

Response letter to reviewer's comments - Kindeberg

Reviewer's comments in black and our response in light blue

Mohr et al. present modelling results of carbon uptake, burial and export in an intertidal seagrass system in a Wadden Sea bay. A seagrass growth model is coupled to a hydrodynamic model including particle tracking and covers four years of seagrass variability to estimate organic carbon burial rates within and outside the seagrass meadows. This combined approach encompassing advective transport, morphodynamics and C cycling provides a source-to-sink assessment of the fate of seagrass-derived organic carbon that is often lacking in the “blue carbon” literature. I commend the authors for this holistic perspective and appreciate their effort. However, I have a few concerns regarding confusing terminology, interpretation and conclusions that should be addressed and clarified before I can recommend this for publication.

Thank you very much for your thoughtful comments and suggestions which greatly helped improve our study. A point-to-point response to your comments is listed below.

First, while the major strength of this model is the holistic perspective on seagrass carbon cycling, encompassing both POC burial rates within the seagrass meadows and export to adjacent ecosystems, none of these processes seem to have been validated by field data. This makes the conclusions less robust, and the lack of in situ measurements should be explicitly addressed as a caveat in the discussion. This is especially important because of the two assumptions that all POC is recalcitrant (L149) and that all POC that enters the surface sediments are sequestered long-term.

- The missing observational data of POC burial rates in the meadows and export to adjacent ecosystems to validate our model is indeed a major caveat in our study. To our best knowledge, there is no such observation data available until now. We highlighted this need in the Discussion:
- L421 (track change version): *‘Especially since there are no observations from the study region for POC burial rates in seagrass meadows or the export of POC and detritus, the values from this study remain a model estimation to be further confirmed by field measurements.’*

Second, I believe there is a mismatch in time scale perspectives. The relevance of longterm storage of POC for climate regulation is acknowledged in the introduction, but the model encompasses only four years. Yet, the authors make claims about long term CO₂ sequestration without any field validation. This time scale discrepancy should be

addressed in the discussion and language referring to long-term sequestration should be toned down or better justified.

- Thank you for pointing this out. We reviewed the terminology related to carbon sequestration and modified the manuscript to make clear that our study focuses on the yearly burial rate of carbon in seagrass meadows and the interannual variations, and that any references to longer term carbon sequestration are estimates based on our yearly budgets.
- We especially added a clarification in the discussion: L359 (track changes version): *'The yearly carbon burial rate of $10.1 \pm 1.5 \text{ gC m}^{-2} \text{ yr}^{-1}$ inside seagrass meadows obtained in this study is lower than estimates of long-term sequestration rates for the seagrass in the German Wadden Sea by other studies, which give sequestration rates of $24 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Mengis et al., 2022) and $44.45 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Oppelt et al., 2024). There are however several limitations for a direct comparison, including a mismatch of timescales.'*

Second, the model estimates fairly low organic carbon burial rates in this system compared to global seagrass estimates, and the authors hypothesize that this could be due to strong hydrodynamics in the bay. While I do not doubt that carbon burial rates are low, I think the potential reasons could be further explored. Considering that an estimated 24% of all “carbon uptake” (I interpret this as being equivalent to the net CO_2 fixation by seagrass primary production) is buried according to the model, it does not seem that the low burial rates are due to low sedimentation rates but rather low productivity. The model estimates annual carbon uptake by the seagrass, and it would be relevant to compare this estimate rates to published rates, similar to what is done with carbon burial rates.

- Thank you for pointing this out. We compared the values of seagrass primary production in our model to that of other regions and indeed our primary production is quite low compared to observations for *Z. noltei* in the Netherlands and France (Vermaat et al (1987), Pérez-Lloréns and Niell (1993), Pérez (1989)). We have added this point to our discussion:
- L408 (track changes version): *'In addition to the hydrodynamic conditions, the seagrass primary production obtained by our model ($40 \text{ gC m}^{-2} \text{ yr}^{-1}$) is smaller than the primary production observed in *Z. noltei* meadows in the Netherlands and France ($115\text{-}184 \text{ gC m}^{-2} \text{ yr}^{-1}$, (Pérez, 1989; Pérez-Lloréns and Niell, 1993; Vermaat et al., 1987)). Since the primary production limits the biomass that is available for burial in the sediments, this might be another reason why the carbon burial is comparatively low.'*

Third, the study focuses on a small geographical area which provides a high spatiotemporal resolution. However, many critical terms in the model (e.g. $f_{exp,AG}$, $f_{exp,BG}$, h_{can} , $LossN$) are based on global and/or first-order estimates from other systems with unknown transferability to this intertidal system. This is to some extent addressed with the sensitivity analysis in Appendix A, but these uncertainties should be acknowledged in the Discussion and especially the uncertainties of the export terms deserve more attention.

- Thank you for emphasizing the importance of uncertainty assessment. In addition to existing assessments provided in the main text, we have added to section 5.4 to further discuss the uncertainty that comes from these terms.
- L421 (track changes version): *‘Especially since there are no observations from the study region for POC burial rates in seagrass meadows or the export of POC and detritus, the values from this study remain a model estimation to be further confirmed by field measurements.’*

Lastly, the terminology concerning seagrass carbon cycling includes several terms describing similar things which leads to confusion. The authors mix carbon “sequestration”, “burial”, “fixation”, “storage”, “stock”, “uptake” and “drawdown” throughout the manuscript, sometimes confusing the terms. For instance, section 4.2 uses “carbon burial rate” whereas section 5.2 discusses “carbon sequestration rates”. I recommend the authors to ensure that the same process is referred to with the same term and if necessary, explicitly define terms to avoid confusion.

- Thank you for pointing out the inconsistencies. We have made following changes throughout the manuscript to have a more concise and consistent use of terminology:
 - we now refer to all our results as ‘carbon burial rates’ instead of mixing the concept with sequestration;
 - we have removed ‘stock’, ‘uptake’ and ‘drawdown’ where they are not particularly referred to in cited publications

Please see my detailed comments below.

L35-43: Carbon storage and carbon sequestration are not the same thing and can be decoupled. Be explicit about what is referred to (e.g. stocks vs rates). For instance, Kennedy et al. 2022 assessed drivers of carbon stocks, not sequestration rates.

- Thank you for pointing this out. We have revised these descriptions (L36-40 in track-change version) to: *‘The subsequent carbon storage in the sediments depends on the seagrass species and meadow connectivity, as well as on environmental factors such as sediment properties and hydrodynamic conditions (Dahl et al., 2016;*

Johannessen, 2022; Röhr et al., 2018; Schaefer et al., 2024). Generally, larger seagrass species with persistent growth in high spatial density have higher carbon stocks than smaller, more sparse species (Kennedy et al., 2022).'

The terminology in the remaining paragraph is consistent with what is used in the cited papers.

L87-93: Is this correct? From Figure 1 there seems to have been a substantial decline in seagrass cover since 2010/2011, especially along the southern shores? Also, it is not clear what “core area” and “core position” mean. Is it where the meadow is continuous? Most dense? Most stable? A brief explanation of the terms would help the reader to follow.

