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Modelling spatial variability of cultivated *Saccharina latissima* in a Dutch coastal bay shows benefits of co-cultivation with shellfish

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Cultivation of *Saccharina latissima*, a brown macroalga, is fast developing in Europe and North America for the sustainable production of food and biorefinery materials and important ecosystem services. Prior studies have demonstrated large spatial variability in the yield and chemical composition of the cultivated *S. latissima*, even within a small coastal bay. Using a validated hydrodynamic-biogeochemical-kelp model, this study examined main drivers of the spatial variability in *S. latissima* growth dynamics in 40 hypothetical farms throughout a Dutch coastal bay, the Eastern Scheldt. Results indicate that temperature plays a primary role in driving the spatial variability. For example, *S. latissima* yield in the deeper and better flushed western part is more than double that in the eastern part, mainly due to its 2–3°C warmer seawater in winter. It is also found that *S. latissima* benefits from co-cultivation with shellfish, since nutrients excreted by shellfish replenish its nitrogen reserve, which fuels a relatively high growth rate in the nitrogen-depleted late spring. The model assessment offers insight into optimal potential locations of *S. latissima* farms in the Eastern Scheldt. Applicability of our modelling approach to other coastal ecosystems and possible further improvements for assisting in seaweed farming practice are discussed.

Keywords: dissolved inorganic nitrogen, Eastern Scheldt, farm-site selection, hydrodynamic-biogeochemical-kelp model, seaweed–shellfish co-cultivation, temperature.

Introduction

Seaweed cultivation is among the fastest expanding components in global aquaculture, especially in European and American countries (Venolia *et al.*, 2020; Monteiro *et al.*, 2021). The cultivated macroalgae provide sustainable food, feed, biofuel, and various biochemical byproducts (e.g. cosmetics, pharmaceuticals) while causing limited negative environmental disturbances (Sharma *et al.*, 2018; van der Molen *et al.*, 2018; Visch *et al.*, 2020b). Additionally, coastal farmed seaweed is capable of extracting excessive anthropogenic carbon and nutrients, stimulating biodiversity, and protecting shorelines (Froehlich *et al.*, 2019; Jiang *et al.*, 2020b; Zhu *et al.*, 2021b). Given these product values and ecosystem services (Hasselström *et al.*, 2018), the European Union considers seaweed farming as a “green” solution for protein supplies and mitigation of the greenhouse effect (Christensen, 2020).

Sugar kelp (*Saccharina latissima*), which has been farmed in European coastal countries ranging from Norway to Portugal, is one of the most commonly cultivated and commercially important seaweed species in Europe (Monteiro *et al.*, 2021; Wang *et al.*, 2022). In the emerging efforts of farming *S. latissima*, large spatial variability in its yield and chemical composition has been found within and among ecosystems. The potential production of *S. latissima* along the Norwegian

coast depends substantially on latitude and distance from the coast (Broch *et al.*, 2019; Forbord *et al.*, 2020). In the relatively homogeneous Danish estuary Limfjorden, yields of the cultivated *S. latissima* vary spatially by a factor of 10, and the pigment and metal contents by a factor of 2–5 (Bruhn *et al.*, 2016). Even over the spatial scale of metres to kilometres along the Swedish west coast, the *S. latissima* growth rate, tissue composition, and biofouling coverage differ significantly (Visch *et al.*, 2020b). The highly site-specific and location-dependent growth dynamics, chemical contents, and bioremediation capacity of *S. latissima* (Grebe *et al.*, 2021) make pilot spatial assessments a crucial step in planning commercially viable and environmentally friendly seaweed farming locations (Zollmann *et al.*, 2021).

Diverse environmental conditions, including temperature (Bolton and Lüning, 1982), light regime (de Jong *et al.*, 2021), nutrient concentrations (Chapman *et al.*, 1978), salinity (Nielsen *et al.*, 2016), and hydrodynamic conditions (Visch *et al.*, 2020c), largely account for the aforementioned spatial variability in its production (Kerrison *et al.*, 2015). Growth and chemical composition of the farmed seaweed are influenced by all these environmental factors. While detecting the dominant factors is key to interpret the *S. latissima* growth dynamics, the dominant environmental factors vary at

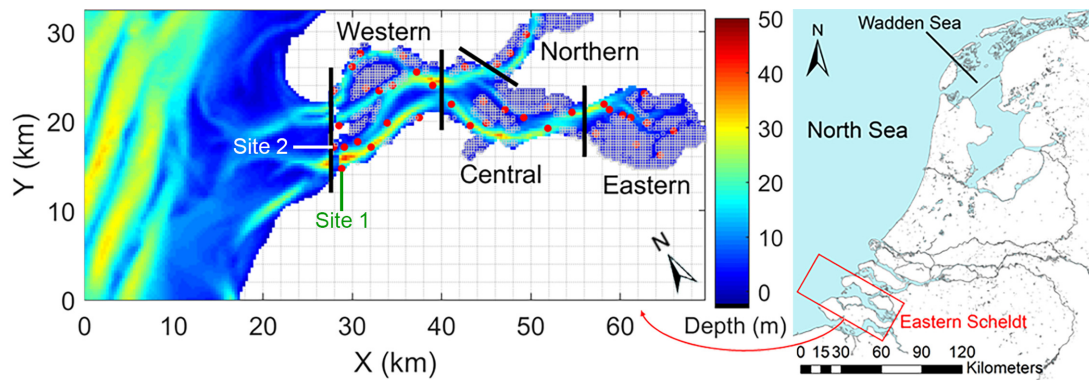


Figure 1. The location of the Eastern Scheldt (the right panel) and the model domain (the left panel). The Eastern Scheldt is divided into four (western, central, northern, and eastern) compartments according to previous studies (e.g. Wetsteyn and Kromkamp, 1994; Jiang *et al.*, 2019b), as separated by black lines. The shaded area and red dots in the left panel denote the surveyed areas of wild and cultured shellfish and the randomly distributed seaweed farms in the hypothetical numerical scenario, respectively. Sites 1 and 2 in the left panel indicate two commercial farms that provide field samples for this study.

different geographic locations and even within a small coastal bay (Grebe *et al.*, 2021). For instance, *S. latissima* grows faster at exposed versus sheltered locations in a Spanish coastal bay due to improved light conditions (Peteiro and Freire, 2013), while a much higher growth rate and lower biofouling coverage are found at sheltered locations compared to exposed locations along the Swedish west coast (Visch *et al.*, 2020c). Moreover, the environmental factor limiting *S. latissima* growth changes over the seasonal cycle (Black, 1950; Sjøtun, 1993; Gevaert *et al.*, 2001; Nielsen *et al.*, 2014), which makes it even more complicated to unravel the spatial variability and select optimal sites in the culture planning phase.

In an integrated multi-trophic aquaculture (IMTA) system, *S. latissima* is often cultured along with salmon, trout, and other fish species and used for sequestering inorganic nitrogen produced in fish farms (Sanderson *et al.*, 2012; Broch *et al.*, 2013; Handå *et al.*, 2013; Reid *et al.*, 2013; Marinho *et al.*, 2015), as well as increasing its own production and nitrogen content (Fossberg *et al.*, 2018). Compared to co-cultivation of fed (i.e. finfish) and extractive (e.g. seaweed) species, cultivating *S. latissima* with another extractive species, i.e. shellfish, has been less examined and conducted commercially (Visch *et al.*, 2020a). Recently, Hargrave *et al.* (2022) revealed that *S. latissima* grown in proximity to blue mussel (*Mytilus edulis*) farms increases yield and pigment concentrations in the Swedish coastal waters. *S. latissima* is also capable of mitigating acidification in coastal waters and thus favouring growth of co-cultivated bivalves in lab experiments and an American oyster farm (Young *et al.*, 2022). Yet, the interplay of these two self-supporting species and the consequent spatial variability in yield and composition of cultivated *S. latissima* remain to be addressed.

