015):

$$\mu = \ln\left(\frac{DW_t}{DW_0}\right) \times \frac{100}{t}$$

The mussel condition index (CI, mg cm^{-3}) was assessed according to Landes et al. (2015):

$$CI = \frac{DW_{tissue}}{SL^3}$$

To compare growth at the different study sites, an ANOVA on ranks (Kruskal–Wallis, SigmaPlot 13.0) was conducted, comparing SLs at three periods after settling. Since samples were not consistently taken at the same days at all sites, a range of up to 24 days between sampling dates for each period was accepted. The WB site was not always included due to a lack of data.

Modeling of Mussel Growth
Model Parametrization
A dynamic energy budget (DEB) model was used to predict mussel growth at for a wide range of salinities using MATLAB version R2019a (Maar et al., 2015). The DEB model is a deterministic, eco-physiological model describing the energy flow through the mussel in response to temperature, salinity and chl-a concentrations (proxy for available food) (**Supplementary Figure S1**). The DEB theory was originally developed by Kooijman (1986, 2010) and the applied DEB model for blue mussels is parameterized according to previous studies (van der Veer et al., 2006; Saraiva et al., 2011; Maar et al., 2015). The DEB model was applied because it has the highest physiological complexity including a salinity response and high accuracy in predicting mussel growth in comparison with other mussel growth models (Beadman et al., 2002). Phytoplankton is considered as the main food source for mussels in micro-tidal, eutrophic coastal areas with high chl-a concentrations (Petersen et al., 2013). Particulate organic carbon (POC) is another potential food source for mussels (Navarro et al., 1996) and highly correlated to the chl-a concentrations in the southern Baltic Sea (Maciejewska and Pempkowiak, 2014). Nevertheless, the food preference and assimilation efficiency of POC is lower than for phytoplankton food and POC was shown to be less important for mussel growth compared to phytoplankton biomass in a similar eutrophic system (Filgueira et al., 2018). Chl-a concentrations were therefore used as a proxy for available food in the calibration of the DEB model. Mussel ingestion follows a Holling type II saturation function versus chl-a concentrations and ceases at chl-a concentrations

<0.5 mg m^{-3} due to valve closure (Dolmer, 2000; Maar et al., 2018). Filtration was not affected by salinity assuming local adaptation (Riisgård et al., 2013a), although abrupt changes in salinity has been observed to induce short-term valve-closure (Almada-Villela, 1984). The ingested food is assimilated by a constant assimilation efficiency up to 17 mg-chl-a m^{-3}, where upon it decreases exponentially due to oversaturation of the digestive system (Riisgård et al., 2013a). The exponential function [$KA = \exp(-0.03 \times (\text{chl-}a - 17)$ for chl-$a > 17$ mg m^{-3})] is based on net growth efficiency data from Riisgård et al. (2013b) with chl-a concentrations varying from 4.1 to 67.8 mg m^{-3} ($n = 7$, $R^2 = 0.85$, their **Figure 5**, ignoring one value at low salinity). The assimilated food goes to the reserve density (mol-C cm^{-3}). Energy is allocated from the reserve density with the fraction $\kappa = 0.7$ to somatic growth (expressed as structural volume, cm^3) and somatic maintenance, whereas the fraction ($1-\kappa$) is allocated to maturity or reproduction (mol-C) and the related maintenance. Maintenance costs were described as a function of structural volume and temperature (**Supplementary Table S1**). The somatic maintenance cost was increased from the value applied in Maar et al. (2015) to get more realistic maximum SLs ($\sim$15 cm at salinity >16.2) for the applied longer growth period of 1–2 years (Dolmer, 1998; van der Veer et al., 2006). The growth response to low salinities is described as an extra maintenance cost due to osmoregulation (Maar et al., 2015). Osmoregulation is assumed to be proportional to mussel surface area and salinity (Kooijman, 2010; Maar et al., 2015). The extra maintenance cost is added to the energy allocation from reserves and distributed to somatic growth and reproduction using the κ-rule. This approach was slightly different from Maar et al. (2015), where only structural growth paid for the extra maintenance cost based on one month of mussel growth data. However, the old approach gave an imbalance between somatic and reproductive tissue for a longer growth period >1 year, including too much spawning. Ingestion and assimilation rates are modified by the Arrhenius dome-shaped temperature function with maximum rates at 20°C (van der Veer et al., 2006; Maar et al., 2018), whereas the maintenance rate is modified by the standard Arrhenius exponential temperature response (Teal et al., 2012). Spawning takes place above a temperature threshold of 9.6°C and above the gonado-somatic index of 0.25. During severe starvation, the somatic and reproductive tissue can pay for somatic maintenance. SL was estimated from the structural volume and a constant shape factor except that SL is not reduced during severe starvation. DEB parameters and equations can be found in **Supplementary Material** (**Supplementary Tables S1, S2**).

Model Calibration and Validation
The salinity response in the model was re-calibrated against Nienhagen mussel growth data for the sampling period 5th Nov, 2014 to 1st Oct, 2015. The salinity maintenance cost coefficient was estimated by an iterative process until the lowest root-mean-square difference (RMSD) between measured and modeled tissue biomass was obtained. The resulting maintenance cost coefficient was adjusted from 1.8×10^{-5} mol-C cm^{-2} d^{-1} to 2.9×10^{-5} mol-C cm^{-2} d^{-1} in the modified salinity response

and we applied a threshold <16.2 for the salinity effect (Almada-Villela, 1984). Regression analysis of measured versus modeled SLs and tissue biomass was used to evaluate the calibration results. Initial mussel data was obtained from the measured SL on 5th Nov (26 mm) converted to structural tissue using the DEB model shape-factor and reserves were assumed to be 50% of maximum. The mussels were assumed not to have developed reproductive tissue. The farm was very small and no severe food depletion was detected within the farm. Time-series of temperature, salinity, and chl-*a* were obtained from monitoring data (**Table 1**) and interpolated linearly over time. Missing values during winter were obtained from monthly means (2007–2017) from the same monitoring station.