- The seagrass cover plotted in Figure 1b is from observations by eyes, with uncertainties in the areas with lower shoot density / less dense coverage (<60%). To avoid confusion and clarify the term “core area”, we have modified L93 (track changes version) to:

‘The seagrass meadows are located in the upper intertidal, preferentially along the leeward side of the islands. In recent years, the core area of meadows (i.e. the area with coverage > 60%) remained relatively stable albeit with annual variations in the less dense (coverage between 20% and 60%) meadow area (Dolch et al., 2013).'

L110-111: Is all lost biomass assumed to be POC? No remineralization, grazing or DOC component included? For instance, on L95 you state that there is “massive grazing”, could this be quantified for the study area and incorporated into the growth model?

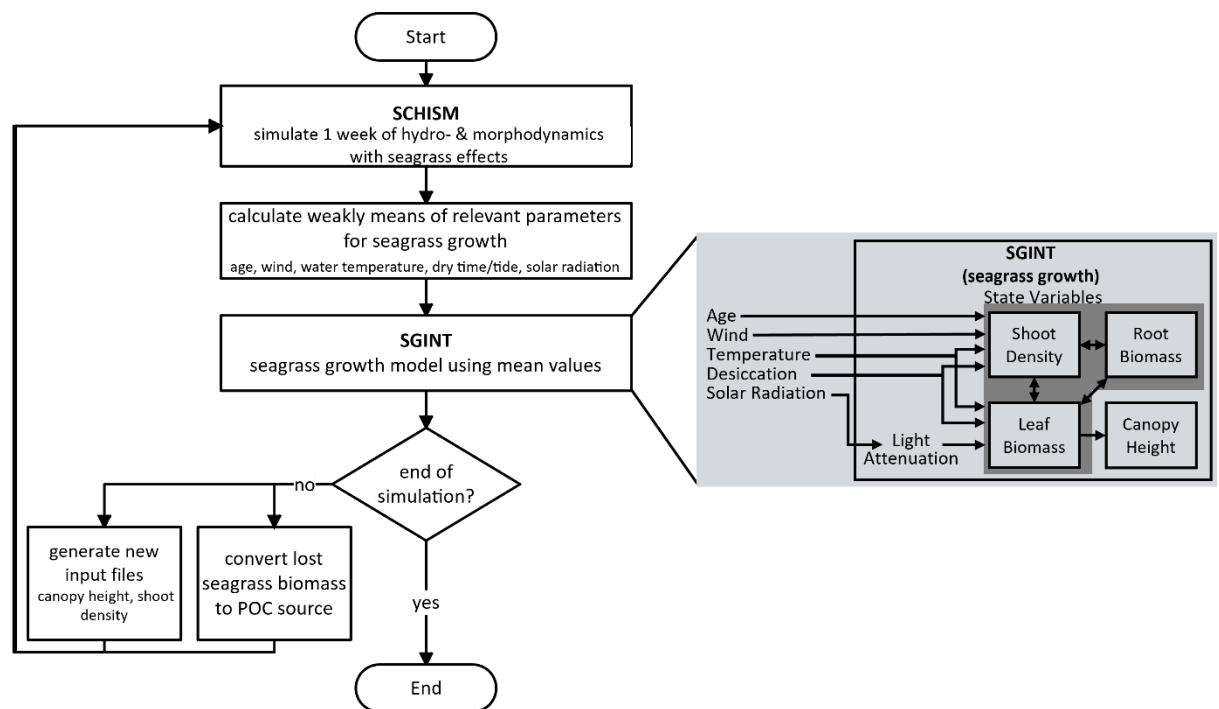
- We would like to clarify that not all lost biomass is transformed to POC. Only the fraction defined by the f_{exp} terms are transformed to POC. Detailed processes of remineralization, grazing and DOC are not explicitly modeled, but the remaining part of the biomass that is not transformed to POC or debris (25%) is considered to be a loss term representing the combined effects of remineralization and grazing (Section 5.1, Fig. 7)
- We added this information to L72 (track changes version)

L126-129: Are the vegetation parameters here defined as constant or varying with season? On L93 you state that the seagrass is featured by a “strong annual growth cycle”, which would render the shoot density, canopy height and ultimately the drag being far from static across seasons. If there is a feedback from the SGINT model for these parameters it should be stated here. This is not entirely clear from Figure 2.

- The vegetation properties (shoot density, biomass, canopy height) vary with the season and are calculated by the seagrass growth model. To make this clearer we have made revisions in the text and to Figure 2 (shown below):

L121 (track-change version): ‘The map of seagrass properties is updated based on the simulation results from the seagrass model, which is used for the hydro-morphodynamic model to simulate seagrass-mediated currents and sediment dynamics for the next round (i.e. 7 days).’

L144 (track-change version): ‘These additional terms depend on the vegetation properties including shoot density N , canopy height h_{can} and stem/leaf diameter D , as well as a vegetation-dependent drag term c_D , which are updated after every timestep of the seagrass growth model.’



Updated Figure 1: Flow chart of the modelling process, including a schematic overview of the intertidal seagrass model SGINT.

L131: So subtidal seagrass in Italy? A brief comment on the uncertainties due to this should be included.

- While our initial model formulation was based on a model originally developed for subtidal seagrass in Italy, our model was adapted to the intertidal environment with several modifications to the growth and decline rates, as well as by parameter tuning to fit the observation data in our study area. These have been described in Appendix A. This information has been added to L149 (track changes version):

The growth model for intertidal seagrass (SGINT) is developed based on the model for *Z. marina* from Zharova et al. (2001) and was adapted to the intertidal environments with

several modifications to the growth and decline rates, as well as by parameter tuning to fit the observation data in our study area.

L145-147: If the study area experiences heavy grazing by birds, using this global estimate would risk overestimating the POC exported relative to production. I believe such heavy grazing is limited to local areas with conditions (e.g. water depth, migratory routes) conducive to herbivory. As far as I can tell, the paper used to tune the shoot loss rate (Laugier et al. 1999) does not incorporate loss from herbivory. Also, assuming that all produced POC ends up in bottom sediments neglects advective transport outside of the system and considering all seagrass-derived POC as recalcitrant is not valid on time scales relevant for long term carbon sequestration. It seems grazing is not considered in the loss term definition (L415-416).

- We do acknowledge that not all terms that are impacting the loss or growth of seagrass are considered in the model, as explained in our previous response regarding the loss by grazing and remineralization. The shoot loss rate $Loss_N$ is the background loss rate, that is further modified by temperature, day of the year (which can also be related to the effects of grazing since grazing by the migratory birds peaks in autumn when the Wadden Sea serves as a key stop for millions of migratory birds from Arctic breeding grounds to wintering areas in West Africa) and inundation time.

We included this information in the loss term definition (L520; track changes version):
'Since the growth and decline of seagrass in the Wadden Sea follow an annual cycle, a general estimation of the age of above-ground seagrass can be made based on the season. At the beginning of the growth season, the mortality is low and then continuously increases towards autumn, before it drops again toward the beginning of the growth season. This loss function also represents other seasonal loss terms not related to the age of the above-ground seagrass. A major contributor to this seasonal increase in loss is the grazing in autumn when the Wadden Sea serves as a key stop for millions of migratory birds (Jacobs et al., 1981).'

