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# Modelling and mapping carbon capture potential of farmed blue mussels in the Baltic Sea region

Annaleena Vaher<sup>a,\*</sup>, Jonne Kotta<sup>a</sup>, Brecht Stechele<sup>b</sup>, Ants Kaasik<sup>a</sup>, Kristjan Herkül<sup>a</sup>, Francisco R. Barboza<sup>a</sup>

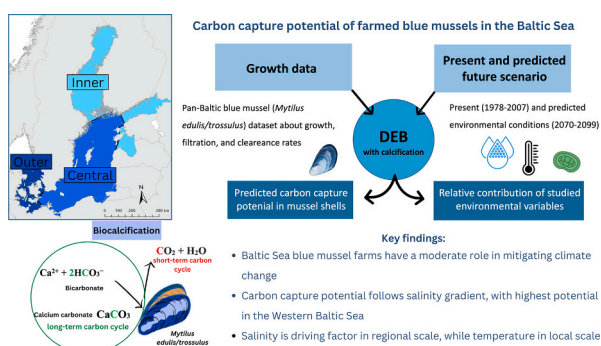
<sup>a</sup> Estonian Marine Institute, University of Tartu, Mäealuse 14, EE-12618 Tallinn, Estonia

<sup>b</sup> Laboratory of Aquaculture & Artemia Reference Center, Ghent University, Ghent, Belgium

## HIGHLIGHTS

- A DEB model was adapted for mapping blue mussel carbon capture in the Baltic Sea.
- We analysed carbon capture in mussel shells under current and predicted future conditions.
- The highest carbon capture potential was found in the Western Baltic Sea.
- Salinity was the most influential factor at the regional scale.
- Results support sustainable aquaculture and environmental conservation.

## GRAPHICAL ABSTRACT



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## ABSTRACT

This study applies a regional Dynamic Energy Budget (DEB) model, enhanced to include biocalcification processes, to evaluate the carbon capture potential of farmed blue mussels (*Mytilus edulis/trossulus*) in the Baltic Sea. The research emphasises the long-term capture of carbon associated with shell formation, crucial for mitigating global warming effects. The model was built using a comprehensive pan-Baltic dataset that includes information on mussel growth, filtration and biodeposition rates, and nutrient content. The study also examined salinity, temperature, and chlorophyll *a* as key environmental factors influencing carbon capture in farmed mussels. Our findings revealed significant spatial and temporal variability in carbon dynamics under current and future environmental conditions. The tested future predictions are grounded in current scientific understanding and projections of climate change effects on the Baltic Sea. Notably, the outer Baltic Sea subbasins exhibited the highest carbon capture capacity with an average of 55 t (in the present scenario) and 65 t (under future environmental conditions) of carbon sequestered per farm (0.25 ha) over a cultivation cycle – 17 months. Salinity was the main driver of predicted regional changes in carbon capture, while temperature and chlorophyll *a* had more pronounced local effects. This research advances our understanding of the role low trophic aquaculture plays in mitigating climate change. It highlights the importance of developing location-specific strategies for

\* Corresponding author.

E-mail addresses: [annaleena.vaher@ut.ee](mailto:annaleena.vaher@ut.ee) (A. Vaher), [jonne.kotta@sea.ee](mailto:jonne.kotta@sea.ee) (J. Kotta), [stechelebrecht@gmail.com](mailto:stechelebrecht@gmail.com) (B. Stechele), [ants.kaasik@ut.ee](mailto:ants.kaasik@ut.ee) (A. Kaasik), [kristjan.herkul@ut.ee](mailto:kristjan.herkul@ut.ee) (K. Herkül), [francisco.barboza@ut.ee](mailto:francisco.barboza@ut.ee) (F.R. Barboza).

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mussel farming that consider both local and regional environmental conditions. The results contribute to the wider discourse on sustainable aquaculture development and environmental conservation.

## 1. Introduction

As the world simultaneously faces the alarming depletion of marine resources and increasing demand for seafood, the sustainable development of aquaculture is emerging as a potential solution to address these interrelated challenges (Klinger and Naylor, 2012; le Gouvello et al., 2022). One possible way to achieve sustainable aquaculture is to minimise the negative environmental impacts of fish farming (Carballeira Braña et al., 2021; Kotta et al., 2023) while advocating for low-trophic aquaculture (LTA) practices (Kotta et al., 2020b, 2022; Krause et al., 2022). Mussel farming plays an important role in LTA practices, providing economic opportunities and contributing to several environmental benefits, such as improving water quality by filtering and capturing excess nutrients (Timmermann et al., 2019).

Aquaculture is one of the fastest-growing food production sectors in the world and is responsible for more than half of global seafood production (Mair et al., 2023). Overall, the global production of farmed bivalve molluscs has steadily increased over the past decades, reaching 2.2 million tonnes in 2020 (EUMOFA, 2022). The total value of mollusc aquaculture reached around 3.8 billion USD out of which 8 % was from farmed blue mussels *Mytilus* spp. (EUMOFA, 2022). The European total farmed blue mussel production decreased from 162,508 t (live weight) in 2002 to 140,000 t in 2022, while revenues increased from 200 million USD (price around 1 USD/kg) in 2002 to almost 275 million USD (price around 2 USD/kg) in 2022 (FAO, 2024). Therefore, even when revenues have increased, farmed blue mussel production across 11 European countries has declined by over 13 % in the past 20 years. The decline in European production is thought to be due to multiple environmental and anthropogenic pressures, including the spread of mussel diseases, pollution, blooms of toxic microalgae, lack of spat, predation, lack of innovation in mussel production, and impacts of climate change (Labarta and Fernández-Reiriz, 2019; Des et al., 2020; Avdelas et al., 2021; Castro-Olivares et al., 2022; van de Vis et al., 2023). The latter is becoming more challenging over time as the global aquaculture sector has to consider mitigation and adaptation strategies to cope with the changing climate conditions (Duarte et al., 2017). Overall, more scientific research, investment, and policy support for the mussel aquaculture industry are needed to increase the various economic and environmental benefits of European mussel production.

Climate change mitigation includes the urgent need to reduce greenhouse gas emissions and to develop innovative and effective solutions for carbon capture (Intergovernmental Panel on Climate Change (IPCC), 2023). Research focused on understanding the role of shellfish farming in climate change mitigation – particularly analysing and modelling shell growth dynamics and the natural process of biogenic carbon sequestration – is crucial to exploring a potential avenue for such solutions (Gallagher, 2015; Filgueira et al., 2016; Aubin et al., 2018; Bertolini et al., 2021; Fuentes-Santos et al., 2021; Sea et al., 2022). The carbon capture potential in shellfish aquaculture continues to be a subject of debate, partially due to the uncertainty associated with the fate of carbon during shell production (Frankignoulle et al., 1994; Filgueira et al., 2015; Aubin et al., 2018; Morris and Humphreys, 2019; Turolla et al., 2020). Bivalve shells are made during biogenic calcification by the precipitation of calcium carbonate ( $\text{CaCO}_3$ ) on an organic matrix (Frankignoulle et al., 1994). Biogenic calcification is a process in which organisms incorporate from water a calcium ion ( $\text{Ca}^{2+}$ ) and dissolved bicarbonate ( $\text{HCO}_3^-$ ), to form shells of  $\text{CaCO}_3$ . During this process,  $\text{CO}_2$  is released into the surrounding water (Emerson and Hedges, 2008). Therefore, the process of biogenic calcification entails two carbon pathways (Tamburini et al., 2022). The first is a “short-term” pathway that involves the immediate release of  $\text{CO}_2$  into the water with an

uncertain fate. The released  $\text{CO}_2$  may be used by primary producers for photosynthesis, or it may follow abiotic pathways, such as re-dissolution in water or release into the atmosphere (Heinze et al., 2015). These processes are influenced by a combination of environmental conditions, including water alkalinity, pH, temperature, salinity, or concentration of primary producers (Emerson and Hedges, 2008). Simultaneously, a carbonate ion is captured in a steadier state under the form of  $\text{CaCO}_3$  and used to build a solid protective shell structure (Munari et al., 2013). By becoming part of the mussel shell, this carbon enters a long-term pathway where it is immobilized and stored (for decades to centuries under adequate environmental and management conditions, Alonso et al., 2021), being an essential process to capture carbon (Bernier, 2003). After mussels die, the cumulated shells may dissolve back to calcium ions and bicarbonate or become limestone over a long period of time, sequestering carbon into the sediment. Humans can prevent the release of captured carbon in shells by harvesting mussels and using their shells for construction materials on roads and other land-based applications, grinding mussel shells and using them in agriculture, or releasing them back into the water column in areas where increasing alkalinity is needed (Martínez-García et al., 2017; Alonso et al., 2021; Álvarez-Salgado et al., 2022).