The DEB model was validated against measured mussel biomass and SL from the mussel farms in Kiel Fjord 2010–2011 and GWB 2017–2018 using regression analysis. WB could not be modeled for the entire sampling period, because there was a drop in SLs over winter 2017–2018 probably due to a loss of larger mussels. Additionally, new settlements of mussel spat occurred in August 2018. The DEB model was therefore applied from April to July 2018 in WB, assuming to follow the same cohort of mussels over time. Initial SL was based on the first field measurement (5.3 mm 6th Sep, 2010 for Kiel Fjord farm, 1.5 mm 12th Jul, 2017 for GWB, and 11 mm for WB 9th Apr, 2018) converted to biomass as described for Nienhagen. Forcing data of temperature, salinity and chl-*a* concentrations was obtained from monitoring data (**Table 1**). Missing values (2 months in Kiel and 5 months in GWB) were replaced by monthly means (2007–2017) from the same monitoring station. Monthly monitoring data did not capture the heat wave during summer 2018 (up to 25°C in July), probably due to the coarse temporal resolution. We therefore applied modeled daily temperatures from the Saltbaltyk database[3] as forcing data to GWB. The Kiel farm is bigger than the other farms and an average chl-*a* depletion of 20% was applied according to observations (Schröder et al., 2014). No severe depletion was detected in the smaller farm of GWB.

The uncertainty related to the threshold for food over-saturation was tested by changing the applied threshold of 17 mg m^{-3} in the standard run to 10, 12, 14, and 20 mg m^{-3} in GWB with the highest food concentrations. We further tested the model sensitivity to the environmental forcing variables and selected DEB parameters by changing the values ± 10% for the GWB, Kiel Fjord, and Nienhagen models for a growth period of 1 year. The sensitivity index, *SI* (%), was estimated as (Bacher and Gangnery, 2006):

$$SI = \frac{1}{n} \sum_{t=1}^{n} \frac{\left| W_t^1 - W_t^0 \right|}{W_t^0} \times 100\%$$

where *n* is the total number of time-steps, *t* is the time-step number, W_t^0 is the tissue biomass at time *t* predicted by the standard run and W_t^1 is the tissue biomass at time *t* predicted by the sensitivity run. The *SI* was estimated as the mean value for each parameter and site. The tested DEB parameters were the Arrhenius temperature coefficient, the salinity maintenance cost

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coefficient, the half-saturation food coefficient (all three related to the environmental forcing variables), the somatic maintenance cost coefficient (which was changed from previous version) and the initial weight of mussel tissue.

Application of the DEB Model

The DEB model was finally applied to twelve monitoring stations at a salinity gradient (7–17 psu) along the German coastline using long-term monthly means of temperature, salinity and chl-*a* concentrations based on monitoring data (years 2007–2017) from each station (**Table 1**). Modeled tissue DWs were transformed into total WWs by the factor 0.086 (Nielsen et al., 2016; Taylor et al., 2019; data of this study) for economic evaluation. The heat wave in summer 2018 was not included in the forcing data period, because it was considered as a special event. We assumed a farm size similar to the Kiel farm with 20% chl-*a* depletion (Schröder et al., 2014). Initial mussel SL was 3.2 mm (GWB 3rd Aug) and the growth period was 18 months until final harvest. Modeled data combined with former studies on mussel farm densities were used to estimate production capacity along the German Baltic Sea as well as generating an outlook of mussel farming in low saline waters.

Economic Profitability

To compare potential mussel harvest and profit, a uniform, 1-ha longline system was adopted, with 10 longlines at a distance of 10 m to each other. A total of 5 cm polypropylene belts served as spat collectors with 0.5 m gaps in between. Collector length varied from 2 to 4 m, depending on the water depth. An average mussel density of 1,700 Ind m^{-1} after 6 months and 280 Ind m^{-1} after 18 months was used based on Taylor et al. (2019) and Haas et al. (2015). Additionally, a mussel loss of 10% was applied throughout the growing period due to natural loss (self-thinning), handling (maintenance, grading, socking, and cleaning), and non-marketable sizes (for human consumption mussels) (Frechette et al., 2010; Cubillo et al., 2015; Haas et al., 2015; Nielsen et al., 2016; Taylor et al., 2019). This might change with salinity, but was not evaluated in former studies or this study. Furthermore, for the production of mussels for human consumption, only half of the farm area can be harvested each year, because new spat is already collected within the other half to ensure a continuous production cycle. Mussels above 45 mm SL are assumed as suitable for human consumption in Denmark (personal communication Petersen and Taylor, 2019) and were adjusted to 50 mm for the German marked, orientated after Krost et al. (2011).

Yearly running costs were defined based on Krost et al. (2011), and separated into pre- and post-initial investment costs. Initial investment costs were divided into the first 5 years of production, following the depreciation rate of a mussel farm outlined by Krost et al. (2011). After the first five years, annual costs were only a function of the running costs (**Table 2**). Costs were differentiated between mussel production for human consumption and for animal feed. The latter is associated with lower production costs, as there is no longer a need for certain materials and machinery (e.g., socks) and the labor is halved (Haas et al., 2015).

TABLE 2 | Yearly costs [EUR, €] for mussel farms of different size and usages: human consumption (HC) and animal feed (AF); divided into running costs including (first 5 years) and excluding (post 5 years) investment cost.