- Again, we would like to clarify that not all seagrass-produced POC ends up in the bottom sediments. POC are modeled as particle tracers. POC originating from the above ground biomass is released from leaves and stems to the water column and subsequently advected to downstream areas by currents. The amount of deposition within the meadows depends on current velocity, direction and POC settling velocity. POC originating from the below ground biomass is added to the sediment POC pool which can be eroded in case of seabed erosion caused by strong waves or during storms..

We added further information on this to Section 3.3:

L159 (track changes version): *'The loss of seagrass biomass provides a source of POC, which is represented as a sediment-class tracer in the model. This allows for deposition and resuspension of the POC depending on the current velocity, direction and POC settling velocity.'*

L168 (track changes version): *'The model continuously releases AG biomass POC to the water column where loss of seagrass biomass occurs.'*

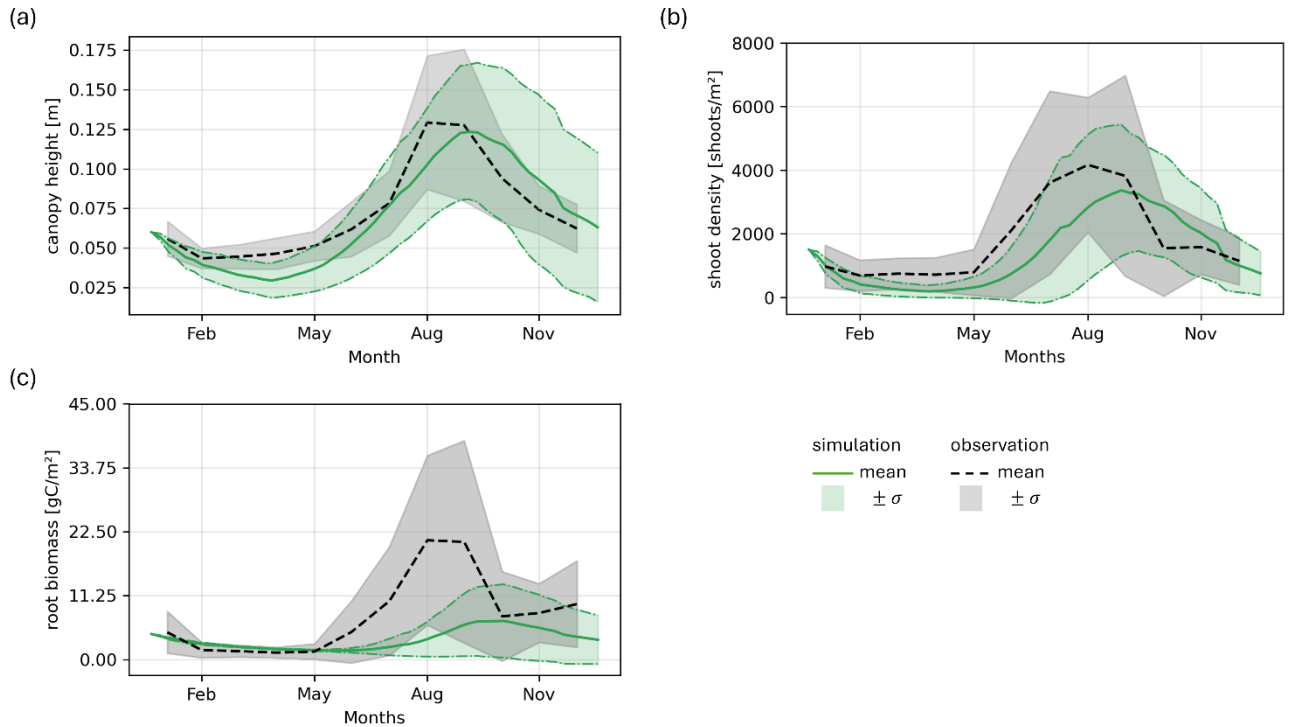
L170 (track changes version): *'The produced BG biomass POC is added to the bottom sediments'*

L165: It is not clear if this decay during transport is incorporated as an additional loss term or DIC/DOC source.

- The decay of the leaves is considered in the sinking velocity of the debris. DIC or DOC are not explicitly included in the model. This sentence has been revised to *"The release of DOC or DIC due to decay is not incorporated in the model and the biomass of the particles does not change.* for clarity (L193 track changes version).

L199-200: Can the uncertainty of this be estimated? What is the monthly range or error bounds around the mean?

- We updated the Figure 3 to include the std of the observations instead of the total range, and also reduced the complexity of the plot by averaging the model results for the different years:



- **Updated Figure 2:** Comparison of observations and model results of (a) seagrass canopy height, (b) shoot density and (c) root biomass. The plots show the mean values and the range between $\pm$ standard deviation σ . The model results are averaged over all computational cells with seagrass. The observation data of the root biomass are derived from the above ground biomass, using the ratio found in between above and below ground biomass in the Netherlands (Philippart, 1995; Vermaat et al., 1987; Vermaat and Verhagen, 1996).

L201-205: How is the large spread between years in December compared to the tight agreement in January in Fig. 3 explained? It seems that the uncertainty of simulations increases as a function of time of year, but how is the convergence in January resolved between different years? For instance, how can canopy height in December 2010 be ≈ 0.09 m but ≈ 0.06 m in January 2011? Also, in Fig. 3b, shoot density $>13\,000$ shoots m^{-2} is quite remarkable. Is this correct?

- We would like to clarify that the seagrass properties are reset to initial conditions at beginning of each year to ensure model consistency with observation. We added this information in the manuscript: L231 (track changes version): ‘*The hydro- and morphodynamics are modelled successively, while the seagrass model is reset at the beginning of each year to account for the changing extent of the seagrass meadows observed in the respective year.*’

- We can confirm that the shoot density of >13000 shoots/m² was observed in a seagrass meadow near Rantum on Sylt in September according to the observation data available to us.

L208: AG and BG biomass is already defined so “BG:AG ratio” can be used here for consistency and to avoid confusion.

- Changed in text

Figure 3: It is not very clear which line represents the observation mean. Can this be made thicker or in a distinct color to clearly separate from simulated std?

- See previous comment on Figure 3.

L227-230: This calculation should be clearly defined in the methods. For instance, does “sedimentary carbon” encompass only surface sediments or deeper layers? This has important implications for the permanence of POC burial and if only surface layers are considered, this calculation would overestimate the POC buried on longer time scales.

- The sediment model uses a single active surface sediment layer to calculate erosion/deposition and our simulation covers only a few years, so all calculated changes of sedimentary POC are confined to the surface sediment layer. We added this information to the model setup (L221, track changes version).
- On the other hand, POC is treated as recalcitrant in our model, therefore the efficiency of POC burial along sediment depth is not accounted for. We have clarified in the methods that we are calculating the yearly burial rates but not the long-term sequestration, and we added information on how the rate is calculated: L176 (track changes version) *‘The burial rate of the seagrass- and non-seagrass-originated POC is calculated as the difference in POC stock in the active surface sediment layer between the initial and the final time step in the year. The resulting value refers to yearly carbon burial rate.’*

L243-244: But still half that of the unvegetated tidal flat (L238). Considering that no other sources of POC are included (phytoplankton, microalgae etc), the comparison of burial in the seagrass meadows compared to the tidal flats seems unbalanced.