In our previous work, we used numerical models to assess the ecological and production carrying capacities of *S. latissima* cultivation in the Eastern Scheldt, a Dutch tidal bay where *S. latissima* farming is recently initiated (Jiang *et al.*, 2022). Here, we present another pilot study, aiming to investigate the intra-bay variations of cultivated *S. latissima* growth and chemical contents in order to facilitate site selection for large-scale (commercial) farming activities. The Eastern Scheldt, renowned for mussel and oyster culture for decades, serves appropriately as a prototype for studying the influence of co-cultivation with shellfish on the farmed

S. latissima. Given the prevalence of spatial variability in cultured and wild seaweed in estuaries and coastal bays (van Tussenbroek, 1989; Stephens and Hepburn, 2014; Zollmann *et al.*, 2021; Wang *et al.*, 2022), our modelling study considering both abiotic and biotic influences offers interesting insights into drivers of the spatial variability. As an essential supplement to cultivation trials in the field, the modelling approach in this study can potentially assist ecosystem managers in optimized planning of seaweed cultivation, especially involving co-cultivation activities.

Methods

The study area

The 350-km² Eastern Scheldt is located in the southwest Netherlands, adjacent to the North Sea (Figure 1). Due to the Delta Works, a coastal engineering project in the Dutch Southwest Delta in the 1980s, it has been largely isolated from freshwater input and transformed from an estuary into a tidal bay (Nienhuis and Smaal, 1994). The Eastern Scheldt is typically divided into four compartments, i.e. the western, central, northern, and eastern, with increasing shallowness and areas of tidal flats, as well as weakening influences of the North Sea (Wetsteyn and Kromkamp, 1994). The average depth of the four compartments is 10.9, 9.1, 7.0, and 4.3 m, and their residence time is 52, 88, 106, and 112 d, respectively (Jiang *et al.*, 2019a). Tidal flats, accounting for nearly one-third of the basin, are home to large populations of wild shellfish, e.g. the burrowing bivalve cockles (*Cerastoderma edule*) and the attached Pacific oysters (*Magallana gigas*). In addition, extensive areas of the Eastern Scheldt are used for culturing blue mussels (*Mytilus edulis*), mainly in the western and central bay, and Pacific oysters, mainly in the eastern bay (Table 1). These species account for >90% of the surveyed shellfish biomass in the Eastern Scheldt (Jiang *et al.*, 2019a). As a result of shallowness and large shellfish stocks, clearance time, defined as the time for shellfish to filter the entire water column, is shortest (~4 d) in the eastern compartment, followed by the northern (9 d), central (19 d), and western (39 d) compartments (Jiang *et al.*, 2019a). Because of the seaward increasing water exchange with the North Sea, landward increasing filtration capacity by cultured bivalves, and their

Table 1. The surveyed bivalve biomass (kilotons fresh weight) in the Eastern Scheldt in 2009 (Source: Wageningen Marine Research).

Species	Eastern	Central	Western	Northern
Cockles (<i>Cerastoderma edule</i>)	4.62	13.64	13.97	8.41
Blue mussels (<i>Mytilus edulis</i> , wild)	0.22	0.00	0.00	0.23
Blue mussels (<i>M. edulis</i> , cultured)	0.00	11.23	18.89	2.98
Pacific oysters (<i>Magallana gigas</i> , wild)	13.89	9.97	8.66	10.67
Pacific oysters (<i>M. gigas</i> , cultured)	6.71	0.00	0.00	0.00
Baltic clams (<i>Limecola balthica</i>)	0.03	0.07	0.16	0.02
Manila clams (<i>Venerupis philippinarum</i>)	0.30	0.00	0.00	0.00
Razor clams (<i>Ensis leei</i>)	0.22	0.05	8.14	0.91
Soft-shell clams (<i>Mya arenaria</i>)	0.01	0.01	0.01	0.01

combined effects, salinity, turbidity, particulate organic matter, and phytoplankton biomass decrease from the western opening to the eastern and northern ends in the Eastern Scheldt (Ysebaert *et al.*, 2016; Jiang *et al.*, 2019b, 2020a).

S. latissima pilot farms have only been initiated in the western bay (Figure 1) since the early 2010s. Given the strong impacts of anthropogenic activities in this basin, the suitability of other parts of the bay for cultivation needs to be assessed. Also, the compatibility with the existing shellfish industry remains to be examined before the commercial scale-up of *S. latissima* cultivation.

Field data

During the growth season 2019–2020, *S. latissima* was collected from the surface water (0.5–1 m) at two existing farming sites in the Eastern Scheldt (Site 1, Jacoba Harbor; Site 2, Neeltje Jans, Figure 1) to monitor the frond area, dry weight, and carbon and nitrogen contents. A total of 30 individuals each time were sampled at Site 1 on 19 February 2020, 2 April 2020, 30 April 2020, and 9 June 2020. Site 2 was also sampled four times on 19 March 2020, 15 April 2020, 7 May 2020, and 26 May 2020 with the sample size of 36, 46, 49, and 48, respectively. These data are used to compare with the model. The sampling and measurement approaches are presented in detail by Jiang *et al.* (2022) and are not repeated here. Note that *S. latissima* was co-cultivated with blue mussels at Site 2.

The numerical model

A hydrodynamic-biogeochemical-kelp model was developed for the Eastern Scheldt and part of the adjacent North Sea to simulate the environmental factors and *S. latissima* growth (Jiang *et al.*, 2022). Tidal elevation, current velocity, temperature, salinity, and other physical variables were solved in the General Estuarine Transport Model (GETM, open-access at <https://getm.eu/>). Dissolved inorganic nitrogen (DIN), detritus, biomass of phytoplankton, zooplankton, and shellfish were modelled by a nutrient-phytoplankton-zooplankton-detritus (NPZD) setup built within the Framework for Aquatic Biogeochemical Models (FABM, available at <https://github.com/fabm-model/fabm>).

The shellfish distribution, density, and filtration capacity were surveyed by Wageningen Marine Research (Table 1 and https://shiny.wur.nl/Schelpdiermonitor_Delta) and imbedded into the model. Bottom cultivation is the dominant form of bivalve aquaculture in the bay, and collection and cultivation of spat is performed in different seasons (deploying spat collectors in summer and collecting them between October and November, Kamermans *et al.*, 2002; van den Brink *et al.*, 2020) from seaweed culture and therefore not included in the model. The presence/absence of shellfish in a grid cell does not change during the simulation. With shellfish grazing plankton and excreting inorganic nitrogen into the water column, nitrogen is looped in the pelagic-benthic coupled system (Figure 2). Driven by realistic boundary conditions and atmospheric forcing, the GETM-FABM setup reached a good agreement with observational data and captured the landward increasing flushing time and seaward increasing salinity and phytoplankton biomass (Jiang *et al.*, 2019a, 2020a). Further detailed description and validation of the hydrodynamic-biogeochemical model are presented in these two earlier papers.