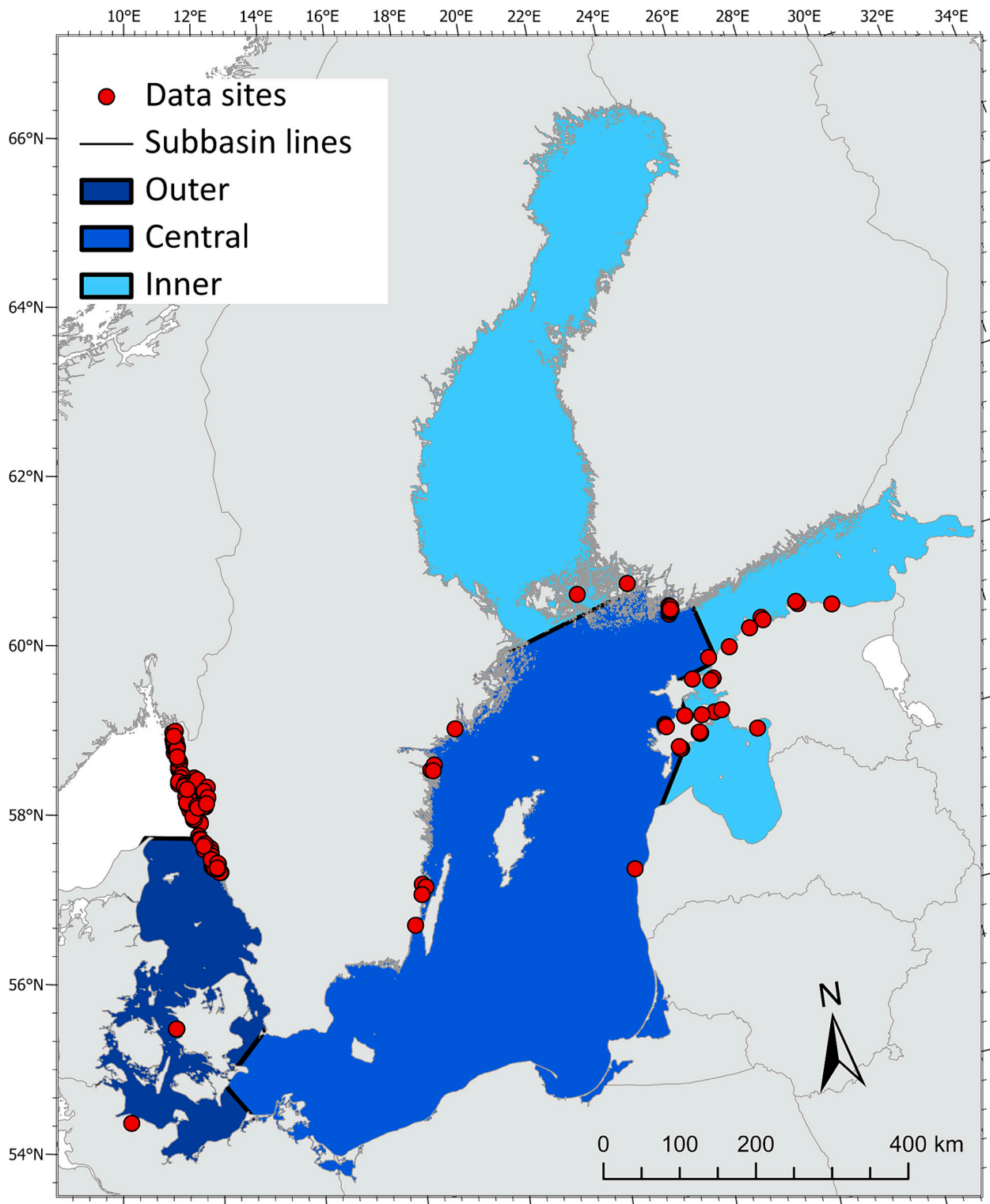
Researchers have developed useful bioenergetic models for carbon sequestration in bivalves (Morris and Humphreys, 2019; Ehrnsten et al., 2020; Bertolini et al., 2021; Dong et al., 2022), but there is still a lack of comprehensive and reliable models for mapping and predicting carbon capture by mussel farming. Implementing Dynamic Energy Budget (DEB) approaches is a promising method to address this complex challenge. DEB theory quantitatively describes the metabolic organisation of organisms using assumptions based on mechanistic principles. DEB models include energy, mass and elemental budgets, with homeostasis (maintenance of constant chemical composition) as a central tenet of the theory (Kooijman, 2010). Although limited examples are currently present in the literature, DEB can be used to quantify nitrogen, phosphorus or carbon fluxes through all living systems (Lavaud et al., 2020, 2021; Kotta et al., 2023). These applications have been used, for example, to estimate the eutrophication mitigation potential (N and P reduction) of mussel farms (Kotta et al., 2020b). However, it is important to ensure that farms are not located in areas with unsuitable conditions, such as sheltered areas with insufficient water exchange, where adverse effects such as increased sedimentation and potential oxygen depletion may occur (Kotta et al., 2020a). Additionally, DEB models can quantify carbon fluxes, offering insights into the effectiveness of climate mitigation measures in complex and dynamic environments. Nevertheless, evaluating carbon capture in shellfish farms requires an adapted approach.

While DEB models have proven valuable for tracking nutrient fluxes, most existing models have not treated shell weights independently of total body mass. Nonetheless, research has shown that shell growth can be decoupled from somatic growth (Campana, 1990; Lewis and Cerrato, 1997), providing an interesting perspective for accurately modelling carbon capture. In theory, the current DEB models for shellfish are only capable of estimating soft tissue dynamics, with shell metrics being currently linked to soft tissue and, therefore, growth. Energy allocation, but also carbon allocation to the shell, follows product rules and should, therefore, be related to the three main DEB fluxes (assimilation, growth, and dissipation). Shells are considered products because they do not require maintenance. In the current paper, we followed the DEB rules for product formation to quantify shell production dynamically (Kooijman, 2010; Pecquerie et al., 2012) instead of correlating shell formation to structural tissue. The methodology established in this study has significant value not only in assessing the carbon capture potential of mussel

farming but also in a variety of other fields, particularly when studying the dynamics of biocalcification in ecosystems such as coral reefs and biocalcifying algal populations (Muller and Nisbet, 2014).

The Baltic Sea region, a data-rich area, presents an ideal setting for developing and applying DEB models of LTA solutions (Reusch et al., 2018). As the region is heavily impacted by eutrophication, the Helsinki

Commission (HELCOM) has set nutrient emission reduction targets to which mussel farming can contribute (HELCOM, 2021). Furthermore, the Baltic Sea is experiencing climate change-related transformations faster than many other marginal seas in the world (Reusch et al., 2018; HELCOM, 2021). In the Baltic Sea, the potential of carbon capture by mussel farms is an understudied topic as mussel farming is a relatively



**Fig. 1.** Study area map showing the three subregions of the Baltic Sea: outer (dark blue), central (blue), and inner (light blue), used to describe and discuss the spatial variation of carbon capture in our study. The red dots indicate the locations from where data used to inform the constructed Dynamic Energy Budget (DEB) model, were collected.

new industry, especially in the more brackish areas where mussel growth is limited due to low salinity. Therefore, there is a need to provide decision-makers with science-based evidence on the capacity of mussel farms to capture carbon in their shells under current conditions and the potential impacts of a plausible future scenario. One focus point is how LTA aquaculture can contribute to environmental targets, specifically in capturing nutrients and carbon from the system.

In this study, we developed a regional DEB model for the Baltic Sea that was adapted to include biocalcification and is, therefore, capable of estimating the carbon capture dynamics of blue mussels under farming conditions. This approach allows mechanistic predictions of carbon capture dynamics in specific environments, such as those characterised by steep salinity gradients or strong seasonality. In addition, we used the same model to assess a plausible future scenario of carbon capture by farmed blue mussels under conditions of nutrient reduction and the ongoing effects of climate change in the Baltic Sea. This application of the DEB model highlights the importance of developing location-specific strategies for mussel farming that consider both local and regional environmental conditions. The results contribute to the wider discussion about the future role of mussel farms in mitigating the negative effects of eutrophication and climate change.

## 2. Material and methods

### 2.1. Study area

The Baltic Sea is a shallow, brackish, and young water body located in northern Europe. It is known for its strong seasonality and highly variable environmental gradients, including salinity, temperature, wave exposure, and nutrient availability (Carstensen et al., 2014; Zettler et al., 2014). Baltic Sea has several major sub-basins, but in this study, we divide the Baltic Sea into three subregions: inner region (Bothnian Bay, Bothnian Sea, Archipelago Sea, Åland Sea, Gulf of Finland, and Gulf of Riga); central region (Southern and Northern Baltic Proper, Western and Eastern Gotland Basins, Gdansk Basin, and Bornholm Basin); and outer region (Kattegat and the Belt Sea) (Fig. 1). This division follows the Baltic Sea salinity gradient, with salinities below 7 in the inner region, below 15 in the central region, and up to 30 in the outer region (transition to the North Sea) (Kotta et al., 2020a).