- The burial rates of non-seagrass carbon are generally lower in the regions where the seagrass meadows are growing, and the presence of the seagrass slightly increases the burial rates (Fig. 5 d). The burial of locally produced (inside the basin or inside the meadows) non-seagrass POC was not modelled, but we included external supply of POC from the offshore open boundary associated with primary production of phytoplankton, to get a general idea of how the seagrass meadows might impact

the burial of allochthonous POC. We acknowledge the fact that our burial rates are not all-encompassing in the discussion (chapter 5.4).

- We added information on the allochthonous POC to the model description: L217 (track changes version): *'The allochthonous POC is supplied from the offshore open boundary associated with primary production of phytoplankton, derived from ECOSMO simulation results (Daewel and Schrum, 2013).'*

Figure 5: It is not clear what the “normal spread for the sequestration rates” refers to. Is this the spatial variability between grid cells? It is also a bit confusing what a median of mean annual burial rates are. Please clarify in the figure caption. Finally, use consistent terminology. The y axis says “Sequestration rate” but the caption uses “burial rates”.

- Thank you for pointing out the inconsistencies. We rechecked our terminology and changed all instances that refer to our results to ‘burial rates’.
- Calling the burial rates ‘median of mean annual burial rates’ is indeed confusing. Ultimately, they refer to the yearly burial rates for each grid cell, averaged over the five years of simulation time. We updated the figure caption:

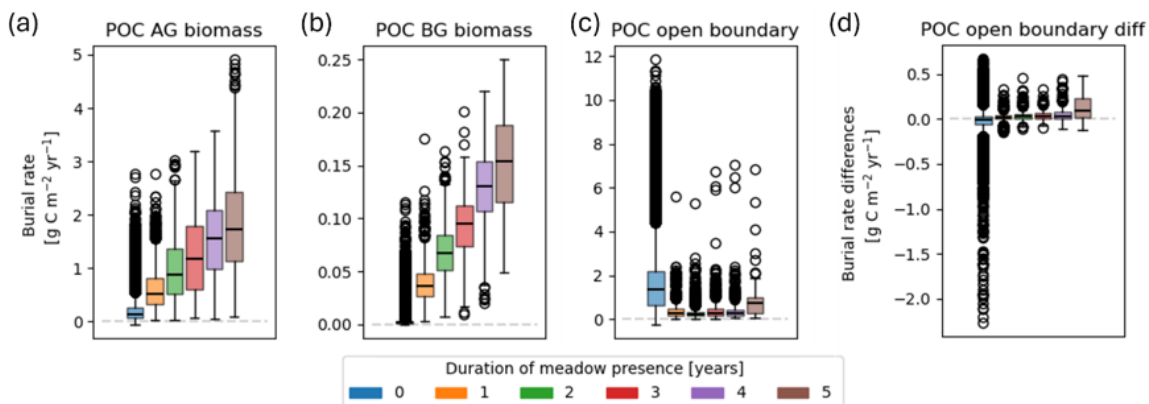


Figure 5: Boxplots of (a-c) annual burial rates on tidal flats for different POC sources, averaged over five years of simulation time and sorted by years with seagrass cover, and (d) difference in the annual burial rates compared to simulations without seagrass, for allochthonous POC from the open boundary. The boxplots show the median and normal spread for the burial rates on the model grid; dots denote outliers from the spread.

L268: There is no estimate of air-sea CO₂ flux in this study so I recommend refraining from saying that atmospheric CO₂ is taken up (unless it is assumed that all primary production by *Z. noltii* occurs during low tide). As far as I can tell, it is not possible to distinguish in the model between atmospheric CO₂ equilibrating with the seawater relative to DIC sources advected laterally into the system.

- Thank you for pointing out this inaccuracy. We now refer to the carbon taken up by the seagrass as carbon taken up during primary production of seagrass biomass, without making any assumptions about the origin. The revised sentences now reads as:

- L 316 (track changes version): *‘ In total, approximately $895 \pm 456 \text{ tC yr}^{-1}$ are taken up by seagrass primary production in the bay, with strong fluctuations among the years characterized by notable change in the spatial extent of seagrass meadows. This corresponds to a primary production of $40.8 \pm 7.7 \text{ gC m}^{-2} \text{ yr}^{-1}$ inside the meadows.’*

L277-280: Here would be a good place to add a sentence about the implications of applying this global estimate to the local intertidal system in this study. The results shown in figure B1 could be referred to here (but see my comment below regarding this figure).

- Thank you for the suggestion. We added a reference to Appendix B at the beginning of the paragraph and added a sentence, to emphasize the uncertainties introduced by the factor f_{exp} .
- L328 (track changes version): *‘The conversion of seagrass biomass to POC by decay and mechanical disintegration in our model depends strongly on the factor f_{exp} (see also Appendix B), which prescribes the fraction of lost biomass converted to POC at each timestep. Using values representative for global seagrass systems ($f_{\text{(exp,AG)}}=40\%$ and $f_{\text{(exp,BG)}}=3\%$) (Duarte and Krause-Jensen, 2017; Zou et al., 2021), the model estimates that $26.1 \pm 3.9 \%$ of seagrass primary production is converted to POC. Uncertainty is introduced by applying the global values to the local system, the magnitude of which cannot be estimated due to a lack of observations. ‘*

L280: I suggest explicitly stating that this refers to inorganic carbon incorporated into seagrass biomass, to avoid confusion with previous discussion about import by allochthonous POC.

- We rephrased the sentence, now referring to ‘carbon by seagrass primary production’ (see previous comment)

L289: So 24% of net primary production each year is buried in the sediments. This seems quite high and would make these seagrass meadows very efficient in comparison to global estimates (e.g. $\approx 14\%$ of NPP for seagrass globally (Duarte and Cebrian, 1996; Arias-Ortiz et al. 2026). Perhaps this is worth highlighting, despite the relatively low estimates of the net sequestration rates?