A kelp model adapted from Broch and Slagstad (2012) was implemented in FABM (Figure 2) to simulate the structural growth and chemical contents of cultivated *S. latissima* during an annual cycle. The individual structural carbon, reserve carbon, and reserve nitrogen are calculated as state variables (in mmol ind^{-1}) in the kelp model, sources, and sinks of which are dependent on environmental factors calculated in GETM-FABM. Governing equations, variables, and parameters are presented by Jiang *et al.* (2022), and here we review the three key processes (i.e. the structural growth, photosynthesis, and DIN uptake) that are directly influenced by the environment and contribute to the spatial variability of *S. latissima* growth.

Growth of the *S. latissima* structural biomass in each time step ($\text{mmol C ind}^{-1} \text{d}^{-1}$) equals the structural biomass (mmol C ind^{-1}) multiplied by a growth rate (μ , d^{-1}). μ [Equation (1)] is a function of the maximum growth rate ($\mu_{\max} = 0.18 \text{ d}^{-1}$), frond size [$f(A)$], daylength [$f(DL)$], temperature [$f_g(T)$], salinity [$f(S)$], and amount of reserve carbon and nitrogen [$f(Q)$].

$$\mu = \mu_{\max} \cdot f(A) \cdot f(DL) \cdot f_g(T) \cdot f(S) \cdot f(Q). \quad (1)$$

In Equation (1), the *S. latissima* growth rate is maximal for smaller plants and slows down when the frond area exceeds 100 cm^2 (Figure 3a) (Broch and Slagstad, 2012). Part of the *S. latissima* seasonal growth variations are associated with photoperiodic effects, which is quantified by daylength (Broch and Slagstad, 2012). Daylength is determined by latitude, and the favourable daylength for *S. latissima* growth is between the winter and summer solstice (Figure 3b). The optimal temperature for *S. latissima* growth is between 10°C and 15°C , and growth stops at $<-2.5^\circ\text{C}$ or $>19^\circ\text{C}$ (Figure 3c) (Broch and Slagstad, 2012). *S. latissima* growth is not stressed in seawater with salinity $>25^\circ\text{C}$ (Figure 3d) (Broch *et al.*, 2019). $f(Q)$, ranging from 0 to 1, quantifies the relative amount of carbon and nitrogen reserves, which is mainly supplied by photosynthesis and DIN uptake. If the nitrogen (carbon) reserve is in relative shortage, $f(Q)$ is calculated based on the ratio of the reserved nitrogen (carbon) to the structural biomass (see details in Jiang *et al.*, 2022).

Photosynthesis is a complex function of temperature and light, i.e. photosynthetically active radiation (PAR). The effects of temperature on the maximal photosynthetic rate follows the Arrhenius law with an optimal temperature of

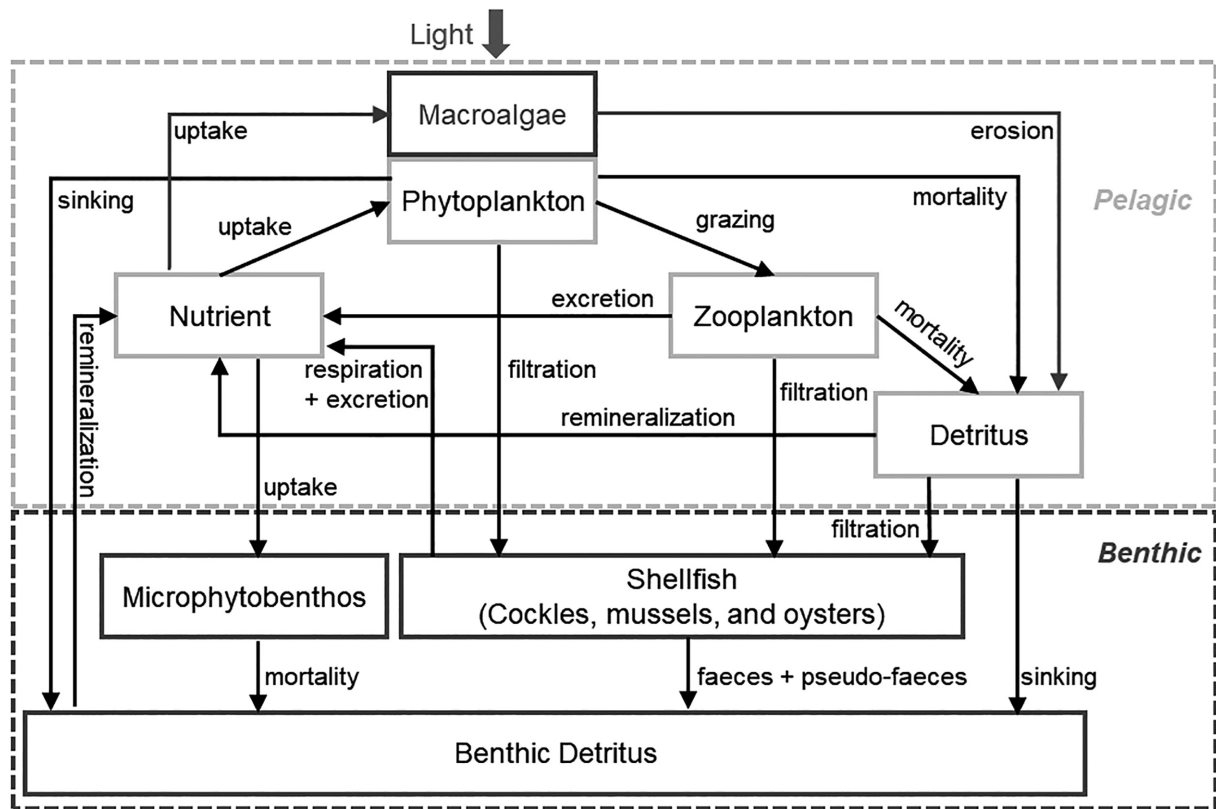


Figure 2. Conceptual diagram of the biogeochemical-kelp model. Boxes and arrows denote state variables and fluxes of nitrogen, respectively.

15°C (Figure 3e). The response of the photosynthetic rate to PAR relies on the saturation PAR ($PAR_{sat} = 200 \mu E m^{-2} s^{-1}$) and temperature-dependent photoinhibition parameter β (Figure 3f). Broch and Slagstad (2012) show the formulations describing the interactive roles of temperature and PAR in regulating the photosynthetic rate.

$$r = r_{max} \cdot f(DIN) \cdot f(U) \cdot f(q). \quad (2)$$

The *S. latissima* DIN uptake rate (r , mol N mol structural $C^{-1} d^{-1}$, Equation 2) depends on the maximum uptake rate ($r_{max} = 0.5$ mol N mol structural $C^{-1} d^{-1}$), DIN concentration in the water column [$f(DIN)$], ambient current velocity [$f(U)$], and saturation of the internal nitrogen reserve [$f(q)$]. $f(DIN)$ follows the Michaelis-Menten relationship with a half-saturation DIN concentration of 4 mmol m^{-3} (Figure 3g) (Broch and Slagstad, 2012). The DIN uptake rate increases with current velocity (Figure 3h), and a weak flow ($<0.1 m s^{-1}$) limits the *S. latissima* nitrogen absorption (Broch and Slagstad, 2012). The lower and upper limit of the *S. latissima* nitrogen reserve in our model is 0.0053 mol N mol structural C^{-1} and 0.0092 mol N mol structural C^{-1} , respectively.