Farm size [ha]	1	4	8	12	16	20
Longline [€]	250	1,000	2,000	3,000	4,000	5,000
Anchoring [€]	250	1000	2000	3000	4000	5000
Sea signs [€]	1,600	1,600	1,600	1,600	1,600	1,600
Buoys [€]	750	3000	6000	9000	12000	15000
Socks [€]	600	2,400	4,800	7,200	9,600	12,000
Collectors [€]	125	500	1,000	1,500	2,000	2,500
Boat [€]	16,000	30,000	40,000	50,000	60,000	70,000
Land station [€]	20,000	20,000	30,000	40,000	50,000	60,000
Machinery [€]	6,000	9,000	12,000	21,000	30,000	39,000
Staff [€]	100,000	125,000	200,000	325,000	450,000	575,000
Yearly costs [€], HC, first 5 years	209,042	260,796	375,157	549,993	724,829	899,665
Yearly costs [€], AF, firs 5 years	151,159	185,851	255,504	355,395	455,286	555,177
Yearly costs [€], HC, post 5 years	157,206	208,961	323,322	498,158	672,994	847,829
Yearly costs [€], AF, post 5 years	99,324	134,016	203,669	303,560	403,451	503,341

In a second step, an increase in farm size was applied to reduce production costs and again estimate profitability (**Table 2**). Subsequently, farm size [ha] was converted into cultivation volume [m^3] to compare 1 ha farms at different cultivation depths, hence, length of collector lines (2, 3, or 4 m), depending on the regional water depth. At water depths <6 m, collector length was set to 2 m, at 6 to 8 m water depth to 3 m, and >8 m water depth, collector length was set to 4 m.

To assess profitability, a sales price of 0.06 € kg^{-1} was assumed for fresh animal feed mussels (Haas et al., 2015; Schernewski et al., 2018). How companies proceed with the feed mussels and which further costs occur by this process was not included in this study. For human consumption mussels, high- and low-end estimates were obtained from existing industry data: Kieler mussels are sold for 11 € kg^{-1} (Kieler Meeresfarm GmbH, 2019[4]) while mussels from the North Sea are sold for 2.19 € kg^{-1} (SH, 2018[5]). The cost-efficiency of mussel farming as a nutrient reduction measure was evaluated by comparison with other mitigation measures studied by Gren et al. (2008). For mussel farming, an average nutrient uptake of 1.2% N and 0.05% P of total WW was assumed based on Petersen et al. (2014). Different from many other measures, mussel farming reduces N and P at the same time. For comparison, all cost and revenue data has been converted into 2018 EUR.

More details on the methodology to assess economic profitability can be found in the **Supplementary Material** (see section "Methodology to Assess Economic Profitability").

RESULTS

Environmental Data

Environmental parameters of the different study sites and years are presented in **Figure 2** (lower graphs). Salinities during the study period were highest in Kiel Fjord (17.0 ± 2.3 psu) and

lowest in GWB (7.10 ± 0.6 psu) (**Table 1** and **Figure 2**). Salinities in Kiel and Nienhagen had a higher variability due to saltwater inflows from the North Sea and their open coast location. Chl-a and water temperature varied naturally throughout the year, but were highest in the shallow and semi-enclosed bays WB and GWB (**Table 1** and **Figure 2**).