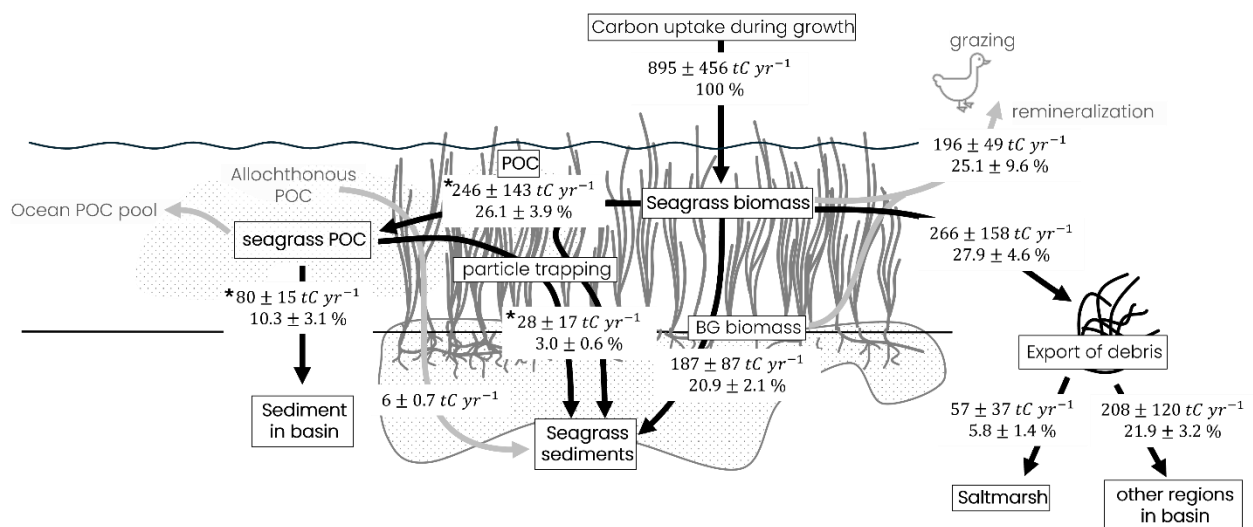
- This is an interesting comparison! We added your suggestion to L 344 (track changes version): *‘Even though the burial rate is lower, the fraction of seagrass primary production buried inside the meadows is higher than global estimates, which suggest that roughly 15 % of seagrass net primary production is buried in situ (Arias-Ortiz et al., 2026; Duarte and Cebrián, 1996).’*

L293-294: Here the grazing and remineralization is brought up. I suggest explaining this earlier in the methods section to make it clear to the reader that these processes are not neglected even though they are not explicitly incorporated in the model.

- Updated manuscript in L70 (track changes version): *‘We further considered the shedding of leaves and used a particle tracker to identify the spatial distribution of shed seagrass leaves biomass and their contribution to carbon burial in adjacent ecosystems such as salt marshes. Other processes related to seagrass carbon such as remineralization or grazing are included indirectly through loss terms, even though they are not modelled explicitly. Our results depict a comprehensive picture of source-to-sink carbon pathways at a basin scale associated with seagrass.’*

Figure 7: In my opinion, there should be an arrow for remineralization in the belowground/sediment compartment as well. Also, it is quite information heavy with a lot of text. Are both annual and total absolute rates and percentages necessary here? I suggest removing the tC yr⁻¹ rates. In the caption, define what black vs. grey arrows represent and what “long-term storage” is.

- Adjusted figure and caption:



Updated Figure 3: Conceptual figure of the carbon pathways of seagrass biomass in the basin. All values are annual values for the study area, averaged over the simulation period from 2010-2014. Values marked with * are dependent on the choice of f_{exp} for the conversion on lost biomass to POC. The percentages are relative to the total annual seagrass primary production (above and below ground). Paths drawn in light grey are not explicitly considered in the model or only considered partially. The area of the seagrass meadows from 2010-2014 is $20.3 \pm 6.3 \text{ km}^2$.

L313-315: Yes, this is a very good point that is often not considered in seagrass blue carbon studies. It would be interesting to know what the net carbon sequestration in the bay would be in the absence of seagrass. Is this something the model could estimate?

- Since we focus on modelling the seagrass-related carbon fluxes, the absence of seagrass was not considered. As can be seen in Fig. 5d, the carbon burial increases at least inside the meadows, compared to a simulation without seagrass influence. On the other hand, one of the major uncertainties is related to allochthonous carbon that is not produced by seagrass, as explained in the discussion. Therefore, we think that it does not make much sense to estimate net carbon sequestration in the bay without seagrass. .

L321-322: I don't find this very surprising considering that the model neglects POC stemming from sources other than seagrass (e.g., marsh plant litter, phytoplankton, microalgae etc)? It could be reiterated here that the study is limited in the sources of POC considered.

- Thank you for pointing this out, it is important that readers know the constraints of the study. We added L386 (track changes version): '*However, non-seagrass carbon is only partially included in this study and the actual burial rates in the seagrass meadows might be higher*'

L328-338: A revised global estimate has been presented by Arias-Ortiz et al. 2026. Depending on timing of publication of that study, it would be a relevant source to cite here.

- Thank you for introducing this study to us, it is very relevant and now cited in our revised version.

L333-334: Repetition from L303-305.

- We want to emphasize the information in both places, since it is relevant for understanding both the uncertainty in transferring values from one region to another and also for contextualizing the global carbon sequestration rates in seagrass meadows. We modified both lines so that the emphasis is for both is clear and the repetition not as strong:
- L363 (track changes version): '*In addition, estimates from both existing studies are extrapolated based on data from other regions and seagrass species, which reduces their direct applicability for the meadows studied here. Sequestration rates are known to vary substantially among species (Duarte et al., 2010; Kennedy et al., 2022; Mazarrasa et al., 2015), among the same seagrass species in different regions (do Amaral Camara Lima et al., 2023; Greiner et al., 2016; Postlethwaite et al., 2018; Prentice et al., 2020) and even on local scales within a single meadow due to local environmental conditions or spatial and temporal continuity of the seagrass cover (do Amaral Camara Lima et al., 2023; Prentice et al., 2020; Schaefer et al., 2025).*'
- L397 (track changes version): '*The consensus is however, that there are large variations in carbon sequestration capacity by seagrass among regions, seasons and*

species (Alongi, 2018; Duarte et al., 2005; Kennedy et al., 2010; Mazarrasa et al., 2015) and that previous global calculations were overestimated (Lavery et al., 2013).'

L342: While this appears to be a reasonable expectation, the model estimated that 24% of carbon fixation is buried in the sediments which is quite high, suggesting that low seagrass productivity (relative to global rates) could explain the low burial rates.

- We added a sentence on the comparatively low primary production: L408 (track changes version): *'In addition to the hydrodynamic conditions, the primary production obtained by our model ($40 \text{ gC m}^{-2} \text{ yr}^{-1}$) is smaller than the primary production observed in *Z. noltei* meadows in the Netherlands and France ($115\text{-}184 \text{ gC m}^{-2} \text{ yr}^{-1}$, (Pérez, 1989; Pérez-Lloréns and Niell, 1993; Vermaat et al., 1987)). Since the primary production limits the biomass that is available for burial in the sediments, this might be another reason why the carbon burial is comparatively low.'*

L345-349: I suggest acknowledging this limitation earlier on (e.g. on lines 277-291).

- We added a line on the uncertainties due to this, as stated above.

L355: Indeed, but it would underestimate carbon sequestration outside of seagrass meadows as well (e.g. tidal flats).

- We amended L429 (track changes version): *'Therefore, the carbon burial rates in this study likely underestimate the amount of carbon buried in seagrass meadows, as well as on the tidal flats.'*

L357: Indeed. Consider adding an arrow for this re-erosion to Figure 7.

- The arrows in Figure 7 represent the net paths by deduction of re-erosion from deposition. We therefore prefer not to add re-erosion arrows to avoid confusion and hope you will agree with that.

L361-366: This discussion diverts from the story and could be removed. Also note that the studies referenced are either from other areas (e.g. carbonate-rich environments) or with other seagrass species making a generalization less applicable to the Wadden Sea.

- We decided to remove this paragraph from the manuscript based on the reviewers comments. Though the TA and DIC fluxes are an important part of the carbon cycle in seagrass meadows, they do not contribute to the carbon fluxes we are looking at in our study.