### 2.2. Blue mussel

*Mytilus edulis* and *Mytilus trossulus* are the dominant habitat-forming mussel species in the Baltic Sea ecosystem. *M. edulis* prefers higher salinity conditions and thrives in salinities above 12, making it more common in the outer subbasins of the Baltic Sea (Sanders et al., 2021). *M. trossulus*, on the other hand, can tolerate lower salinities from 5 to 8 and is found throughout the entire Baltic Sea, except in the northernmost and easternmost regions where the species reach their tolerance limit (Kijewski et al., 2019). For both species, the salinity threshold is <5, where the species can no longer survive and the ecosystem function is severely reduced (Elmgren and Hill, 1997; Vuorinen et al., 2002). There are also extensive hybrid zones between *M. edulis* and *M. trossulus* in the Baltic region, resulting in the widespread presence of this hybrid species in Baltic mussel farms (Stuckas et al., 2009; Väinölä and Strelkov, 2011; Larsson et al., 2017). In the Baltic Sea, the morphological characteristics and physiological state of blue mussels depend mainly on salinity levels but are also affected by temperature and food availability (Tedengren et al., 1990; Bonsdorff and Pearson, 1999; Kotta et al., 2015). Due to lower salinity levels slowing down the growth rate, the Baltic Sea blue mussels can reach a maximum size of about one-third of that observed in mussels from the North Sea (Tedengren et al., 1990). Compared to their North Sea counterparts, Baltic mussels typically have thinner, more translucent, and elongated shells – a characteristic attributed to the lower calcium content in their shells (Remane and Schlieper, 1971; Tedengren et al., 1990; Knöbel et al., 2021).

### 2.3. DEB model

The standard DEB parameter values for *M. edulis*/*M. trossulus* have been estimated and validated for spatial application in the Baltic (Kotta et al., 2023) using chlorophyll *a*, temperature, and salinity as environmental model forcings. Although the model prediction area of Kotta et al. (2023) focused on the Northeastern Baltic Sea region, the model was trained using data spanning the entire salinity gradient of the Baltic Sea and beyond, making it suitable for the current pan-Baltic application. DEB model applications to shellfish generally relate shell metrics exclusively to structural volume and, therefore, to the somatic growth flux. However, observations clearly show that shell production can be decoupled from somatic growth. Shell production, for example, has been observed during prolonged starvation in molluscs (Yang et al., 2010). Bivalve shells are, in DEB terminology, clear examples of persistent products (Kooijman, 2010), which are formed in association with the three main fluxes (assimilation, dissipation, and growth). For this work, the approach proposed by Pecquerie et al. (2012) to simulate fish otolith biocalcification is adapted to enable estimations of bivalve shell production.

Bivalve shells are composed of an organic fraction, the organic matrix, and an inorganic fraction, the precipitated CaCO<sub>3</sub> on the organic matrix. The organic fraction of the shell ( $\dot{p}_p$ , J d<sup>-1</sup>) is a DEB-product and amounts to the weighted sum of the growth and dissipation fluxes, with  $v_G$  and  $v_D$  the contribution coefficients (dimensionless) of the growth and dissipation flux, respectively.

$$\dot{p}_p = \dot{p}_G v_G + \dot{p}_D v_D \quad (1)$$

The contribution of assimilation, the third basic flux in DEB theory, is neglected because the formation of the organic matrix is a gene-regulated process and, therefore, an anabolic process. Dissipation includes both anabolic and catabolic processes, while growth only includes anabolic processes. However, assimilation is exclusively a catabolic process, and its contribution to shell formation is, therefore, negligible (Fablet et al., 2011; Pecquerie et al., 2012).

The organic matrix regulates the precipitation rate of CaCO<sub>3</sub>. Precipitation of CaCO<sub>3</sub> occurs through the active transport of Ca<sup>2+</sup> ions to the extrapallial fluid. The active regulation of CaCO<sub>3</sub> precipitation ( $\dot{p}_{CaCO}$ , J d<sup>-1</sup>) on the organic shell matrix comes with an energetic cost which is given by:

$$\dot{p}_{CaCO} = \dot{p}_p / y_{CO} \quad (2)$$

with  $y_{CO}$  the yield of calcium carbonates on organic matrix. The value of  $y_{CO}$  relates to the ratio of organic to inorganic fractions in the shell. Since the shell constitutes of an organic and an inorganic fraction, the variation of shell volume through time ( $\frac{dV_s}{dt}$ , cm<sup>3</sup> d<sup>-1</sup>) is given by:

$$\frac{dV_s}{dt} = \frac{\dot{p}_p}{[E_{GO}]} + \frac{\dot{p}_{CaCO}}{[E_{GI}]} \quad (3)$$

With  $[E_{GO}]$  the volume specific cost for organic matrix (cm<sup>3</sup> J<sup>-1</sup>), and  $[E_{GI}]$  the volume specific cost for inorganic matrix (cm<sup>3</sup> J<sup>-1</sup>). Shell matrix such as shell weight ( $W_s$ , g) and shell length ( $L_s$ , cm) are obtained from the volume through:

$$W_s = V_s d_s \quad (4)$$

$$L_s = \frac{V_s^{\frac{1}{3}}}{\delta_{Ms}} \quad (5)$$

Considering the strong homeostasis assumption of DEB theory, energy and weight fluxes can be converted to element fluxes enabling the estimation of carbon budgets for shellfish.

The values of DEB shell parameters (Table 1) were extracted from the literature or were estimated through the standardized Add-my-Pet procedure (Lika et al., 2020). During parameter optimization, primary

DEB parameters for *M. edulis/trossulus*, estimated in Kotta et al. (2023), were kept constant. Shell parameters  $v_G$ ,  $v_D$ , and  $\delta_{M_s}$  were estimated based on the Kotta et al. (2023) dataset, as well as a dataset from mussels collected at a commercial farm in Tagalaht Bay, Estonia (58.46°N, 22.05°E). This comprehensive dataset includes 378 growth observations, encompassing measurements of mussel total wet weight, shell length, total dry weight, and dry tissue weight from various sites across the Baltic Sea region (Fig. 1, Supplementary Material 1). These observations cover the full range of key environmental conditions essential for mussel growth and shell formation, such as chlorophyll *a* (0.2–2.5  $\mu\text{g L}^{-1}$ , indicating food availability), salinity (4.4–26.1) and summer temperatures (15–18 °C). In this pan-Baltic dataset, the experimental setups were highly variable, with differences in rope type, deployment and incubation times, and depth contributing to the heterogeneity of the data.

The standard practice for estimating parameters from univariate datasets is to use growth data, which typically uses constant (average) environmental predictors - such as temperature, salinity and food availability - specific to the growth data (Lika et al., 2011). During parameter estimation, chlorophyll *a* values were considered to be constant during the year and were based on winter or summer observations. Salinity was also considered constant throughout the year. Seasonal fluctuations in sea water temperature ( $T$ , °C) were predicted based on the maximum summer temperature ( $T_{max}$ , °C) using Eq. (6).

$$T = \frac{T_{max}}{2} \sin\left(\frac{2\pi}{365}(t + t_0)\right) + \frac{T_{max}}{2} \quad (6)$$

In this equation,  $t$  represents the day of the year for which the temperature is calculated, and  $t_0$  is the start day of each growth experiment. In this case, summer values were chosen because the growth experiments varied in their start and end dates, and some did not last a full year. This variability made it impractical to use annual average temperatures for these growth records.

Model to data fits were evaluated based on the mean relative error (MRE) value. MRE values below 0.20 are generally considered 'good', MRE values between 0.2 and 0.3 are 'acceptable' and estimates with values above 0.3 are considered 'off'. The datasets used for parameterisation as well as the AmP DEB parameterisation files are included in the Supplementary Material 1.

#### 2.4. Implementing the DEB model at farm scale

We used a commercial *M. edulis/trossulus* hybrid farm located in Tagalaht Bay as the 'standard mussel farm' for the study. This blue mussel farm is self-regulating since the farming relies on the recruitment of free-swimming larvae from wild populations that disperse passively from natural mussel reefs. After dispersal, the larvae attach themselves to the farm substrates. Our test farm uses a smart farm system, i.e., mussels are grown on nets placed at 1–5 m depth and attached to long buoyancy lines. The mussels are cleaned and harvested by specialized machines, which run along the nets. The mussel farm has an area of 0.25 ha and consists of six 100 m long farm lines. The stocking density of such mussel farm is approximately 40 million individuals (Kraufvelin and Diaz, 2015; Kotta et al., 2020a, 2023). The cultivation period is from the 1st of June to the 31st of October of the following year, i.e., the biomass

is harvested 17 months after the establishment of the farm (Kotta et al., 2023). This standard mussel farm unit was used to express the predictions of the DEB model for the whole Baltic Sea region.