Blue Mussel Farms in the German Baltic Sea: Settling and Growth
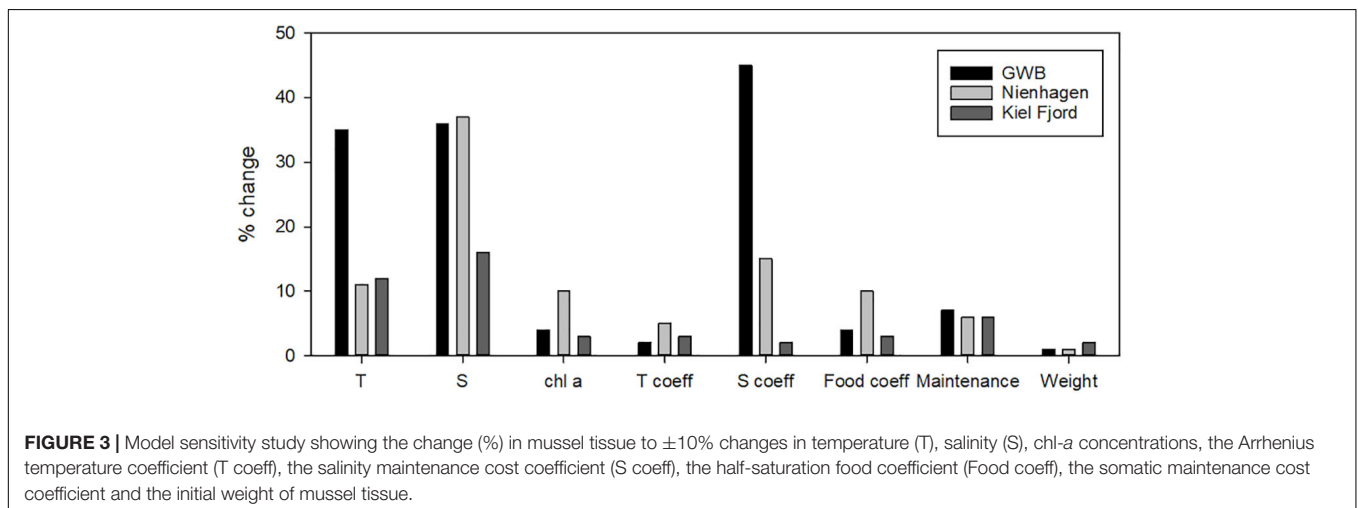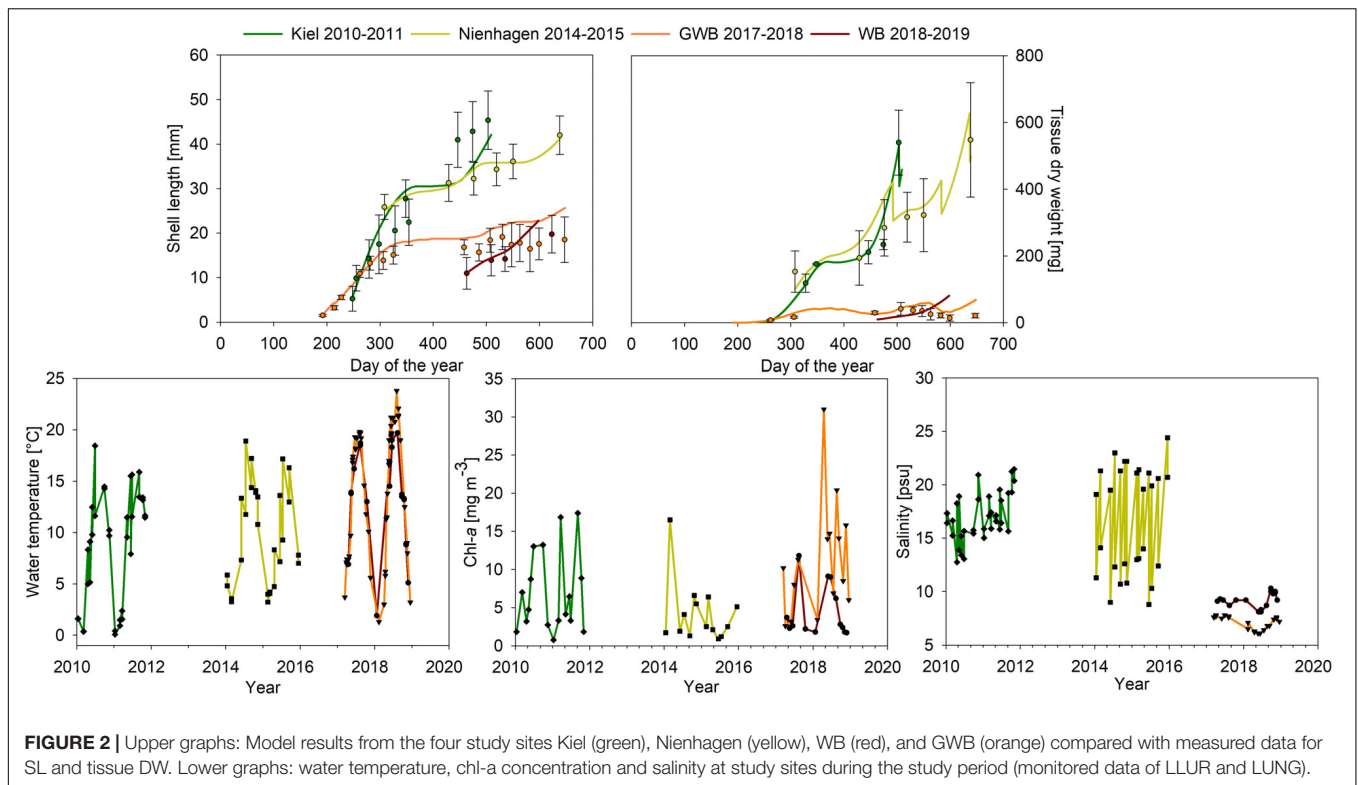
Results showed high variation of mussel density between sites, but also seasonally (from spat fall to harvest) for each site (**Table 3**). Shell growth rates decreased with salinity from the North Sea to GWB. Specific growth rates were based on tissue DW and these results were fewer than for SLs as well as negative for GWB, since weight decreased during the heat wave in summer 2018 after approximately one year of growth (**Table 3** and **Figure 2**).

Settling took place in June and July at all sites except for Nienhagen, which provided settling substrate only in August. Nonetheless, the mussels in Nienhagen picked up growth fast. Mussel CI showed on average lower values at low salinities (GWB and WB) compared to the other, more saline areas (**Tables 1**, **3**). The CI had the highest range in Kiel Fjord, where it was high during winter (13.6 mg cm^{-3} in November 2010) and low in spring (3.0 mg cm^{-3} in April 2011) after spawning. In Nienhagen, CI varied only slightly, with higher values (8.7 mg cm^{-3}) in winter (November, 2014) and lowest values (6.2 mg cm^{-3}) in spring (March, 2015). In WB, CI was 4.7 mg cm^{-3} in November 2018 and 3.8 mg cm^{-3} in June 2018. In GWB, CI was lowest in October 2018 after the heat wave (3.3 mg cm^{-3}) and highest in September 2017 (6.3 mg cm^{-3}).

Significant differences in SLs after settling appeared between sites after (i) 79–98 days between Nienhagen and the other sites ($p < 0.001$), (ii) 153–167 days between Kiel Fjord and GWB ($p < 0.001$) and Nienhagen and GWB ($p < 0.001$), and (iii) 314–338 days between all sites ($p < 0.001$) except between GWB and WB (Kruskal–Wallis One Way Analysis of Variance on Ranks, SigmaPlot 13.0).

FIGURE 2 | Upper graphs: Model results from the four study sites Kiel (green), Nienhagen (yellow), WB (red), and GWB (orange) compared with measured data for SL and tissue DW. Lower graphs: water temperature, chl-a concentration and salinity at study sites during the study period (monitored data of LLUR and LUNG).

FIGURE 3 | Model sensitivity study showing the change (%) in mussel tissue to ±10% changes in temperature (T), salinity (S), chl-*a* concentrations, the Arrhenius temperature coefficient (T coeff), the salinity maintenance cost coefficient (S coeff), the half-saturation food coefficient (Food coeff), the somatic maintenance cost coefficient and the initial weight of mussel tissue.