In order to explore the spatial variability of cultivated *S. latissima* in the Eastern Scheldt, a total of 40 modelled farms were distributed nearly evenly in $\sim 1\%$ of the domain (Figure 1). Note that locations of these farms are randomly designed without considering other use of the basin (e.g. waterway, windfarms, and recreational sites). Each farm covers a grid cell (300 m \times 300 m), in which the *S. latissima* individuals were placed in the upper 3 m of the water column. The density of farmed *S. latissima* at Site 1, ~ 71 individuals m^{-2} , is applied in the model. The model was run over an annual cycle of cultured *S. latissima*, i.e. outplanting in November 2009

and harvest in June 2010. Of the total 40 modelled farms, 17, 10, 10, and 3 are located in the western, central, eastern, and northern compartments, respectively (Table 2). Fourteen seaweed farms sharing the same grid cell with benthic shellfish are named “co-cultivation farms” hereafter. In this model scenario, the cultivated *S. latissima* populations exert a $<3\%$ reduction in the phytoplankton stock or shellfish production (Jiang *et al.*, 2022). On the other hand, how shellfish and other environmental factors (e.g. temperature, DIN, irradiance) affect the cultivated *S. latissima* and shape its spatial variability are examined.

Results

Spatial variations of environmental factors in the Eastern Scheldt

As a consequence of the relatively intensive tidal exchange with the North Sea and large water depth, seawater around *S. latissima* farms in the western compartment is warmer in winter and cooler in summer compared to other modelled sites of the Eastern Scheldt (Figure 4a). In contrast, the seasonal temperature range is the greatest in the eastern section (Figure 4a). The difference in temperature across the bay can reach as much as 3°C in winter (Figure 4a).

PAR over *S. latissima* farms is low and nearly homogeneous in winter but shows spatial variations since March, when phytoplankton start to accumulate (Figure 4b). The landward decrease in spring chlorophyll *a* (chl *a*) concentrations, which is induced by enhanced bivalve grazing in the northern and eastern compartments and tidal import of microalgal biomass from the North Sea (Jiang *et al.*, 2020a), mainly accounts for the landward increase in light penetration (Figure 4b).

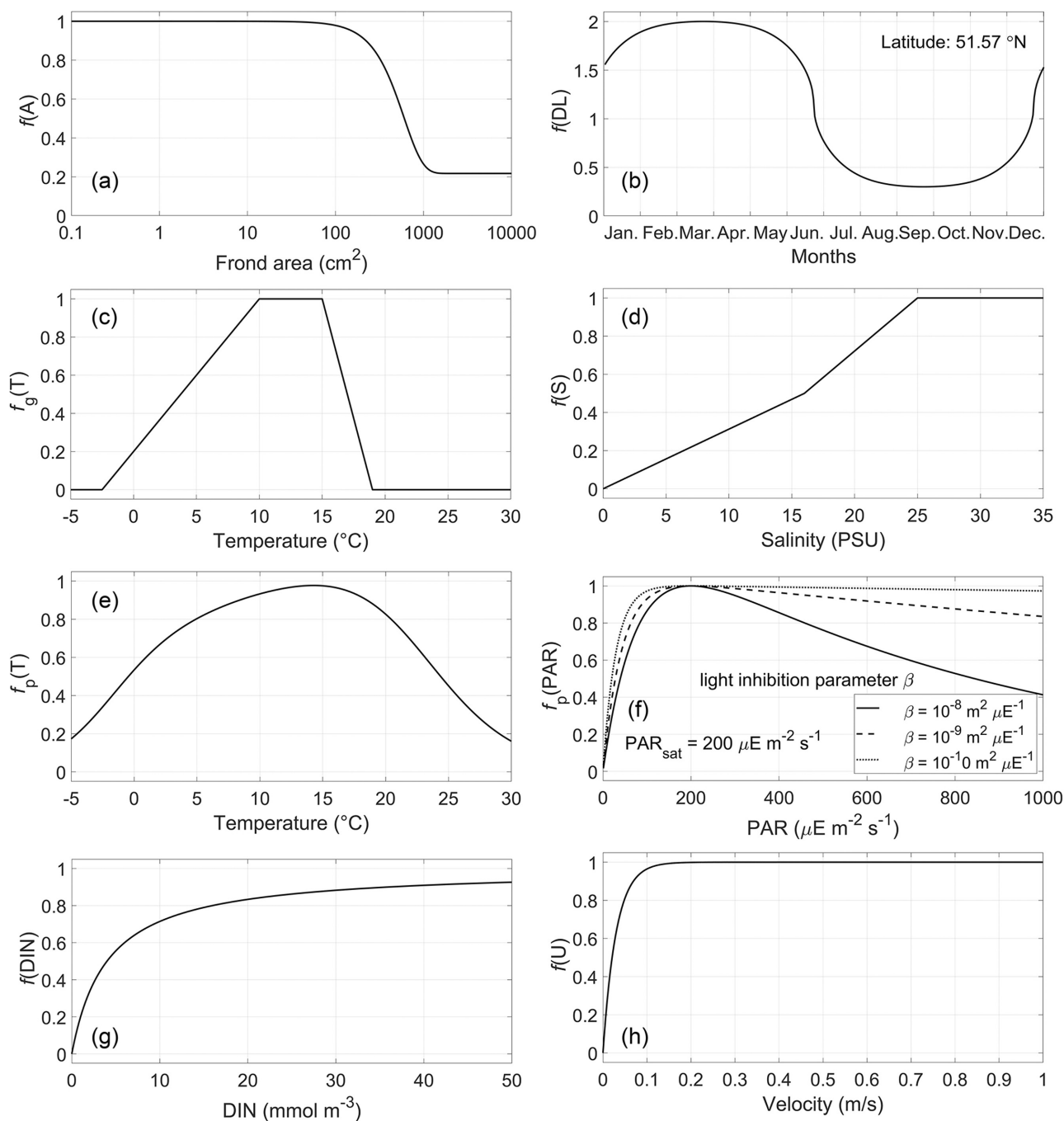


Figure 3. Quantitative growth responses of the modelled *S. latissima* to various environmental factors: effects of (a) the frond area, (b) daylength, (c) temperature, and (d) salinity on the growth rate; effects of (e) temperature and (f) PAR (photosynthetically active radiation) on the photosynthetic rate; effects of (g) DIN concentrations and (h) current velocity on the DIN uptake rate. The subscripts *g* and *t* in panels c and e and f represent growth and photosynthesis, respectively. Note that y-axes in all panels are dimensionless scale parameters instead of real physiological rates.

In addition to 15-d fluctuations driven by the spring-neap tidal cycle, DIN accumulates in winter, is consumed in spring, and stays low in summer (Figure 4c). DIN concentrations reduce from the North Sea landwards into the Eastern Scheldt, as indicated by a gradient between the western and eastern farms (Figure 4c). The DIN concentration around northern *S. latissima* farms is higher than in other regions (Figure 4c), because all three farms in the northern compartment are located at or near shellfish farms/habitats (Figure 1), which regenerate nitrogen into the water column.