To force the DEB model, we used environmental layers derived from simulations of two different scenarios to assess the potential of carbon capture by mussel farming: the first represents the present conditions, and the second projects a future state, considering nutrient reduction and the continuing impacts of climate change as described in detail in Meier et al. (2012). Here, the Baltic Sea coupled physical-biogeochemical model RCO-SCOBi (the Swedish Coastal and Ocean Biogeochemical Model coupled to the Rossby Centre Ocean Circulation Model; Meier et al., 2003; Eilola et al., 2009) was forced with regionalized atmospheric data from the global climate model ECHAM5 (Roeckner et al., 2006) and the A1B emission scenarios (provided by the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios, Nakicenovic and Swart, 2000). The regionalization of the atmospheric forcing was simulated with the coupled atmosphere-ocean model RCAO (the Rossby Centre Atmosphere Ocean model developed at the Swedish Meteorological and Hydrological Institute; Döscher et al., 2002), using an atmospheric horizontal grid of 25 km (Meier et al., 2011). The RCAO, a Bryan-Cox-Semtner primitive equation circulation model, was operated with a horizontal resolution of 3.7 km and 83 vertical levels (each 3 m thick) and open boundary conditions in the northern Kattegat (Webb et al., 1997). Runoff changes were projected using a hydrological model for the Baltic Sea catchment (Lind and Kjellström, 2009). Comprehensive details on the downscaling and the RCAO model can be found in Meier et al. (2011, 2012). The ECHAM5/RCAO model output included physical and chemical data layers such as Secchi depth, salinity, temperature, nitrate ( $\text{NO}_3$ ), phosphate ( $\text{PO}_4$ ) and phytoplankton. Daily averages were calculated for the periods 1978–2007 (current conditions) and 2070–2099 (projected future climate).

To achieve a healthy environmental status of the Baltic Sea, HELCOM has proposed reducing nitrogen (N) and phosphorus (P) concentrations in the sea. This will be achieved by setting the Maximum Allowable Inputs (MAI) and Country Allocated Reduction Targets (CART) for each HELCOM country. In the Baltic Sea, the MAI targets require a reduction of N and P of 11.2 % and 27.5 %, respectively. However, when comparing the model setup referred to by Meier et al. (2012), the reduction targets are 18 % for N and 42 % for P. Therefore, the future scenario tested encompassed the achievement of the HELCOM nutrient reduction MAI target (HELCOM, 2017).

Daily environmental data were used to run the DEB model, covering the cultivation season from the 1st of June to the 31st of October of the following year. The DEB model, which operates at a daily time step, evaluates nutrient and carbon fluxes, including assimilation processes within a single mussel. This approach provides a dynamic understanding of how environmental factors influence individual mussel physiological responses and associated nutrient cycling. To upscale biomass growth from a single mussel to an entire farm, we considered realistic densities in our test mussel farm (40 million individuals). High-density mussel farms are recognised for their ability to significantly reduce phytoplankton levels in seawater. The flux of food into a mussel farm depends on phytoplankton concentration and horizontal flow velocity. In our study, the daily mean absolute horizontal flow velocity for the upper 10

**Table 1**  
Parameters used in the DEB-shell module.

Parameter	Unit	<i>M. edulis/trossulus</i>	Description	Reference
$v_G$	–	0.0270	Contribution of growth flux to shell formation	Calibrated
$v_D$	–	$5.4 \cdot 10^{-5}$	Contribution of dissipation flux to shell formation	Calibrated
$y_{CO}$	–	0.047	Yield coefficient of $\text{CaCO}_3$ to organic matrix	Calculated from Kotta et al. (2023)
$[E_{GO}]$	$\text{J cm}^{-3}$	39,000	Volume-specific cost for organic matrix	(Kooijman, 2010)
$[E_{GI}]$	$\text{J cm}^{-3}$	2700	Volume-specific cost for inorganic matrix	(Palmer, 1992, 1983)
$\delta_{M_s}$	–	0.434	Shape coefficient of shell	Calibrated
$d_S$	$\text{g cm}^{-3}$	2.7	Density of $\text{CaCO}_3$	

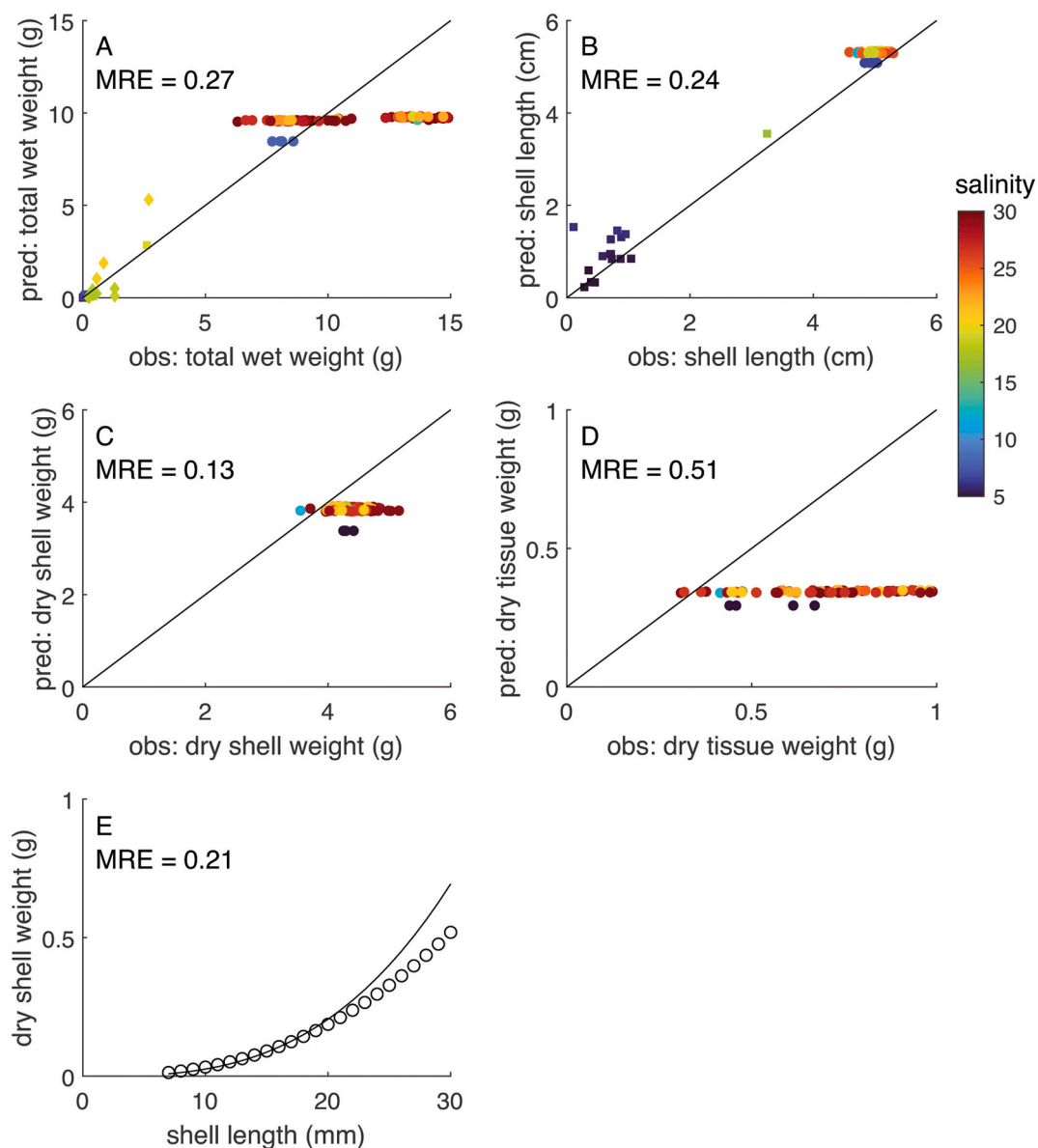
m water column was used as an indicator to determine whether hydrodynamics was sufficient to prevent food limitation or whether food was being depleted, resulting in farmed mussels growing at lower phytoplankton concentrations than indicated by the forcing data. In cases of food limitation, the DEB model estimated the expected phytoplankton uptake within the mussel farm. At the same time, the forcing data provided the influx of food from the surrounding area. From this, we calculated the adjusted phytoplankton density, which was then used in the DEB model to simulate realistic phytoplankton ingestion and biomass growth on a farm scale (Holbach et al., 2020).

For spatial prediction of growth and carbon sequestration by farmed mussels across the study area, we ran the mussel DEB models independently for each 1 km<sup>2</sup> grid cell. These models assumed that there were no mussel farms in neighbouring grid cells, reflecting the nascent state of mussel farming in the Baltic Sea, where multiple farms in the same area are unlikely. This setup allowed us to assess how environmental variation between cells affects nutrient and carbon dynamics on the farm, and

to isolate and understand the impact of individual farms.