Sites in WB and GWB recorded a high mussel loss in the summer of 2018 of around 80% (mostly due to fall offs). Densities in GWB declined from 4,000 Ind m^{-1} in November 2017 to 218 Ind m^{-1} in October 2018. Shell growth of the remaining mussels stagnated and decreased (**Figure 2**), while tissue DW and hereby mussel condition (CI) also reduced (**Figure 2**). In GWB, no new spat settlement took place in this summer, while in WB, new settlement occurred in late summer (August/September).

DEB Modeling of Mussel Growth

The salinity response in the DEB model was re-calibrated against measured growth data from Nienhagen (2014–2015) by

minimizing the RMSD and model results showed a significant correlations with measured biomass ($r^2 = 0.92$, $n = 6$, $p < 0.0001$) and SL ($r^2 = 0.97$, $n = 5$, $p < 0.0001$). The DEB model was validated against data from Kiel (2000–2011) and showed significant correlations with biomass ($r^2 = 0.94$, $n = 5$, $p < 0.0001$) and SL ($r^2 = 0.81$, $n = 9$, $p < 0.0001$).

During the heat wave in summer 2018 for GWB, the model predicted a decrease in biomass although less pronounced than for observations, but overestimated growth in October 2018 after the heat wave (**Figure 2**). Hence, the correlation between data and model was only significant for mussel tissue if the last data point from 19th Oct, 2018 was ignored (tissue DW: $r^2 = 0.47$,

Site	Density [Ind m^{-1} CL]	G [mm d^{-1}]	μ [% d^{-1}]	CI [mg cm^{-3}]		
				Mean	**Max**	**Min**
North Sea*	11,000–64,000	0.13	n.a.	n.a.	n.a.	n.a.
Kiel Fjord	200–40,000 (36,000)	0.11	1.35	6.7 ± 3.9	13.6	3.0
Nienhagen	n.a.	0.09	0.43	7.6 ± 0.9	8.7	6.2
Wieker Bay	820–2700	0.06	n.a.	4.2 ± 0.4	4.7	3.8
Greifswald Bay	218–4,000	0.05	−0.29	5.0 ± 1.0	6.3	3.3

*Values of Walter and De Leeuw (2007).

$n = 9$, $p = 0.04$), whereas it was significant for all data points for SL ($r^2 = 0.93$, $n = 15$, $p < 0.0001$).

The model test of using other thresholds for food oversaturation did not improve the model fit (lower r^2) for GWB compared to the standard run and underestimated the mussel biomass especially during the spring bloom (data not shown). The model sensitivity study showed that mussel growth in GWB responded strongly to changes in temperature and salinity, but not to food levels (**Figure 3**). Nienhagen responded strongly to changes in salinity and moderately to temperature and food. The responses of the Kiel farm were less than for other farms and related to temperature and salinity. The model formulation was most sensitive to the salinity stress coefficient, but not to the Arrhenius temperature coefficient, the half-saturation food coefficient (except for Nienhagen), somatic maintenance cost or the initial weight of the mussels (**Figure 3**).

The comprehensive modeling of individual SL and tissue DW for 12 stations revealed a high variability along the natural salinity gradient of the German Baltic coast (**Table 4** and **Figure 4**).

Mussels at sites west of Rostock with salinities above 10 psu (**Table 4** and **Figure 4**) reached the 50 mm threshold within 18 months, except of Nienhagen, where chl-a concentrations were lower than for other sites (**Table 4**). Modeled individual tissue DW after 6 (18) months ranged from 0.02 (0.2) g in the DZBC to 0.4 (4.2) g by Flensburg. Mussels east of Rostock did not reach 50 mm SL after 18 months but varied from 27 mm (DZBC) to 42 mm (Strelasund) (**Table 4**).

Economic Profitability

Based on modeled mussel yields (**Table 5**), mussel farms east of Rostock are unable to produce mussels for human consumption (>50 mm) within 18 months, hence, they are no longer considered for profitability in this regard. As for animal feed production, none of the studied farms were found to be profitable, even with increasing farm size. This is due to the low market prices of 0.06 € kg^{-1}.

Production costs decreased with increasing farm size, but the minimal threshold of 0.7 € kg^{-1} as in the Limfjord was not reached at any of the farm sites (**Figure 5a**). If sold as a local specialty for 11 € kg^{-1}, mussel farming in Kiel Fjord could already be profitable at a cultivation volume of 40,000 m^3 (1 ha). If sold at a marked price of 2.19 € kg^{-1}, profitability would start below a cultivation volume of 160,000 m^3, 4 ha (**Figure 5b**). If mussel farming was used as a nutrient mitigation measure in Kiel

Fjord (6 month production cycle), nutrient removal costs would range between 44 to 172 € kg N^{-1} and 964 to 3,804 € kg P^{-1} yearly, depending on the farm size (**Figure 5c**).

DISCUSSION AND CONCLUSION

Mussel farming represents an environmentally friendly alternative for a high quality protein source that at the same time can be a measure against eutrophication in the brackish Baltic Sea. In the present study, a combination of environmental monitoring data, mussel growth data from four test farms and DEB modeling was used to assess the farm production and nutrient removal potential at a salinity gradient along the German coastline. It was shown that suspended mussel cultures growing at salinities above 10 psu (west of Rostock) could reach market size of 50 mm for human consumption within 18 months, except for Nienhagen. The Nienhagen site showed relatively low mean chl-a concentrations of 3 mg m^{-3} and the model sensitivity test indicated higher food limitation here compared to the other sites, together with a high sensitivity to salinity changes (**Figure 3**).