L390: Again, that a quarter of all carbon taken up is buried in the sediments suggests a high burial efficiency which I find quite remarkable for an intertidal seagrass system in a hydrodynamically active area.

- We agree with this observation

L392: On L289 you state it is $23.9\% \pm 2.2\%$ percent of “seagrass-originated carbon”

- See next comment

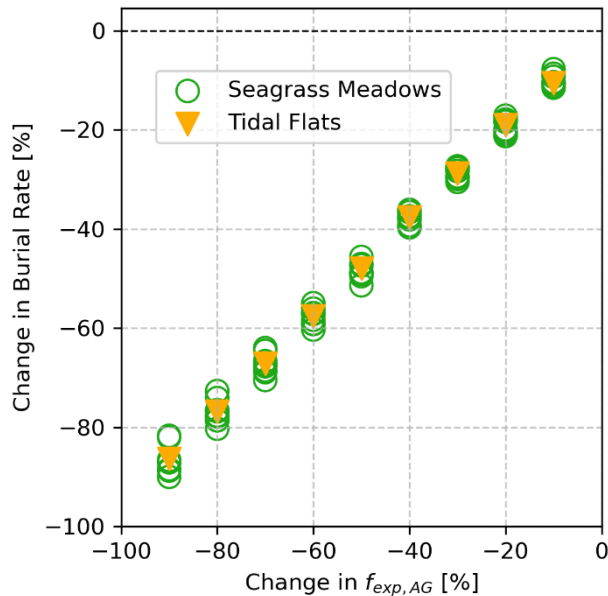
L394-395: This is confusing. Is this a different form of total annual carbon uptake or why does it differ from L392 and L16?

- Regarding these three comments: 23.9% is the sum of the BG biomass that remains in the sediment (20.9% or PP) and the POC from AG and BG biomass (3% of PP). We rephrased the paragraph and hope that it is clear now: L464 (track changes version):
‘The majority of seagrass-originated carbon buried into the seagrass sediments originates from the BG biomass. Approximately $20.9 \pm 2.1\%$ of the total annual primary production remains buried in the sediments from the BG biomass. In addition, POC formed by decay and mechanical forces from AG and BG biomass contributes to the seagrass-originated carbon in the seagrass sediments. Approximately $3.0 \pm 0.6\%$ of the total annual primary production of the seagrass is retained in the sediments as POC. In total, $23.9 \pm 2.2\%$ of the primary production are buried in the sediment by the dead BG biomass and seagrass POC.’

Appendix B: Figure B1 is not clear to me, perhaps the caption and/or axes just needs to be modified. a) It is not obvious which sites on the x axis are tidal flats or seagrass meadows. b) It is not obvious why a fixed value of 90% is chosen. This seems quite extreme and it may be relevant to include smaller offsets as well to inform the uncertainty estimates of the rates presented on e.g. L280; c) The y axis says sequestration rate but the caption burial rate.

- We added further description to Appendix B in general and updated figure B1:

‘The conversion of above ground biomass to POC is determined by the conversion factor $f_{exp,AG}$. The factor is based on literature values (Duarte and Krause-Jensen, 2017; Zou et al., 2021). The burial rate of carbon inside the seagrass meadows depends linearly on the amount of locally produced carbon, as can be seen in Fig. B1, where a reduction of the biomass that is converted to POC leads to an equally large reduction in POC that is buried in the meadow sediments.’



-
- *Figure B1: Relative change in burial rate of AG POC for tidal flats without seagrass cover in general and for several seagrass meadows, for different values of $f_{exp,AG}$, the fraction of seagrass biomass loss that is converted to POC.*

Appendix C: Only tidal regime, temperature and sediment transport seems to be “validated”. Was there no validation or ground-truthing for POC export, POC burial etc? If not, this should be brought up as a caveat in the model interpretation.

- The missing observational data of POC burial rates in the meadows and export to adjacent ecosystems to validate our model is indeed a major caveat. We have pointed out this caveat and emphasized the need for observation/field measurements for future studies in Discussion. Please see our response for your first major comment.

Minor technical corrections:

Thank you for catching all the small oversights!

L38: “Zostera marina”

adjusted

L64: “integrated it into”

adjusted

L76: The “resulting bay” seems odd. Perhaps just say “the bay”?

adjusted

L155: “Zostera noltii” for consistent spelling

Corrected all instances of ‘*notii*’ to ‘*noltei*’, since this is the most common used spelling in our references

L183: Should it not be “two classes”?

No, this refers to the sediment classes (mud, fine sand and coarse sand).

L189: Zostera is the genus, Zostera noltii is the species

adjusted

L198: “Z. noltii”

See above

L230: “the beginning”

adjusted

L251: “is still located”

adjusted

L271: I suggest not starting a new sentence (and paragraph) with a number.

adjusted

L283: Same here, consider rephrasing

adjusted

L285: Repetition: “ $12.8 \pm 5.1 \%$ 12.8 ± 5 ”

adjusted

L292: In Figure 7 it is $25.1 \pm 9.6 \%$ not $25.1 \pm 6.38 \%$. Are these different uncertainty estimates? If so, specify.

corrected after checking in the results

L316: “therefore”

corrected

L317: Letters missing in “role in string carbon”?

corrected

L319: Repetition of “sequestration rate”. Consider rephrasing.

corrected

Literature referred to above:

Arias-Ortiz et al. 2026 : <https://doi.org/10.21203/rs.3.rs-8462059/v1>

Duarte and Cebrian, 1996 : <https://doi.org/10.4319/lo.1996.41.8.1758>; Arias-Ortiz et al.
2026 : <https://doi.org/10.21203/rs.3.rs-8462059/v1>

[Thank you for the helpful literature, which has been added in the revised version.](#)

Response letter to reviewer's comments - Vermaat

Reviewer's comments in black and our response in light blue

I have now reviewed this interesting manuscript. I have a substantial list of minor editorial issues that I will present below, but there is also a few issues in my view that are at the moderate-to-major scale and in my view deserve attention and revision before the paper is to be published. In summary, I think that the paper (a) needs a more complete description of the two modelling components that are combined here, (b) they should choose a different parametrization for the seagrass component based on values available in the literature for their specific intertidal seagrass species rather than values from subtidal stands or different species, and (c) they need to make their validation/verification explicit. Furthermore, I have quite a list of small things that will easily improve the paper. The overall message, that we should moderate our high expectations of the potential blue carbon sequestration by intertidal Wadden Sea seagrass beds, in my view stands convincingly.

First of all, we would like to thank the reviewer for the thorough review of our manuscript. We appreciate the time and effort invested in this review and think that our manuscript profited greatly from the remarks. We hope that the reviewer will agree with our answers and find the revised manuscript satisfactory.