Due to the overwhelming size of the full simulation output summary figures were based on sampling which also allowed us to visualize different regions of the Baltic on a common and comparable scale. To visualize cumulative carbon capture in mussel shells and wet weight increment 100 random cells were chosen from each Baltic Sea region (separately for present and future scenario). The respective carbon captures and wet weights were recorded from the simulation data and then averaged. This process was repeated 100 times allowing the calculation of the 5 % and 95 % quantiles together with the mean of the averages.

To visualize the relative contributions of salinity, temperature, and chlorophyll *a*, these variables were first converted to a common numerical scale and then once again 100 random cells were chosen from each region and a linear model was fitted with shell carbon capture as the dependent variable and the environmental variables as the independent variables. The contribution of each environmental variable was



**Fig. 2.** The DEB parameter estimation was evaluated by comparing observations and predictions of mussel growth across the Baltic Sea. The mean relative error (MRE) was used as the metric for this evaluation. MRE values around 0.2 indicate acceptable results and a good fit, suggesting that the parameter values used in our model are realistic. In plots A to D, the colours of the symbols indicate the average salinity during cultivation, while the shapes of the symbols represent datasets from the same experiment.

calculated as the absolute value of its regression coefficient divided by the sum of the absolute values of all environmental regression coefficients (and then multiplied by 100 %). Repeating the process 100 times allowed estimation of the variability of the estimates.

To visualize the effect of these variables on a spatial scale a random origin cell was first chosen from each region and then a sample of 100 cells was constructed by selecting cells no farther than some fixed distance from the origin cell. A linear model was once again fitted to the sample and the relative importance metric  $lmg$  was calculated for each environmental variable using the R package *relaimpo* (Groemping, 2006) with the restriction that these need to sum up to one. This process was then repeated 100 times to assess the variability of the estimates.

### 3. Results

#### 3.1. DEB model performance

The DEB parameters  $v_G$  and  $v_D$ , and  $\delta_{M_i}$  were calibrated using a comprehensive dataset of mussel growth across the Baltic Sea, consisting of 378 observations (Fig. 1). This dataset included experiments from different locations in the Baltic Sea region and observations of mussel growth metrics such as total wet weight, shell length, dry shell weight, and dry tissue weight. The parameterisation achieved a good model-to-data fit with a mean relative error (MRE) of 0.18. Predictions for total wet weight and shell length were satisfactory (MRE between 0.2 and 0.3, Fig. 2a and b). Estimates of the correlation between shell length and shell weight were acceptable (Fig. 2e). However, estimates for dry tissue weight were less accurate (MRE > 0.3). Overall, the results indicate a good estimation of the calcification process under highly variable environmental conditions.

#### 3.2. Spatial patterns of carbon capture in mussel farms: Current vs. future scenario

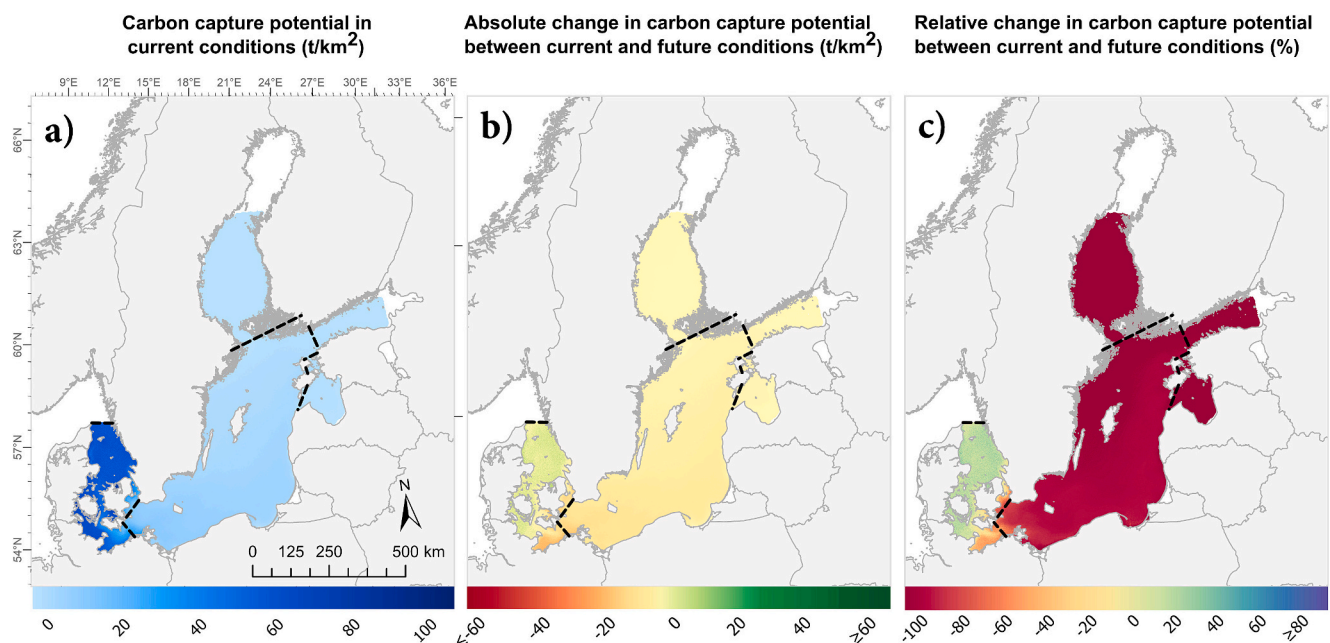
Overall, spatial changes in carbon capture in shells align with the salinity gradient of the Baltic Sea (Fig. 3a). The carbon captured in mussel shells produced in standard farms reaches its highest values (30–90 t C) in the outer Baltic Sea (Kattegat and Danish straits), where

high salinity conditions prevail. In the area between outer and central region, carbon capture decreases rapidly (10–30 t C), following the sharp decrease in salinity, continuing to gradually decline across the rest of the central region. The lowest values of carbon capture in shells are estimated in the inner region (Gulf of Finland and Bothnia Bay), where mussels reach their lower salinity tolerance limit ( $\leq 1-10$  t C).

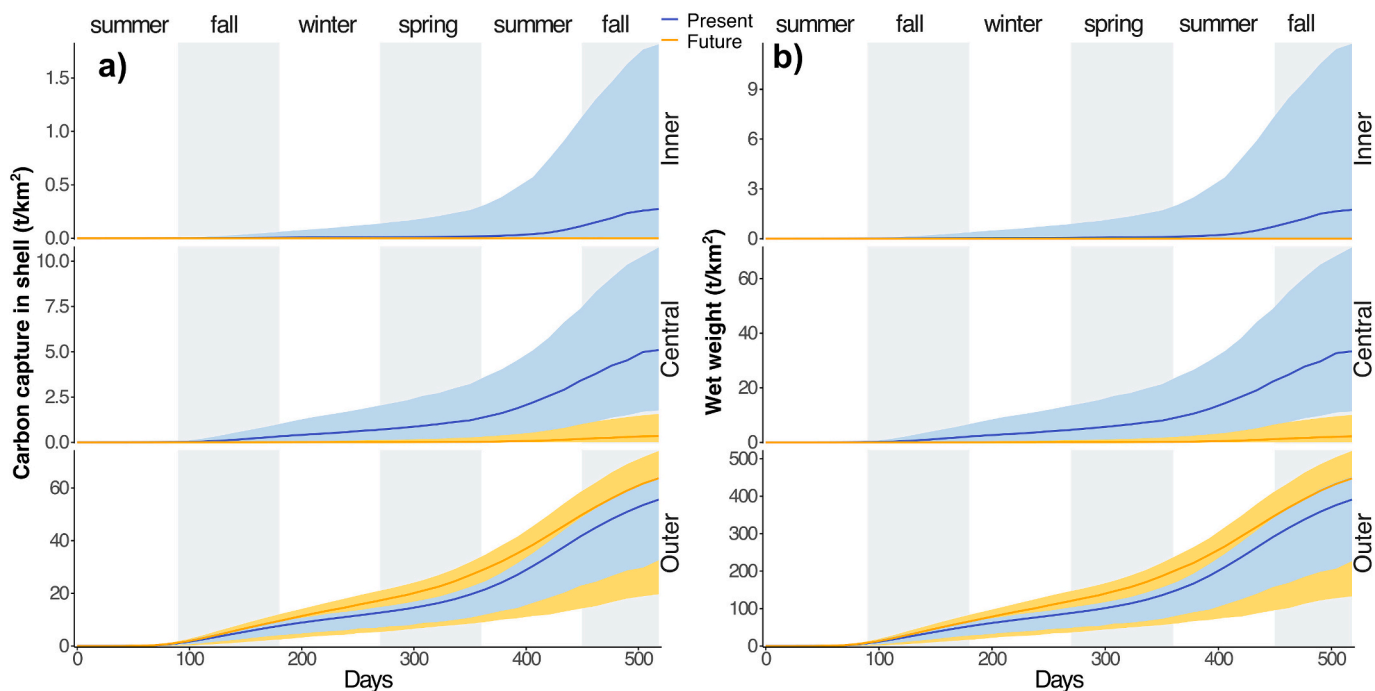
The amount of carbon capture in shells is expected to increase by  $\leq 1-20$  t C (0–30 % increase with respect to present conditions) in the outer Baltic Sea under future environmental conditions – the only region predicted to experience any carbon capture enhancement (Fig. 3b,c). This is likely due to more favourable environmental conditions for blue mussels predicted by the end of the century in this area, where high salinities will persist alongside an increase in sea surface temperatures. A sharp decrease in carbon capture capacity (–10 to –30 t C) is predicted between the outer and central regions in the evaluated future scenario (Fig. 3b). Although the absolute changes in the central and inner regions are not as drastic as those observed in the outer area ( $\leq -10$  t C), projected relative changes show a dramatic and, in extreme cases, almost complete loss (over 90 %) of carbon capture capacity in these regions by the end of the century (Fig. 3c).