Since, the Eastern Scheldt ranges only 0.3 latitude (51.4°N–51.7°N), the across-bay difference in daylength is negligible. Subject to the North Sea influence, salinity maximizes in the western compartment and decreases landwards. However, salinity in the Eastern Scheldt is hardly <28 throughout the year (Jiang *et al.*, 2019a) and does not restrict the *S. latissima* growth (Figure 3d). Current velocity in the mesotidal Eastern Scheldt is <0.1 m s⁻¹ for only shorter than 5% of a tidal cycle (Jiang *et al.*, 2019a), which barely affects the daily *S. latissima* DIN uptake (Figure 3h). Thus, these three factors (daylength,

Table 2. Information of modelled *S. latissima* farms (see the locations in Figure 1) in this study.

Compartments	Number of farms	Overlapping with wild or cultured shellfish (co-cultivation)	Average water depth (m)
Western	13	No	12.2
	4	Yes	7.0
Central	6	No	15.4
	4	Yes	3.4
Eastern	6	No	8.8
	4	Yes	3.0
Northern	1	No	10.9
	2	Yes	4.4
Total	26	No	12.1
	14	Yes	4.5

salinity, and current velocity) are not discussed further in the study. It needs to be mentioned that the modelled temperature, salinity, tidal currents, chl *a*, and DIN presented above have been validated by field observations, as discussed in previous papers (Jiang *et al.*, 2019a, 2020a).

Spatial variations of cultivated *S. latissima* in the Eastern Scheldt

Due to the environmental effects, specifically temperature, PAR and DIN variations, the growth and production of cultivated *S. latissima* vary substantially in different areas. The frond area, an indicator of structural mass, and the dry weight, which includes the structural and reserve biomass, exhibit similar spatial patterns, that is, highest (lowest) in the western (eastern) compartment (Figures 5a and b). *S. latissima* cultivated in the western compartment can be more than twice as large and heavy as that in the eastern compartment in June (Table 3). *S. latissima* farmed in the central compartment is second highest with respect to the frond area and dry weight until April when it is surpassed by that in the northern compartment (Figures 5a and b). The spatial variation in biomass yield can be explained by the growth rate (Figure 5c).

During winter (from December to February), the growth rate varies by a factor of two in different regions of the Eastern Scheldt (Figure 5c). The main driver is neither PAR, low but similar all over the bay (Figure 4b), nor DIN, which is abundant (>20 mmol m^{-3} , Figure 4c) and does not limit the nitrogen assimilation (Figure 3g). The low (-2 – $4^{\circ}C$) but spatially variable temperature (Figure 4a) limits the growth rate to no more than half of its optimal value (Figure 3c) and is primarily responsible for the difference in growth (Figure 5c). In winter, the nitrogen reserve is at the maximum of the year (full), and the *S. latissima* nitrogen content does not follow the spatial pattern of DIN concentrations in seawater (i.e. northern $>$ western $>$ central $>$ eastern, Figure 4c), but rather that of the growth rate and structural biomass (i.e. western $>$ central $>$ northern $>$ eastern, Figures 5e). Spatial variations of the *S. latissima* carbon content is opposite to nitrogen (Figure 5d).

The second period of large spatial variations in the *S. latissima* growth rate starts in late March, which is characterized by the successive decrease in the growth rate in the western, central, northern, and eastern compartments (Figure 5c). The sharp deceleration in growth does not result from tempera-

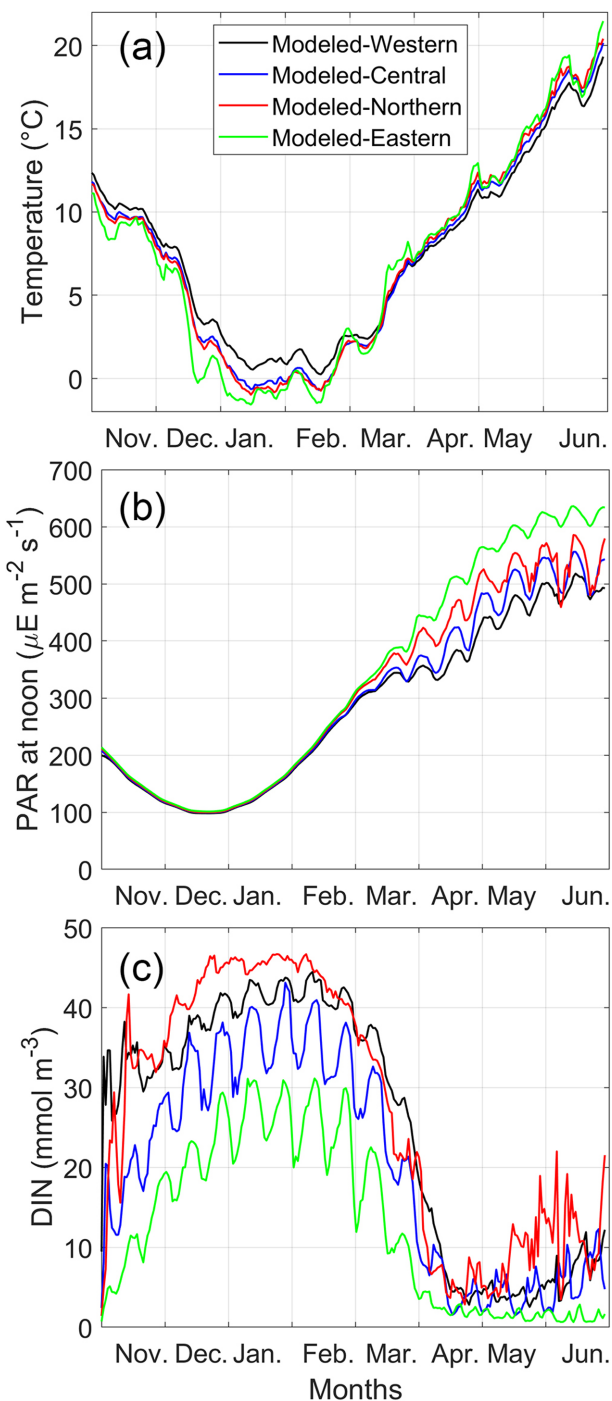


Figure 4. The modelled average (a) water temperature, (b) PAR (photosynthetically active radiation), and (c) DIN concentrations at 2 m from the surface, where *S. latissima* grows, in four compartments of the Eastern Scheldt. See Table 2 and Figure 1 for information of *S. latissima* farms.

ture, PAR, or DIN. Temperature increases towards the optimal range for growth (10 – $15^{\circ}C$) in this period (Figures 3c and 4a). PAR in the meantime is above the saturation value (200 $\mu E m^{-2} s^{-1}$) and increasing (Figures 3f and 4b). DIN (e.g. in the western compartment) is still abundant when the growth rate reduces in late March (Figures 3g and 4c). It turns out that the reduced growth rate is a consequence of increased frond size, which is of considerable magnitude particularly when