Moderate/major issues

Parametrization and description of the seagrass growth model. I have no problem with the use of just a few biomass state variables or boxes, but

(a1) But I see no good reason why canopy height data are derived from a permanently submerged *Z. noltii* bed from a Mediterranean lagoon (L135), when values for intertidal stands are readily available in the literature. We have them from SW Netherlands and Mauretania, but more importantly, Schranz & Asmus (2003, MEPS 261) provide such numbers for the Sylt-Rømø bight: 11 cm in exposed and 17 cm in sheltered systems. Also, we have shown that shoot dimensions do not change very much during the growing season, but the beds get denser and expand (Vermaat & Verhagen 1996). Finally, but why do we actually need canopy height from biomass? For estimating sediment roughness and hence have a factor for the entrainment of POC? Or for estimating the depth of the canopy for light availability?

Notice that we found that most of the photosynthesis occurred during low tide. It would be good to explain this here.

- Thank you for pointing this out. We would like to clarify that there was a mistake in the writing and the wrong formula was inserted into the text. The formula inserted

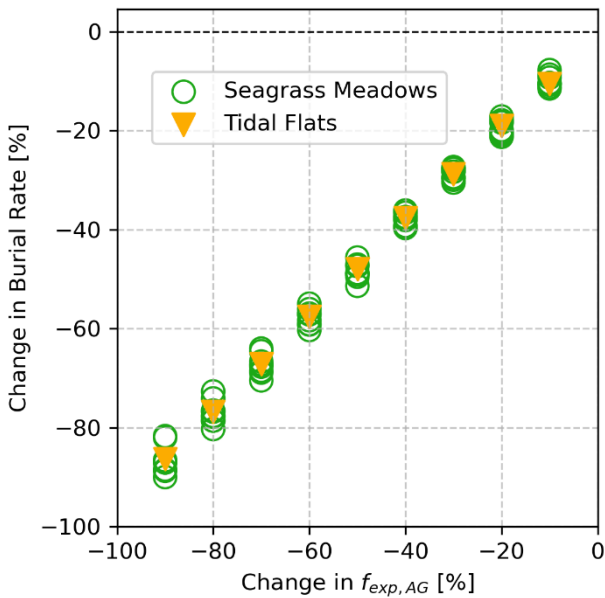
here refers to a previous formulation of the seagrass model, where the total above ground biomass was calculated instead of the single shoot biomass. The formula has been adapted and now reads $h_{can} = B_s \cdot 20 \text{ m } gC^{-1}$. The conversion factor is still based on the observations from Laugier et al. (1999) but has also been checked against the observations from Schanz & Asmus (2003), where the relationship between single shoot biomass and canopy height in the exposed areas is approximately the same (Schanz & Asmus: $h_{can}/B_s = 19.3 \pm 4.3 \frac{m}{gC}$).

- The canopy height is used by the physical model for calculating the impact of the vegetation on hydrodynamics and subsequently on the sediment (including morphodynamics) and POC transport, as described in L142-146 (track change version).

(a2) The function fexpAG reflects leaf loss and is set at 40% (L152). We have quantified this leaf loss during the season and came to 51% in our 1987 paper and likely even higher in our 1996 paper (75% if I now quickly subtract mean net growth rate from mean gross growth rate). As the authors say on L 151, this is an important variable for POC loss, but the paper does not present a sensitivity analysis on this aspect. Or, at least I could not trace this in the table A1 and figure A1. Table A1 does include leaf loss and shoot loss (LossN), but I failed to reconstruct how these translate to fexpAG of L 152. As an aside, this figure A1 is very hard to decipher and I suggest the authors to really make the sensitivity analysis more readable. Further, I fail to follow what is described in appendix B. Here we need a more elaborate explanation too.

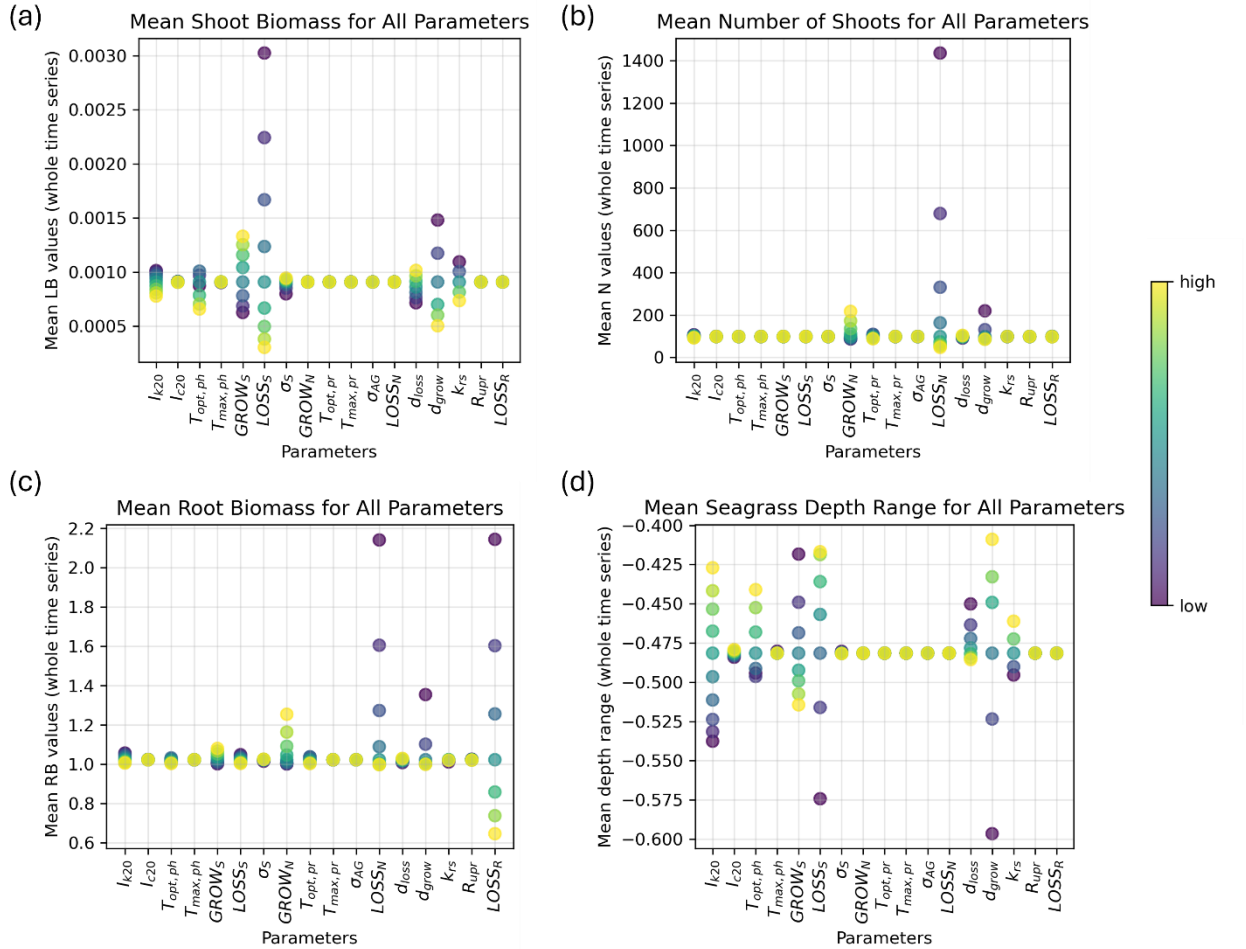
- We would like to clarify that $f_{exp,AG}$ is a parameter related to leaf loss, but not the leaf loss itself. Leaf loss is calculated as described in Appendix A, equation A9 as a function of inundation time per tide, the day of the year (as a proxy for the age of the leaf) and wind strength. f_{exp} refers to the specific fraction of the lost leaf biomass that is converted to POC. The values are based on estimates of the fate of carbon originating from seagrass biomass by Duarte & Krause-Jensen (2017) and Zou et al. (2021). To avoid misunderstanding in the manuscript, the descriptions are now rephrased as: ‘... $f_{exp,AG}$ is the fraction of lost biomass exported from the meadows as P...’ in L166 (track change version).
- Since f_{exp} is not influencing the seagrass growth model, it is not included in the sensitivity analysis in Appendix A, but has a separate description in Appendix B. We added further information to Appendix B to help understand the figure: ‘The conversion of above ground biomass to POC is determined by the conversion factor $f_{exp,AG}$. The factor is based on literature values (Duarte and Krause-Jensen, 2017; Zou et al., 2021). The burial rate of carbon inside the seagrass meadows depends linearly on the amount of locally produced carbon, as can be seen in Fig. B1, where a