At lower salinities <10 psu, mussels were stressed due to the extra maintenance costs from osmoregulation (Riisgård et al., 2013a; Landes et al., 2015; Maar et al., 2015) and reached a size of 30–45 mm after 18 months (**Figure 4**). The model sensitivity study showed that mussels in GWB (2017–2018) responded strongly to changes in both salinity and temperature indicating that the mussels were severely stressed and sensitive to environmental change. A heat wave occurred in summer 2018 and high water temperatures (>20°C) weaken mussel condition (Hutchins, 1947; Braby and Somero, 2006) and byssus threads (Van Winkle, 1970; Allen et al., 1976; Young, 1985; Newcomb, 2015). Furthermore, studies have shown a reduced temperature resistance for mussels at decreasing salinities (Hiebenthal et al., 2012). The observed decrease in mussel tissue during summer 2018 could partly be explained by the DEB model due to a lower net growth efficiency at temperatures >20°C as the decrease was less severe than observed (**Figure 2**). The GWB model was very sensitive to changes in temperature and salinity; hence, small deviations in the forcing data could have caused the discrepancy between data and DEB model results. In addition, it was observed that the mussels in GWB detached from the collector line and settled to the bottom, which was most likely a result of weak

TABLE 4 | Modeled shell length and tissue dry weight (DW) as well as calculated total wet weight (WW) after 6 and 18 months.

| Site	Shell length [mm]		Tissue dry weight, DW (total wet weight, WW) [g]				Salinity [psu]	Chl-*a* [mg m^{-3}]	Water temperature [°C]
	6 months	18 months	6 months		18 months				
Flensburg	36	81	0.4	(4.2)	4.9	(47.6)	17.5	7.1	11.0
Eckernförde	35	74	0.4	(3.7)	3.7	(35.8)	16.7	3.8	10.9
Kiel	36	77	0.4	(3.9)	4.3	(41.2)	16.1	5.7	10.2
Lübeck	30	59	0.2	(2.0)	1.7	(16.0)	13.6	3.5	10.8
Salzhaff	29	60	0.2	(1.9)	1.8	(17.6)	11.6	6.8	11.6
Nienhagen	25	46	0.1	(1.0)	0.9	(8.2)	11.8	3.0	10.2
Rostock	26	53	0.1	(1.2)	1.2	(11.4)	10.9	9.9	11.0
DZBC	14	27	0.02	(0.2)	0.2	(1.4)	7.7	35.4	11.7
Strelasund	20	42	0.05	(0.5)	0.7	(6.4)	8.5	11.7	11.3
WB	19	41	0.05	(0.5)	0.6	(6.1)	8.9	7.2	12.2
GWB	18	35	0.04	(0.4)	0.5	(4.3)	7.2	12.4	12.2
Usedom	16	31	0.03	(0.3)	0.3	(2.5)	6.2	13.7	11.2
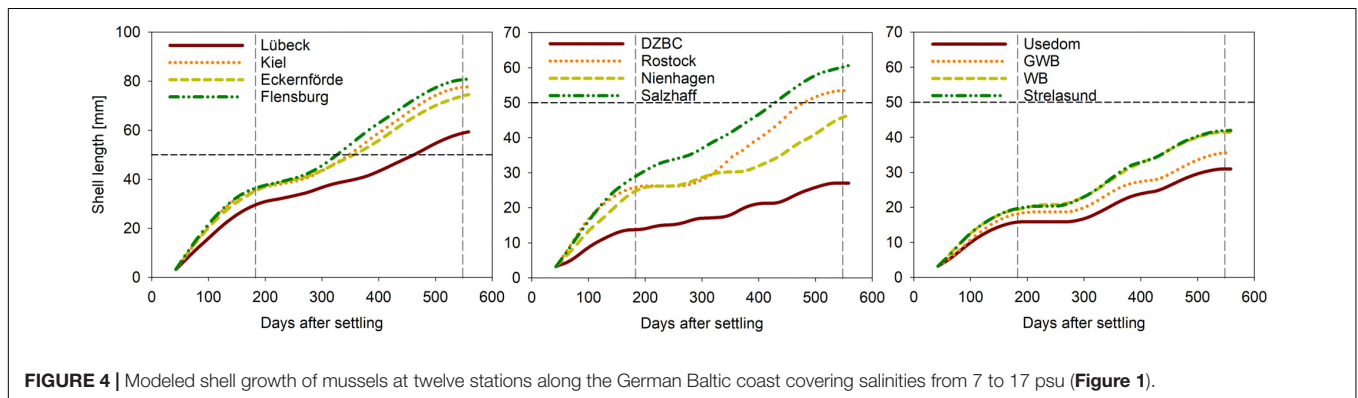
FIGURE 4 | Modeled shell growth of mussels at twelve stations along the German Baltic coast covering salinities from 7 to 17 psu (**Figure 1**).

TABLE 5 | Potential yearly mussel harvest (total wet weight, WW) for animal feed (AF) and human consumption (HC) for an established 1 ha farm, production costs for each (without upfront investment costs), as well as yearly nutrient removal [kg ha^{-1} a^{-1}] if harvested as animal feed mussels. Production volumes result from water depth and applicable collector length (2, 3, or 4 m).