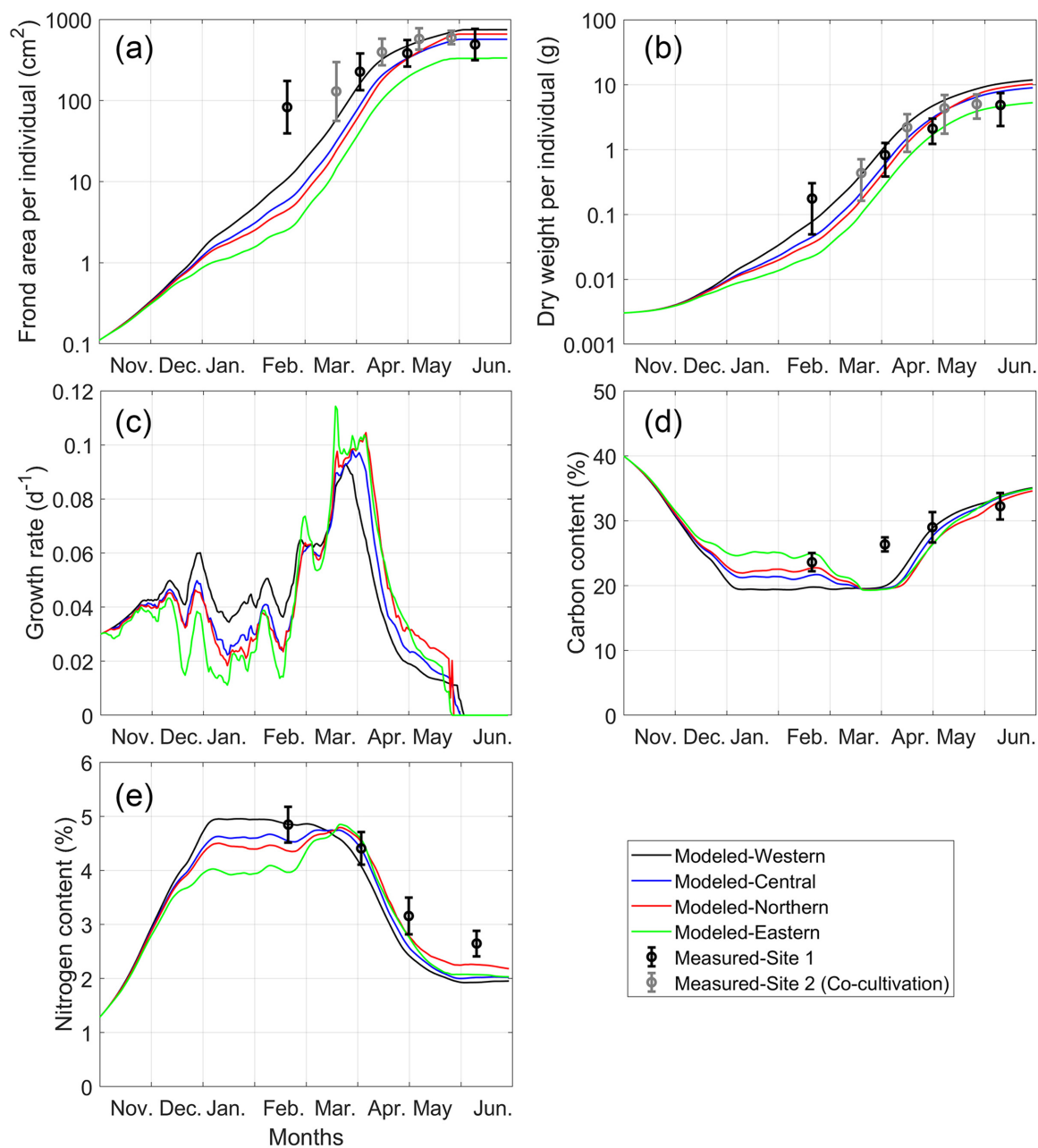


Figure 5. The modelled average (a) frond area, (b) dry weight, (c) growth rate, (d) carbon content, and (e) nitrogen contents of the cultivated *S. latissima* farms in four compartments of the Eastern Scheldt. The field data measured at two *S. latissima* farms are listed for comparison. See Table 2 and Figure 1 for information of modelled and realistic *S. latissima* farms. Note the y-axis of panels (a) and (b) uses the logarithmic scale.

Table 3. The modelled *S. latissima* frond area, dry weight, and carbon and nitrogen contents at harvest time (30 June 2010) in the Eastern Scheldt.

Compartment/Category	Number of farms	Frond area (cm ²)	Dry weight (g)	Carbon content (%)	Nitrogen content (%)
Western	17	747 ± 142	11.8 ± 2.2	35.0 ± 0.3	1.95 ± 0.13
Central	10	569 ± 161	8.9 ± 2.5	34.9 ± 0.2	2.02 ± 0.11
Eastern	10	334 ± 70	5.3 ± 1.5	34.9 ± 0.3	2.03 ± 0.08
Northern	3	659 ± 98	10.2 ± 1.1	34.6 ± 0.1	2.18 ± 0.03
Co-cultivation	26	678 ± 186	10.6 ± 2.9	34.7 ± 0.2	2.09 ± 0.06
Others	14	546 ± 212	8.7 ± 3.3	35.1 ± 0.3	1.96 ± 0.13

Data are shown as averages and standard deviations.

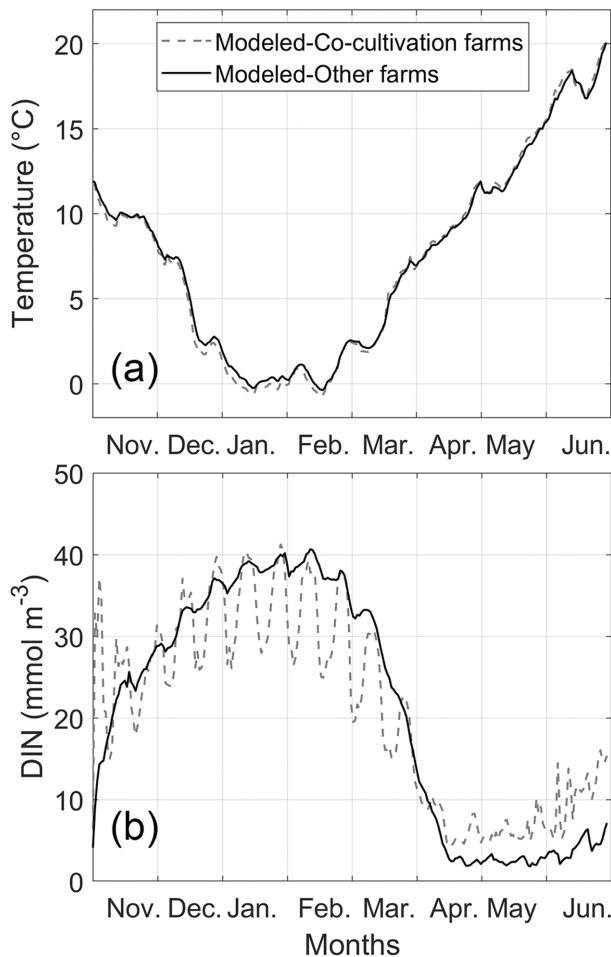


Figure 6. The modelled average (a) water temperature and (b) DIN concentrations at surface 2 m of co-cultivation versus other *S. latissima* farms. See Table 2 and Figure 1 for information of *S. latissima* farms and shellfish culture plots.

the frond size is $>100\text{ cm}^2$ (Figures 3a and 5a). In late April and May, with the diminished DIN in seawater (Figure 4c), *S. latissima* is consuming the reserved nitrogen for growth (Figure 5e). In the northern compartment, the *S. latissima* growth rate and nitrogen content are higher, when the rest of the bay is short of DIN (Figures 4c, 5c and e).

To summarize, temperature and DIN concentrations are key players driving spatial variations of *S. latissima* growth in the Eastern Scheldt. Warmer water in winter in the western compartment is favourable for increasing the *S. latissima* yield, and the higher regenerated DIN concentration in late spring in the northern compartment also boosts the kelp production.