#### 3.3. Temporal dynamics of carbon capture in mussel shells and wet weight over the production cycle

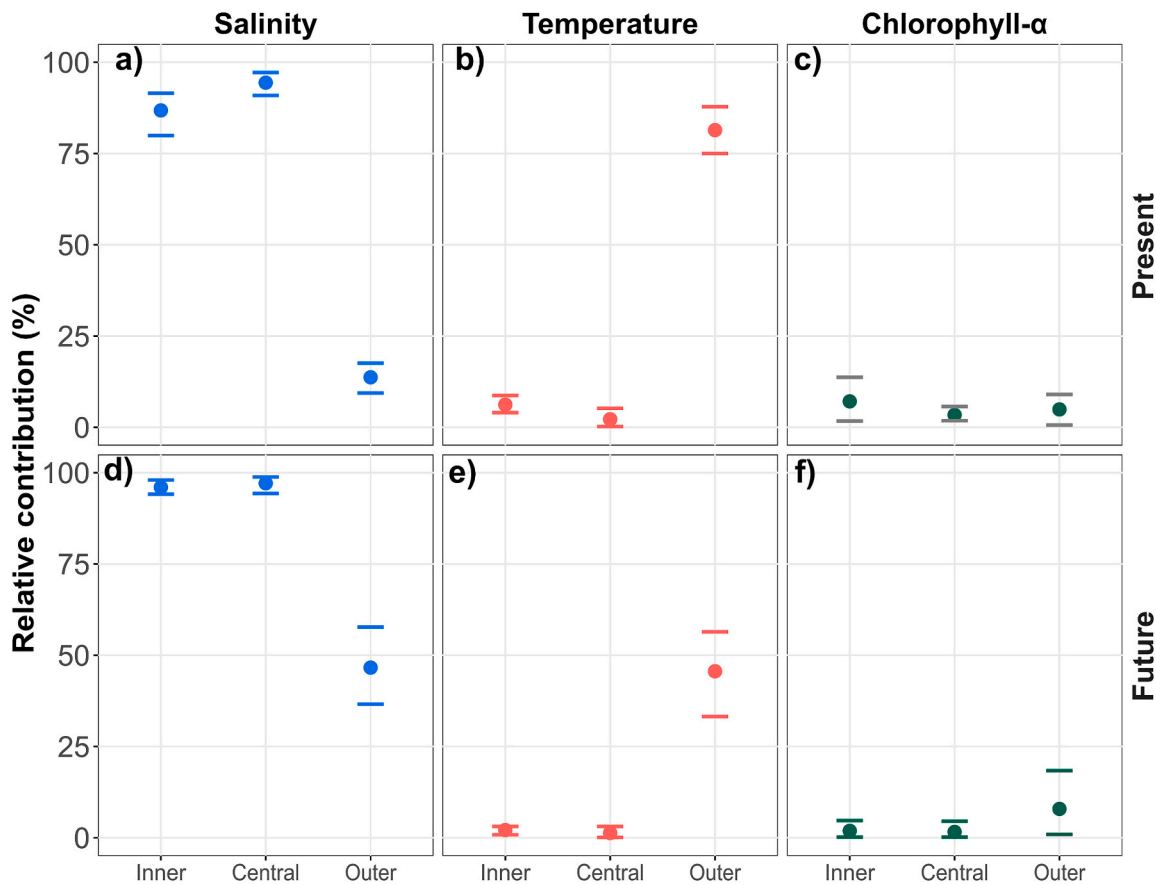
As the mussels grow, the carbon capture in the shells gradually increases over the first year of production under both present and future scenario (Fig. 4a). There is a noticeable acceleration of growth in the summer of the second year, reaching a plateau at the end of the fall (when mussels are harvested). In the present scenario, the amount of carbon captured in shells increases by the end of the cultivation cycle approximately tenfold between each region and the model predicts the highest capture in the outer region (mean values around 55 t in present and 65 t in future scenario at the end of a production cycle) (Fig. 4a). In the inner and central regions of the Baltic, the carbon captured in shells is noticeably higher under present conditions; however, this pattern changes in the outer region where future conditions are predicted to slightly improve the capacity (Fig. 4a). The variability increases over time, marking the inner region as the most unpredictable area for



**Fig. 3.** Predicted total incorporated carbon in farmed blue mussel shells (expressed in tonnes) under present environmental conditions (a) as well as the future change expressed as an absolute (b) and relative (c) difference with respect to the present. Additional insights into the current and projected scenarios are provided in the main text and Supplementary Material 2.



**Fig. 4.** Predicted cumulative carbon capture in mussel shells (a) and wet weight increment (b) of farmed blue mussels in tonnes over the production cycle of a standard mussel farm (17 months). Trends highlighted in blue represent predictions under present environmental conditions, while trends highlighted in orange are the predictions under future conditions for the inner, central, and outer regions of the Baltic Sea. Mean values are represented with lines and confident intervals at 95 % by shaded areas. Each alternating background box represents 90 days/a season, starting from summer. Results are analysed using the bootstrapping method.



**Fig. 5.** Relative contributions of salinity (a,d), temperature (b,e), and chlorophyll *a* (d,f) to the observed changes in carbon capture capacity of farmed blue mussel shells in inner, central, and outer regions of the Baltic Sea. The upper panel shows the contributions under present conditions, while the lower panel shows the contributions estimated under the evaluated future scenario. Mean values are represented by points and confident intervals at 95 %.



accurate quantification of carbon capture in shells.

Mussel wet weight increment and carbon capture in shells are closely linked, suggesting a strong correlation in the observed patterns between the two. For the present scenario the wet weight in inner region is on average around three tonnes by the end of the cultivation cycle and in the central region stays around 40 t (Fig. 4b). In the outer region where the salinity is higher and mussels can grow larger, the current wet weight stays around 400 t (Fig. 4b). The predicted wet weights are just slightly above zero tonnes in future conditions in both the inner and central regions, indicating the constraints imposed by the forcing environmental factors (Fig. 4b). The highest wet weights are estimated at the outer region (around 450–500 t in the future scenario at the end of a production cycle) (Fig. 4b).

### 3.4. Relative contributions of environmental factors to observed patterns

Salinity is the dominant environmental factor contributing to the observed changes in the carbon capture capacity of mussels in the inner and central regions of the Baltic Sea under both evaluated scenarios (86.8 % and 94.4 % in the present and 96.0 % and 97.1 % in the future, respectively) (Fig. 5a,d). Temperature and chlorophyll *a* both have a marginal contribution in these regions (Fig. 5b,c,e,f). However, the importance of temperature for outer region is highest among considered predictors but its relative contribution drops and becomes comparable with the influence of salinity in the future (Fig. 5a,b,d,e). Chlorophyll *a* contributed marginally to explain observed spatial and temporal changes in carbon capture in all regions, remaining below 20 % under both scenarios (Fig. 5c,f).