Site	Water depth [m]	Production volume [m^3]	WW total AF 6 months [t ha^{-1} a^{-1}]	WW total HC 18 months [t ha^{-1} a^{-1}]	Production costs [€ kg^{-1}]		Nutrients 6 months [kg ha^{-1} a^{-1}]	
					AF	HC	N	P
Flensburg	18.3	40,000	50.9	48.6	2.0	3.2	612.7	27.7
Eckernförde	20.9	40,000	45.8	36.5	2.2	4.3	552.1	25.0
Kiel	12.8	40,000	47.9	42.0	2.1	3.7	576.5	26.1
Lübeck	8.5	40,000	24.5	16.3	4.1	9.6	295.3	13.4
Salzhaff	5.6	20,000	11.6	9.0	4.3	8.8	279.6	12.7
Nienhagen	22.7	40,000	12.4	8.4	8.0	18.7	149.0	6.7
Rostock	13.9	40,000	14.5	11.6	6.9	13.6	174.2	7.9
DZBC	3.6	20,000	1.0	0.7	48.4	108.1	24.7	1.1
Strelasund	4.1	20,000	3.1	3.3	15.8	24.0	75.6	3.4
WB	5.1	20,000	3.0	3.1	16.7	25.4	71.8	3.3
GWB	7.7	30,000	3.7	3.3	20.0	35.9	59.9	2.7
Usedom	6.5	30,000	2.4	1.9	31.3	60.8	38.3	1.7

byssus threads. The loss of mussels could also have affected the average SLs and biomass of the mussels in the farm, if more of the larger individuals were lost indicated by the decrease in population SL during the heat wave (**Figure 2**). Not only adult mussel growth is negatively influenced by high temperatures (Gonzalez and Yevich, 1976; Almada-Villela

et al., 1982), but also larvae survival is drastically reduced, especially under low salinities (Brenko and Calabrese, 1969). This might explain the late or absent settlement in WB and GWB. Nonetheless, further confirmation, by specific experiments at low salinities, is required to proof heat waves as a cause for reduced mussel growth, condition and/or mussel loss as observed in the field.

Chl-*a* concentrations were used as a proxy for food availability in the calibrated DEB model, whereas POC could be another potential food source as observed for more tidal areas, e.g., the North Sea, with high amount of resuspension (Jago et al., 1993; Van Raaphorst et al., 2003). In the southern Baltic Sea, POC is mainly derived from primary production and associated processes (Dzierzbicka-Głowacka et al., 2010) and there is a positive correlation between POC and chl-*a* concentrations (Maciejewska and Pempkowiak, 2014), supporting our approach of using chl-*a* as a food proxy. However, during periods with low phytoplankton biomass, detrital complexes may be an important food source for bivalves (Newell et al., 1998; Hedberg et al., 2018; Adams et al., 2019) not accounted for by the model. The maximum chl-*a* concentration for optimal mussel growth is uncertain and was set to 17 mg m^{-3} in the present study, whereupon the assimilation efficiency was reduced due to overloading of the digestive system with undigested algae cells passing the gut (Kiørboe et al., 1981; Riisgård et al., 2013b). Previous studies found maximal growth rates at chl-*a* concentrations up to 10–17 mg m^{-3} and that growth was severely reduced at >41 mg m^{-3} (Clausen and Riisgård, 1996; Petersen et al., 1997; Riisgård et al., 2013b), but there is to our knowledge a lack of experimental data conducted from 17 to 41 mg-chl-*a* mg m^{-3} to support a better model description. However, the other tested thresholds (10, 12, 14, and 20 mg m^{-3}) did not improve model performance for GWB. The sites with highest average chl-*a* concentrations were Strelasund (12.3 mg m^{-3}), GWB (13.7 mg m^{-3}), Usedom (14.2 mg m^{-3}), and DZBC (36.2 mg m^{-3}). Hence, the DEB growth estimates are more uncertain from these areas, especially DZBC. Nevertheless, the salinity response was calibrated for the Nienhagen site with chl-*a* concentrations below 6.4 mg m^{-3} (**Figure 2**) and was therefore not influenced by a negative response to high food conditions. We therefore believe that the new salinity calibration is robust.

Within 6 months, a 1-ha farm can produce from 1.0 t (DZBC) to 51 t (Flensburg) and remove 1.1 to 27.7 kg P and 24.7 to 612.7 kg N, respectively. In comparison, a 1-ha farm in the eutrophic Limfjorden (salinities of 20–35 psu) could remove 40 to 100 kg P and 600 to 1,270 kg N by harvesting of mussels (Taylor et al., 2019). In the Eastern Baltic Sea with salinities around 6 psu, the same farm size could remove 6.4 to 10.8 kg P and 83 to 140 kg N by harvest (Kotta et al., 2020). Hence, the estimated nutrient removal along the German coastline was in between previous estimates from higher and lower salinity areas as would be expected from the strong influence of salinity on mussel growth. The potential to use mussel farming as a nutrient reduction measure, and its economic value in this regard, is highly discussed (Lindahl and Kollberg, 2008; Stadmark and Conley, 2011; Hedberg

et al., 2018; Gren, 2019; Petersen et al., 2019). Compared with other nutrient remediation measures, mussel farming at high productive sites lies roughly in the middle of previously reported costs. Optimization of farm set up and harvesting techniques can greatly increase the biomass yield and hereby reduce costs (Taylor et al., 2019).