Effects of shellfish on cultivated *S. latissima*

S. latissima farms with co-cultivated shellfish are mostly located in shallow waters with an average depth of 4.5 m (Table 2). Because of the shallowness, these co-cultivation farms are in waters that are $<1^\circ\text{C}$ colder than the others in winter (Figure 6a). The difference in temperature induces a lower *S. latissima* growth rate and nitrogen content in the co-cultivation farms in winter (Figure 7).

Given that a higher percentage of co-cultivation farms are located in the landward compartments (Figure 1 and Table 2), DIN concentrations at co-cultivation farms are

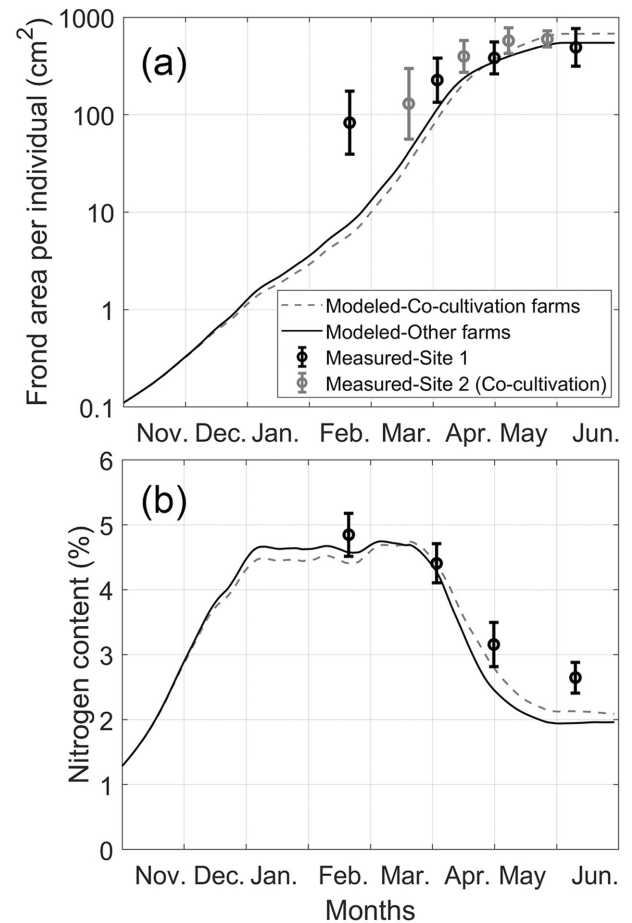


Figure 7. The modelled average (a) frond area and (b) nitrogen contents of the cultivated *S. latissima* in co-cultivation versus other farms. The field data measured at two *S. latissima* farms are listed for comparison. See Table 2 and Figure 1 for information of *S. latissima* farms and shellfish culture plots.

slightly lower in winter months (Figure 6b). During the nitrogen-limited season (mid-April to June), the DIN concentration at co-cultivation farms is always above the half-saturation concentration for uptake (4 mmol m^{-3} , Figure 3g) and approximately twice as much as that at the other farms (Figure 6b). The recycled DIN from these filter feeders enhances the DIN accumulation of the *S. latissima* cultivated near the water surface, which therefore catches up and eventually exceeds the individual production at farms without benthic shellfish (Figure 7b). At co-cultivation farms, the averaged *S. latissima* frond area at harvest in June is 24% higher, and dry weight 23% higher (Table 3). It is noteworthy that the measured *S. latissima* frond area and dry weight at the co-cultivation Site 2 are also higher than those at Site 1, especially in April and May (Figures 5a and b).

Discussion

The optimal locations for *S. latissima* farms in the Eastern Scheldt

Over the 8-month cultivation season, significant spatial variations of the *S. latissima* growth and carbon and nitrogen contents occur in two periods. In winter months, seaward increasing temperature results in increasing growth rates. Until

nitrogen depletion, the western compartment thus appears an ideal region for implementing *S. latissima* farms, owing to the mild water temperature and tide-induced DIN import from the North Sea. When nitrogen is mostly depleted in late spring, DIN regenerated from benthic shellfish populations sustains a relatively high growth rate and nitrogen reserve for *S. latissima* in ambient surface water. If all 40 *S. latissima* farms in this study were located at co-cultivation sites, the total yield in dry weight could potentially increase by 320 t, creating extra revenue of ~10 million euros referring to the seaweed price of van den Burg *et al.* (2021). These two factors (temperature and DIN) suggest that a strategy for maximizing the *S. latissima* yield and nitrogen content would be deploying the cultivation lines initially in the western compartment and transplanting them near shellfish farms or beds. This of course does not consider the translocation cost and space availability.

Spatial variations of temperature and DIN availability contribute most to variations of *S. latissima* production in the Eastern Scheldt. Temperature plays a regulatory role in seaweed biomass accumulation, photosynthesis, and all enzymatic reactions, and the optimal temperature for *S. latissima* is 10–15°C (Bolton and Lüning, 1982). While most prior studies focus on the stress of elevated temperature on the cold-water species *S. latissima*, including tissue deterioration, reduced pigment concentrations, increased biofouling, etc. (Andersen *et al.*, 2013; Bruhn *et al.*, 2016; Diehl *et al.*, 2021; Wang *et al.*, 2022), our results highlight that the low winter temperature in shallow waters can substantially diminish the growth rate. Nitrogen availability, another main limiting factor of *S. latissima* production in our study, has been extensively considered to affect the seaweed growth rate and internal nitrogen content, particularly after the spring bloom in coastal systems (Chapman *et al.*, 1978; Wheeler and North, 1981; Ahn *et al.*, 1998; Jevne *et al.*, 2020).

In addition to temperature and DIN, other environmental factors either lack spatial variability in the Eastern Scheldt (e.g. PAR in winter, daylength) or are within the suitable range for the *S. latissima* growth (e.g. PAR in spring, salinity, current velocity). Considering these additional aspects, the dominant environmental factors affecting the *S. latissima* yield may differ in other systems. For instance, Broch *et al.* (2019), Forbord *et al.* (2020), and Wang *et al.* (2022) find that nutrient availability, temperature, salinity, and turbidity are jointly responsible for the different kelp productions, biofouling extents, and protein contents between inshore and offshore waters of Norway, as well as across latitudes. Light and nutrients are important in modulating the *S. latissima* growth dynamics in the Danish Aarhus Bay (Nielsen *et al.*, 2014) and Limfjorden (Bruhn *et al.*, 2016), while salinity may determine the contents of protein, fermentable carbohydrates, and pigments in *S. latissima* in inner Danish waters (Nielsen *et al.*, 2016).

Combined with our results, these studies demonstrate that detecting main drivers of spatial variability in cultivated *S. latissima* is a site-specific effort, and conclusions drawn from a coastal system cannot be easily transferred to another system. For example, in the Eastern Scheldt and the Spanish estuary Ría de Ares y Betanzos, the region exposed to the adjacent sea is more suitable for *S. latissima* cultivation (Peteiro and Freire, 2013), whereas *S. latissima* grows better in sheltered areas along the Swedish west coast (Visch *et al.*, 2020c). Behind these distinct findings are the differences in dominant

environmental drivers, as well as interactions of multiple environmental factors.