When assessing the relative contribution of environmental forcing variables at different spatial scales, the influence of salinity on carbon capture in mussel shells increases with the spatial scale in both

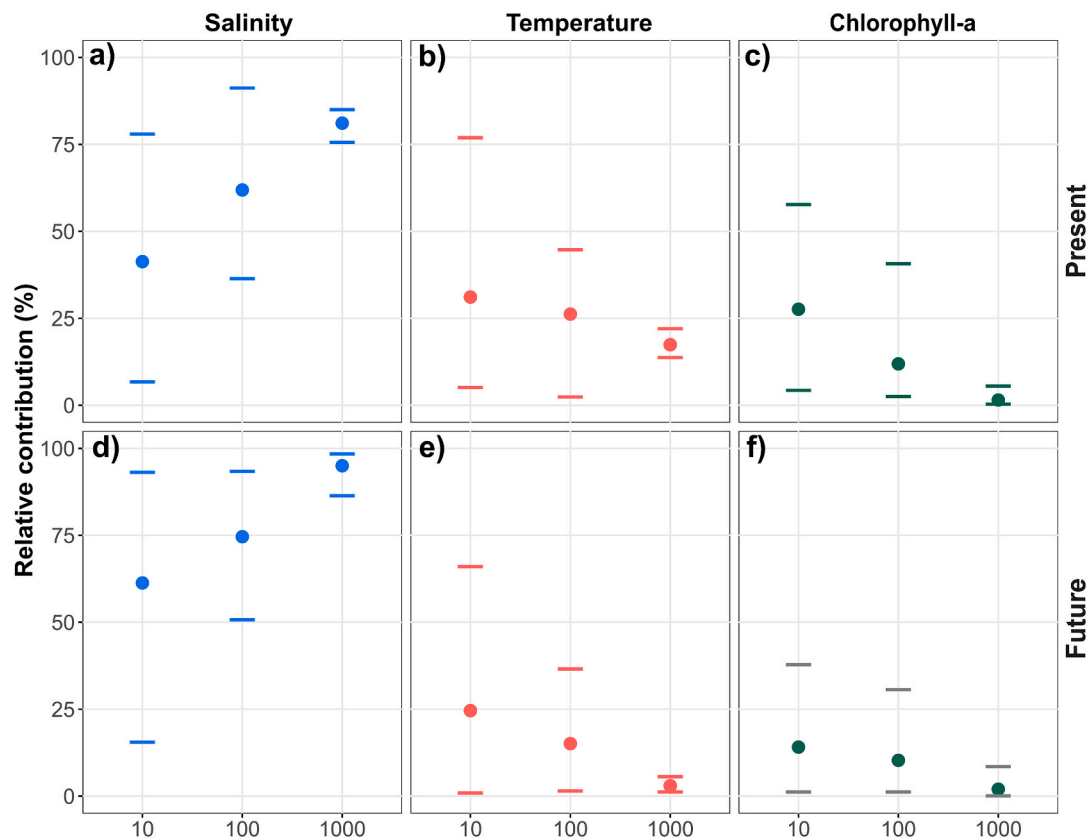
scenarios, with a greater effect at larger scales compared to local scales (81.1 % vs. 41.3 % in the current and 96 % vs 58 % in the future scenario, respectively) (Fig. 6a,d). In contrast, the contributions of temperature and chlorophyll *a* decrease with increasing spatial scales, suggesting that these factors contribute more locally to carbon capture in mussel shells (Fig. 6b,c,e,f).

## 4. Discussion

Our results represent the first spatial and temporal analysis of carbon captured in cultured blue mussel shells for the Baltic Sea and provide a detailed assessment of how environmental variables contribute to carbon capture under different scenarios. These results are useful to inform both regional and subregional decision-making processes on whether and where to place blue mussel farms considering carbon capture patterns and trends. We developed a DEB model that specifically quantifies shell production following the rules of the DEB theory for product formation (Kooijman, 2010; Pecquerie et al., 2012). Unlike traditional methods, which typically relate shell formation directly to structural tissue, this novel approach allows a more accurate determination of the carbon capture capacity associated with shell formation. This is especially valuable in the Baltic Sea region, where low salinity limits mussel growth and functioning. Salinity and temperature are critical aspects in the marginal habitat of the Baltic Sea, setting the limits for the distribution and capacity to thrive of marine species (Bonsdorff and Pearson, 1999).

### 4.1. Carbon capture potential under present scenarios

Before going into a detailed discussion of the obtained results, it is relevant to mention that we have not attempted to quantify the net



**Fig. 6.** Relative contributions of salinity (a,d), temperature (b,e), and chlorophyll *a* (c,f) to the observed changes in carbon capture capacity of farmed blue mussel shells across different scales of the Baltic Sea (distance radius of 10, 100, and 1000 km). The upper panel shows the contributions under present conditions, while the lower panel shows the contributions estimated under the evaluated future scenario. Mean values are represented by points and confident intervals at 95 %.

contribution of sea-based blue mussel farming in the Baltic Sea as an overall carbon source or sink. To do so, an overall carbon budget estimation and a detailed life cycle assessment of cultivated blue mussels and the harvesting process should have been performed (Filgueira et al., 2015; Turolla et al., 2020). Instead, we used our DEB model to quantify the carbon capture potential of farmed blue mussel shells across the Baltic Sea regions. In this sense, our focus was solely on estimating the long-term immobilization of carbon in the form  $\text{CaCO}_3$  (Tamburini et al., 2022) by blue mussels under different environmental contexts, a process that prevents carbon's immediate release into the surrounding water and might contribute to mitigating global warming.

According to our model's calculations under current conditions, the most effective regions for establishing mussel farms to maximise long-term carbon capture are the outer subbasins of the Baltic Sea (the Danish Straits, the Belt, and the Kattegat Sea). In these high salinity subbasins, our standard mussel farm is expected to capture between 30 and 90 t (average of 55 t) of carbon in mussel shells by the end of the considered cultivation cycle (17 months). In the central and inner subbasins, where brackish waters prevail, our model predicts a significantly lower carbon capture potential (<10 t). While carbon sequestration in these areas of the Baltic Sea is considered moderate, such LTA practices are of substantial value. This is particularly true as many other food production systems result in high carbon emissions, and mussels have the added benefit of sequestering excess nutrients in these regions (Kotta et al., 2020b). Extending the duration of the cultivation cycle and, thus, allowing mussels to grow longer might help increase carbon capture in low salinity areas of the Baltic Sea. However, this possibility requires further assessment of the potential economic trade-offs of delaying the harvest to maximise environmental benefits.

#### 4.2. Carbon capture potential under future scenarios

Predicting the plausible impacts of climate change in the spatially heterogeneous and temporally variable Baltic Sea region is extremely challenging. The observed changes in response to the assessed future scenario in our study are based on the latest publicly available hydrodynamic model predictions (Meier et al., 2012). As with many marine species that extend their range into brackish waters, the carbon sequestration potential of mussel shells is mainly driven by salinity. However, significant knowledge gaps remain in estimating future salinity levels, making it difficult to predict shellfish carbon capture potential under future climate conditions accurately (Lehmann et al., 2022). Predicting long-term salinity levels in the Baltic Sea is complex as various factors such as wind direction and speed, net precipitation, river runoff, inflow of seawater, and sea level rise are involved (Lehmann et al., 2022; Meier et al., 2022). Recent studies predict that the salinity of the Baltic Sea might exhibit a milder decrease or even an increase under projected future scenarios (Lehmann et al., 2022; Meier et al., 2022). Therefore, the future desalination scenario assessed in our study should be regarded as the "worst-case" scenario for blue mussel farms in the Baltic Sea.

The evaluated future scenario predicts a dramatic decrease in salinity, especially in the central and inner subbasins of the Baltic Sea, where salinity levels are expected to drop below (Supplementary Fig. 2). In general, with the decrease in salinity, the levels of  $\text{CaCO}_3$  will also decrease, causing undersaturation of calcium carbonate in the water, compromising calcification rates and carbon capture particularly in salinities below 6 in the Baltic Sea (Sanders et al., 2018). Based on the tested scenario, carbon capture potential will dramatically decrease in the central and inner Baltic Sea, exhibiting up to 90 % declines due to the uninhabitable salinity conditions that will prevail in the area. In this case, it is plausible that species such as the invasive bivalve *Dreissena polymorpha*, which currently thrives in the low salinity areas of the Baltic Sea, could replace blue mussels to some extent. However, *D. polymorpha*, with its different environmental requirements, is less suitable for cultivation in mussel farms and overall, this topic requires further research,

as the carbon capture potential of *D. polymorpha* and other species, as well as their responses to environmental conditions in the Baltic Sea, remain largely unexplored.

Our results indicate that under the evaluated future conditions carbon capture potential in farmed mussel shells might increase up to 50 % in the outer Baltic region. These results are explained by the predicted increase in salinity and temperature in these subbasins, which will create more suitable conditions for blue mussel growth and shell formation. However, when salinity is the primary environmental driver in carbon capture processes at a regional scale then improved temperature conditions or increased food availability can lead to significant, multi-fold variations in carbon sequestration at the local scale. This requires the development of strategic, region-specific adaptations in shellfish farming to optimise both shellfish yield and carbon sequestration potential under changing climate conditions, thus ensuring sustainable aquaculture development in the Baltic Sea.

#### 4.3. Novel dynamic energy budget models to assess carbon capture in bivalves

Several approaches have been used to evaluate the carbon storage potential of shellfish aquaculture. These studies generally apply a life cycle carbon budget of shellfish (Munari et al., 2013; Aubin et al., 2018; Ray et al., 2018; Alvarez-Salgado et al., 2022; Martini et al., 2022; Tamburini et al., 2022; Feng et al., 2023). These approaches do not include kinetic processes and, therefore, do not account for the interactions between the local environment and the metabolism of organisms, which largely determines the carbon fluxes through cultivation systems. Although limited examples are currently present in the literature, DEB models can be used to quantify nitrogen and phosphorus fluxes through living systems dynamically (Lavaud et al., 2020, 2021; Dong et al., 2022). These applications have been used, for example, to estimate the eutrophication mitigation potential (N and P reduction) of mussel farms (Kotta et al., 2023). Additionally, DEB models can dynamically quantify carbon fluxes, offering insights into the effectiveness of climate mitigation measures in complex and dynamic environments. Our study is the first to use a DEB approach to carbon budgeting in animal production systems, uniquely separating shell production from somatic growth.