Further, mussel farms can be established and repositioned more freely, targeting specific areas in need of nutrient reductions. Moreover, mussel farming reduces N and P simultaneously. As a result, the price for nutrient reduction decreases. At the same time, mussel farming is also found
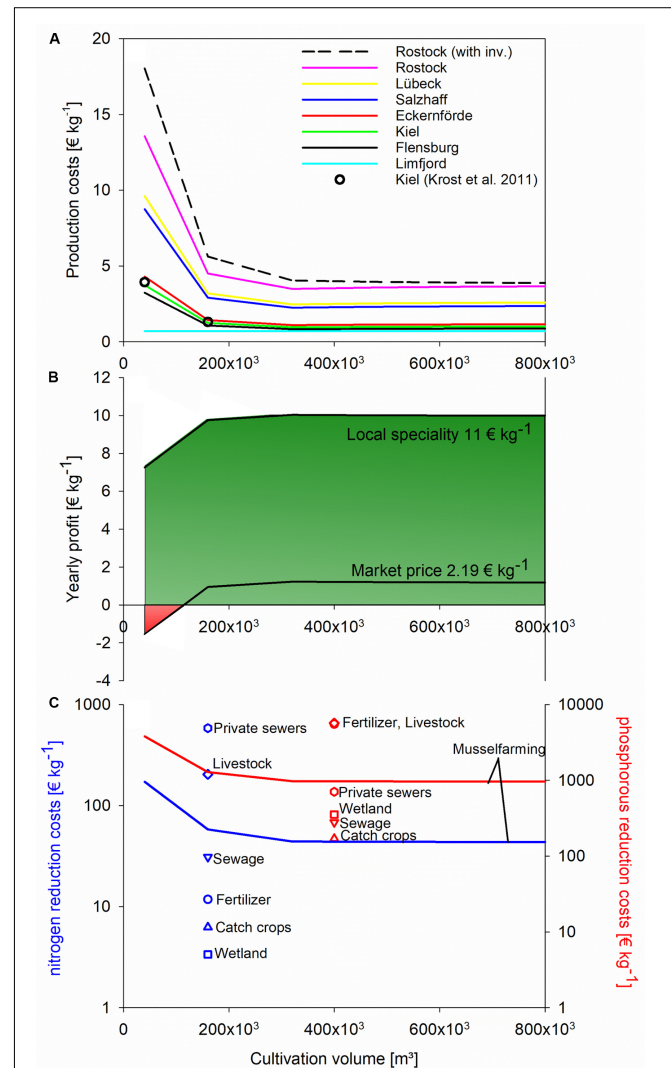

FIGURE 5 | (A) Yearly operational costs of mussel production for human consumption west of Rostock, excluding investment costs (with investment costs for Rostock as comparison), inclusion of cost data by Krost et al. (2011) (black circle) and inclusion of minimal reported production costs of 0.7 € kg^{-1} (Limfjord production); **(B)** profitability for mussel farming in Kiel Fjord, if sold for human consumption, following two market price scenarios (neglecting upfront investment costs); **(C)** costs for phosphorus (red) and nitrogen (blue) removal: comparing mussel farming (example of Kiel Fjord, neglecting upfront investment costs) with other measures after Gren et al. (2008).

to increase water clarity (Schröder et al., 2014; Nielsen et al., 2016; Friedland et al., 2019). This can have important economic implications for coastal communities, as higher water transparency makes waterbodies more attractive to visitors. Studies in Sweden (Soutukorva, 2001) and Finland (Vesterinen et al., 2010) revealed a statistically significant, positive coefficient, demonstrating the preference visitors have for higher water transparency. For example, the aggregate benefit to Stockholm and Uppsala counties following a 1 m rise in water transparency was SEK 85-273 (EUR 11-35) million year^{-1} (Soutukorva, 2001).

Nonetheless, unpredicted biomass losses will affect the profitability of mussel farming. They could not be included in calculations of this study, since there are no long-term observations of mussel spat settlement and/or potential losses along the German Baltic coast. Neglecting these unpredicted losses, profitability of mussel farming is very much size, site and sales price dependent. Enlarging farms can reduce production costs, but also cause an increase in food depletion (not included in extrapolations here) (Nielsen et al., 2016). Additionally, large mussel farms can have negative effects on the environment, such as increased local sedimentation rates (Dahlbäck and Gunnarsson, 1981; Callier et al., 2006) and hereby organic matter below the farm (Kautsky and Evans, 1987; Christensen et al., 2003), changes in the benthic communities (Kasper et al., 1985; Callier et al., 2008) and microbial assemblages (Mirto et al., 2000), alterations in oxygen and nitrogen dynamics (Nizzoli et al., 2005; Carlsson et al., 2012) and resulting hypoxia below farms (Lee et al., 2016). However, environmental impacts of mussel farms are still under discussion, not always clearly visible and often site dependent (Chamberlain, 2002; Crawford et al., 2003; Fabi et al., 2009).

Furthermore, an increase in farm volume to a profitable size is not always possible due to multiple coastal uses, stakeholder conflicts and protected areas (Gimpel et al., 2018). Aquaculture areas can be designated in national or regional marine spatial planning and site specific spatial analyses are required before establishing and expanding a mussel farm (Backer, 2011; Karka et al., 2011; Holbach et al., 2020).

Besides the reduction of production costs, the sales price also differs depending on the mussel usage (e.g., animal feed or human consumption) and the current market need. As for human consumption mussels, higher marked prices of up to 11 € kg^{-1} can be reached, if promoted and sold as a regional product, as it is in Kiel. Usually, mussels in Germany will be sold for human consumption above 50 mm SL. The Danish market accepts 45 mm (pers. com. J. Petersen) and even so called "mini-mussels" of 30–35 mm (Larsen and Riisgård, 2016). Site specific market analyses need to be done, to determine the demand and acceptance of consumers to small-size, local-specialty mussels, with higher prices.

For the Baltic Sea, a combination of uses could be a lucrative supplementary and seasonal work for fishermen (who already possess many of the working equipment, as e.g., a working boat), if financial contribution for nutrient remediation is given or if mussel farming as mitigation measure allows for new fish aquaculture. After harvest, small size mussels could be used for mussel meal production to supplement, e.g., fish feed. However, this requires high tonnages to be accepted by processing companies (10,000 t WW; Schernewski et al., 2018). While this could barely be realized by a single mussel farm, the collective effort of several farms under a single state authority, could supply this quantity to processing companies. On the other hand, if promoted as local specialty, mussels as small as 30 mm could be sold for human consumption and at the same time, increase the touristic value of an area.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

A-LB was responsible for overall structure of the manuscript, writing the manuscript, and data collection. MM was responsible for the DEB modeling and contributed to the writing. MN and GS were responsible for the economic calculations and contributed to the writing. PK, FP, SD, LR, and RF provided data for the mussel farms in Kiel, Nienhagen, WB, and GWB, respectively. LR and RF also contributed to the writing.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2020.00371/full#supplementary-material

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