Co-cultivation of *S. latissima* and shellfish

Co-cultivation with shellfish adds extra dimensions to the spatial variability of *S. latissima*. The most significant effect of co-cultivation is increasing the concentration of inorganic nutrients in the water column, which maintains the relatively high growth rate of the cultivated *S. latissima* in nutrient-depleted late spring. The fact that bivalves are mostly populated in shallow waters or on tidal flats, as well as the strong tidal mixing in the Eastern Scheldt (Wetsteyn and Kromkamp, 1994; Jiang *et al.*, 2019a), facilitates the surface-bottom nutrient exchange. The co-cultivation *S. latissima* farms defined in this study are those within the same grid cell as shellfish, both wild and cultured. In part of the tidal cycle, the regenerated DIN is also accessible to other *S. latissima* farms within the tidal excursion distance (typically <5 km for tidal flats) of the shellfish bed. The amount of DIN supply to these farms is related to the distance to the shellfish beds, as similarly found in IMTA applications (e.g. Sanderson *et al.*, 2012; Fossberg *et al.*, 2018).

The benthic shellfish populations, as filter feeders, moreover contribute to the improved water clarity and light penetration, potentially also benefiting the cultivated *S. latissima in situ*. However, as the modelled seaweed is implemented in the light-abundant surface layer, the shellfish-induced improved light conditions are not a key player in accelerating the seaweed growth in our model. Additionally, due to its shallowness, the low winter temperature over shellfish beds, despite not a direct biotic factor, is a noteworthy disadvantage of the seaweed-shellfish co-cultivation.

The seaweed-shellfish interaction is critical when planning co-cultivation of these two extractive species that sequester anthropogenic nutrients from coastal waters. On one hand, shellfish mainly removes organic matter in the water column, and excretes inorganic nutrients fueling the seaweed production. Co-cultivation with shellfish enhances the benthic-pelagic coupling and nutrient cycling in coastal waters and increases the efficiency of seaweed to assimilate nutrients, as indicated by this study and Hargrave *et al.* (2022). Namely, our findings suggest bivalves have an overall positive effect on *S. latissima*. On the other hand, our previous work indicates that the cultivated *S. latissima*, as an introduced primary producer and competitor against phytoplankton, might reduce the phytoplankton biomass and thus shellfish yield in the Eastern Scheldt, if the seaweed culture exceeded its ecological carrying capacity (Jiang *et al.*, 2022). Therefore, although seaweed is not as competitive in nutrient assimilation as phytoplankton (Pedersen and Borum, 1996; Miller *et al.*, 2011), the *S. latissima* farming scale should be carefully planned to avoid the negative effects of seaweed on bivalves in the Eastern Scheldt. In other systems with much lower shellfish populations per basin volume (e.g. Jiang *et al.*, 2019a), our findings imply that the co-cultivation of *S. latissima* and shellfish may potentially increase the seaweed production, as well as improve the bioremediation capacity in eutrophic waters and nutrient utilization efficiency in oligotrophic waters.

Applicability and limitations of the modelling approach

The hydrodynamic-biogeochemical-kelp model is capable of capturing the seasonal variations of the environmental

conditions, *S. latissima* growth dynamics, and its carbon and nitrogen contents in the Eastern Scheldt, as revealed in our results and previous works (Jiang *et al.*, 2019a, 2020a, 2022). Spatial variability and site selection for seaweed cultivation, a fast-growing industry and likely solution for sustainable seafood production and bioremediation, rely on a comprehensive consideration of environmental influences (Kerrison *et al.*, 2015). The modelling approach presented in our study integrates the combined effects of multiple environmental factors, including abiotic (temperature, salinity, daylength, current velocity, nutrient concentrations, and light) and biotic (shellfish and phytoplankton), and offers a practical tool in addition to field cultivation trials for suggesting suitable seaweed mariculture sites. Besides assisting in carrying capacity estimates (Jiang *et al.*, 2022) and site selection (Broch *et al.*, 2019) in the planning phase of seaweed culture, our model has the possibility to underpin farming strategies during the culture season. For example, if forced with an operational weather forecast product (e.g. the Atmospheric Model high resolution 10-d forecast by the European Centre for Medium-Range Weather Forecasts), the coupled kelp model is able to predict the seawater temperature variations near *S. latissima* farms and recommend the harvest date to avoid the high-temperature stress, as suggested in our model (e.g. $>19^{\circ}\text{C}$, Figure 3c) and many empirical studies (e.g. Bolton and Lüning, 1982; Andersen *et al.*, 2013).

It is feasible to transfer our modelling application in the Eastern Scheldt to other coastal ecosystems in the world. The key elements in the transfer process are to collect sufficient field observational data of seaweed and environmental variables and to validate the model accordingly. Because of similar physiological processes, the mechanistic kelp model has general applicability to other macroalgal species with species-specific parameters, such as applications in *S. latissima* (Venolia *et al.*, 2020) and *Ulva fenestrata* (Lavaud *et al.*, 2020).

Like others, the model in our study is not perfect. The *S. latissima* simulation can be improved at least by including the interactive effects of several environmental factors, biofouling simulations, blade reorientation in response to hydrodynamic changes, and so on. Data from continuous field and lab studies (e.g. Boderskov *et al.*, 2016; Lubsch and Timmermans, 2019; Jevne *et al.*, 2020; de Jong *et al.*, 2021; Zhu *et al.*, 2021a, c) are necessary to potentially unravel these questions and improve the model. The bivalve–seaweed interaction is modelled on a spatial scale of one grid cell (300 m \times 300 m), and a refined model resolution will benefit resolving spatial variability with increased accuracy. Additionally, our model is nitrogen-based and does not consider phosphorus. If phosphorus limitation occurs in late spring, our model tends to underestimate the DIN concentration and overestimate the positive effects of shellfish excretion on *S. latissima* growth. Moreover, our findings suggest that translocation of the cultivated *S. latissima* to near shellfish farms in late spring would benefit the overall yield. When assessing such activities, incorporating economic (expense versus income; e.g. Timmermann *et al.*, 2014) and social (e.g. Grebe *et al.*, 2019) dimensions into the simulation would further benefit the industrial management.

Conclusion

This study examines the spatial variability of cultivated *S. latissima* in the Eastern Scheldt with a validated hydrodynamic-biogeochemical-kelp model. In a model

scenario, the hypothetical *S. latissima* farms are evenly placed in the basin. In one culture cycle (November to the next June), the individual frond area and dry weight of cultivated *S. latissima* vary substantially. The highest biomass yield, found in the better flushed western compartment, is more than double of that in the eastern compartment, which results mainly from the 2–3°C warmer winter temperature. Co-cultivation with shellfish can increase the *S. latissima* production significantly (by $>20\%$) and the nitrogen content slightly (by 0.1%), since shellfish accelerates the nutrient cycling through excretion. The shellfish-induced DIN replenishment plays a particularly important role in maintaining the growth rate during the nitrogen-depleted late spring. Therefore, our results support the idea of shellfish–seaweed co-cultivation in the Eastern Scheldt unless their carrying capacities are exceeded. If the labour/facility cost or space is not considered, the optimal culture practice would be growing *S. latissima* over winter in the western bay and transferring it close to shellfish farms or beds before nutrient drawdown in late spring.

Our study suggests that identification of the dominant environmental influences, abiotic and biotic, is key to elucidate the spatial variability of cultured seaweed. Our coupled kelp model, taking the combined effects of various environmental factors into account, is suitable for such research. The modelling approach is applicable to other coastal ecosystems with sufficient field data and model validation, and can provide increasingly useful assistance in aquaculture management with further development.

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