Hamer and Foekema (2023) published a report evaluating carbon fluxes during shell formation in bivalve molluscs, while Ehrnsten et al. (2020) provided an overview of current modelling capabilities to quantitatively describe how benthic fauna, including bivalves, influence carbon processing in coastal zones. Our model for simulating biocalcification processes is based on different assumptions than those proposed by them. The earlier models simulate shell formation based on the assumption that shell length is related to growth. They split the energy flux to growth in two, allocating energy to shell formation and energy to growth. Relating shell to growth is a standard procedure in DEB and has been done since the start of DEB 45 years ago. A typical approach to calculating shell length in DEB is to relate structural length (the state variable that changes during tissue growth) to shell length. However, there are some problems with their proposed method. If shell formation is related to growth, then shell size is related to the DEB state variable structural volume (e.g., functional tissue). Maintenance costs are paid based on the size of the structural volume (larger animals pay more maintenance costs and respire more). If the growth flow is split in two, one part going to the tissue and one part to the shell, this means that maintenance costs are paid on the shell. Shell is a DEB product and is not part of the actual living animal and should not contribute to maintenance costs (e.g. a small individual with a large shell should not respire more than a small individual with a small shell).

Shell dynamics do not depend solely on growth. For example, even during periods of starvation, when no growth is expected, shell weight can still increase. Similarly, individuals that have reached their final size stop growing, just as humans typically stop growing around the age of

16. Despite this, numerous observations have shown that shells continue to grow in a similar way to hair and nails. Processes such as shell repair are crucial beyond this point of growth cessation. However, these phenomena cannot be accurately modelled using the model developed by Hamer and Foekema (2023), which does not account for these continuous shell dynamics.

In this paper, we have taken a distinctly mechanistic approach to modelling shell formation, supported by the DEB theory. This theory postulates that product formation, including shell formation, is based on assimilation, growth, and dissipation fluxes. This approach has previously been tested in DEB frameworks specifically for otoliths. While in some cases the shell dynamics may appear similar between our proposed model and that of Hamer and Foekema, there are numerous instances, particularly under suboptimal environmental conditions, where the dynamics of shell formation differ significantly. These differences are discussed in detail in Stechele and Lavaud (under review) and in previously published research on otoliths by Fablet et al. (2011) and Pecquerie et al. (2012).

#### 4.4. Limitations of the applied model and future developments

Our DEB model was generally able to capture metabolic processes in a wide range of environments. Results had acceptable MRE values, indicating good model-to-data fitting, but precision remains an issue when estimating shellfish metabolic performance. For example, high variability in tissue growth is observed. This can be attributed to metabolic inter-individual variability, environmental variability, variability in experimental setup, and variability on the initial conditions of the individuals of the experiments from where the data to construct the DEB model were obtained. A better fit could have been achieved if our model accounted for inter-individual variability. However, our focus was on carbon fluxes through populations, so the model represents the average individual within the population, ensuring that the estimates align as closely as possible with the typical individual. However, the estimates of shell length and shell weight were accurate and precise, with shell metrics showing less variability compared to tissue metrics.

The environmental factors incorporated into the DEB model in this study included salinity, temperature, and food availability. Although these are important variables that determine metabolic performance, our model omits other factors, such as oxygen levels and suspended solids, which may also affect mussel physiology. However, based on existing research (Kotta et al., 2015), these factors are not critical in our study area, especially for farmed mussels, as mussel farms are placed in well-oxygenated, dynamic environments away from sedimentation zones, minimising the impact on mussel feeding and growth. Other environmental variables might become important in the future. Climate change is expected to induce heat waves, altered currents, shifts in phytoplankton blooms, and changes in the ocean's carbonate system (IPCC, 2023). Although all these variables can be linked to metabolic performance, including biocalcification rates, through the DEB framework, more physiological research is required to quantify the effect of these variables on the metabolism of mussels. Especially relevant is the potential impact of acidification, saturation states, or pH on metabolic performance and biocalcification. Research on this topic is still contradictory (Tan and Zheng, 2020; Gold and Vermeij, 2023). Increasing pCO<sub>2</sub> levels and changing pH and alkalinity may affect the carbon sequestration potential of organisms such as mussels. However, available field and experimental evidence also show that Baltic Sea mussels might exhibit tolerance to ocean acidification in the Baltic Sea (Thomsen, 2012). Integrating the effects of alkalinity and pH into the energy budget and performance assessment could deepen our understanding of these dynamics. The DEB model, which is commonly used to assess non-lethal environmental effects on physiology, is suitable for this analysis. While pH and alkalinity are not yet included in the DEB framework, research by Stechele and Lavaud (under review) is advancing this integration.

Daily averages of temperature and salinity predictions used in our model, integrate information throughout the periods 1978–2007 and 2070–2099, overlooking extreme weather events. However, in the future, not only average temperatures are expected to increase but also the frequency, duration, and intensity of extreme weather events (Pansch et al., 2018). Marine heatwaves are expected to severely impact marine ecosystems as the global warming is proceeding. Our predicted future temperatures will be closer to mussel's optimal thermal performance than the current temperatures, therefore our model predicts an increase in carbon capture capacity in mussel shells. However, when considering the impacts of more frequent and intense heat waves, temperatures will most likely exceed the optimal thermal performance of 25 °C and become intolerable for blue mussels (Jones et al., 2009). Moreover, a single heat wave is less likely to cause mussel mortality than repetitively occurring long lasting heat exposures (Pansch et al., 2018; Seuront et al., 2019). If this happens, the prolonged extreme sea surface temperatures can have sublethal or lethal effects on Baltic Sea mussel populations causing mass mortality events as already observed with *Mytilus* populations in the English Channel (Seuront et al., 2019) and have been documented across various coastal regions of the Baltic Sea (personal observations by J. Kotta). Therefore, the impacts of heat waves are extremely important to consider in predicting the growth and shell formation of blue mussels. Additionally, in the process of planning blue mussel farms, decision-makers and farm owners must also be aware of the potential areas of impact such as shallow and enclosed waters that are expected to heat up under future climate conditions. In our future work, once more data and experimental research are available about the expected frequencies, durations, and intensities of the marine heat waves, we can improve our model and understand better how extreme events affect blue mussel populations and carbon capture potential in the Baltic Sea.

## 5. Conclusion

Assessing and harnessing multipurpose nature-based solutions that address the impacts of global and climate change pressures while providing economic benefits is crucial for promoting the sustainable development and use of marine ecosystems. In this context, our study presents a novel regional Dynamic Energy Budget (DEB) model that improves the way in which biocalcification processes are considered to evaluate the carbon capture potential in farmed blue mussel shells across the Baltic Sea under various environmental scenarios.

Our findings show that carbon capture potential follows the regional salinity gradient of the Baltic Sea. The highest carbon capture occurs in the outer Baltic Sea, where salinity is higher, and decreases remarkably in the central and inner sub-regions where lower salinity levels prevail. The analysed future scenario considered a worst-case scenario based on the best available evidence. The results suggest an increase in carbon capture potential in the outer region towards the end of the century, while a dramatic decline is expected in central and inner sub-regions. In these sub-regions, predicted salinity drops below 5, creating lethal conditions for blue mussels by potentially decimating both farmed and natural populations. While salinity dominates carbon capture in shells at a regional scale, temperature and chlorophyll *a* have more localized effects. Our study emphasises the need for region-specific strategies in mussel farming to tailor farming practices with the aim to optimise the productivity of mussel farms, ensuring their viability and contribution to carbon capture.

The DEB model we developed is not just a scientific tool but a powerful resource that provides decision-makers and stakeholders with quantitative evidence to assess the carbon capture potential of farmed blue mussels and its dynamics across the Baltic Sea. The model can be modified and extended beyond the Baltic Sea region and blue mussels to measure the carbon capture potential in other bivalve species around the world, both in farmed or natural populations. Understanding and estimating the carbon storage capacity of bivalve-dominated biogenic

systems under varying environmental conditions is crucial for evaluating their functioning and the condition of the ecosystem services they provide. This information is essential for designing and optimizing area-based conservation and restoration measures in bivalve-dominated marine habitats. Additionally, the tool supports developing mitigation measures that rely upon the biological activities of marine calcifying organisms.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.174613>.

### CRedit authorship contribution statement

**Annaleena Vaher:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Jonne Kotta:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Brecht Stechele:** Writing – review & editing, Writing – original draft, Validation, Methodology, Formal analysis, Data curation. **Ants Kaasik:** Writing – original draft, Formal analysis. **Kristjan Herkül:** Validation, Investigation. **Francisco R. Barboza:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Conceptualization.

### 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.

### Data availability

Data will be made available on request.

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