reduction of the biomass that is converted to POC leads to an equally large reduction in POC that is buried in the meadow sediments.’ (L 616-619, track change version) and we also updated figure B1 with a range of different values for $f_{exp,AG}$:



Updated Figure B1: Relative change in burial rate of AG POC for tidal flats without seagrass cover in general and for several seagrass meadows, for different values of $f_{exp,AG}$, the fraction of seagrass biomass loss that is converted to POC.

- We have also improved figure A1 (see below) for better readability:



Updated Figure A1: Impact of different parameter settings on seagrass growth, shown as the changes to mean (a) single shoot biomass, (b) number of shoots, (c) root biomass, and (d) mean depth of the distribution. Each parameter was changed over its scope defined in Table A1 while the other parameters were kept constant. For comparison purposes, the parameter values are marked high to low instead of the actual values. The range for each variable is listed in Table A1.

(a3) the paper is accompanied by a more detailed description of the seagrass model in appendix A. I suggest the authors to revise the text and leave variable explanation fully to the appendix and only describe the generic principles. Particularly how and why the environmental variables are derived from the hydrodynamic model and then shunted into the seagrass model in a weekly timestep.

- We have moved the equations from the seagrass model description (section 3.2) to Appendix A.
- We agree that adding the calculation of the environmental variables from the hydrodynamic model to the model description is beneficial. The following descriptions have been added to appendix A:

“Growth of seagrass in the model is driven by weekly averaged values of temperature, solar radiation, mean inundation time, and wind speed, which are calculated based on the simulation results of the hydrodynamic model.

The weekly averaged temperature represents the mean value for both water temperature when the seagrass meadow is inundated and air temperature otherwise:

$$T = \text{avg}(T_t). \quad (\text{A13})$$

The radiation is given by

$$I_{wc,n} = I_{n-1} \cdot \exp(-k_{e,n} \cdot d_{z,n}/2), \quad (\text{A14})$$

$$I_n = I_{n-1} \cdot \exp(-k_{e,n} \cdot d_{z,n}), \quad (\text{A15})$$

where $I_{wc,n}$ is the radiation reaching the middle of layer n counted from surface water, I_{n-1} is the radiation reaching the bottom of the layer $n - 1$, I_n is the radiation reaching the bottom of layer n and $d_{z,n}$ is the layer thickness of layer n . $k_{e,n}$ is the light extinction coefficient in layer n , which is calculated as

$$k_{e,n} = k_w + k_{sed} \cdot tsc_n, \quad (\text{A16})$$

where k_w is the background attenuation by water, k_{sed} is the light extinction coefficient by sediment turbidity and tsc_n is the sediment concentration in layer n . The radiation used as forcing is the average radiation reaching the middle of the bottom-most computational cell ($I_{wc,bot}$) of the hydrodynamic model, which is the same as the incoming radiation at the surface for the timesteps at which the cell is dry:

$$I = \text{avg}(I_{wc,bot}). \quad (\text{A17})$$

The mean inundation time per tide in hours is calculated as

$$t_{dry} = t_{dry,week}/n_{tides}, \quad (\text{A18})$$

where $t_{dry,week}$ is the accumulative time when a computational cell is dry during a whole week, and n_{tides} is the number of tidal cycles in the same period. ”

-

(a4) L419 Your I_k estimate is from Kohlemeier (2016), this reference is absent in the refile. I_c is from Olesen & Sand-Jensen (1993) and hence for *Zostera marina*. Personally I would have used readily available seasonally variable values for *Z. noltii* from Vermaat & Verhagen (1996) for intertidal *Z. noltii*, for photosynthesis, but also for growth. Your compensation light level I_c for growth should be plm 5 E/m²/d from our fig 3a for leaf RGR), which converts to plm 12-15 W/m² PAR. This is not a trivial difference from the value of 9 you used, and I think this is a serious issue to consider, since *Z. noltii* is a high-light adapted plant compared

to *Z. marina*. Also Leuschner & Rees (1993, AQBOT 45) present PI curves for *Z. noltii* taken on the mudflats of Sylt during emersion, and these data would have been preferable over literature values for *Z. marina*. On L465 you write that ‘no definitive values are available from literature for the different parameters affecting growth of *Z. noltii*’. Obviously, I dispute this here, you could have used ours, for a starter.

- Thank you for pointing out the missing references. We rechecked all references in Table A1 and made sure that all of them are included in the reference list.
- Also thank you for the valuable insight on the light dependency of *Z. noltei* and the additional references. We have now added Vermaat & Verhagen (1996) and Leuschner & Reese (1992) to the references for I_c . For this study, we keep the value for I_c at 9 W/m^2 , since values ranging between 1 and 15 W/m^2 for I_c have no apparent difference in the growth of the seagrass in the model according to our calibration (see figure A1; only the depth range in which the seagrass grows changes slightly). The reason for this is that the values for I_c are low compared to the incoming mean weekly solar radiation in the seagrass meadows, which is $> 50 \text{ W/m}^2$ during the growth season (March – September). The weekly averaging leads to a reduced importance of the compensation irradiance for the growth of seagrass in the model, while the saturation irradiance is more important.
- Sorry for causing the misunderstanding. There are of course published studies providing values for the parameters that are used in the model, such as those listed by the reviewer. Our meaning is that although values of some parameters have been recommended, not every parameter has been provided for *Z. noltei* in the Wadden Sea environment. We have rephrased the sentences in L545 - 550 (track change version) for clarification: ‘As definitive values were not available from literature for the Wadden Sea for all of the different parameters affecting the growth of the *Z. noltei*, the values used as a base for tuning are additionally based on values either reported for *Z. noltei* from different regions, mainly from the Mediterranean and southern France (Kombiadou et al., 2014; Laugier et al., 1999; Peralta et al., 2000, 2002; Plus et al., 2003) or values reported for *Z. marina* (Abe et al., 2003; Bach, 1993; Dennison and Alberte, 1982; Olesen and Sand-Jensen, 1993; Rasmussen, 1973; Verhagen and Nienhuis, 1983).’

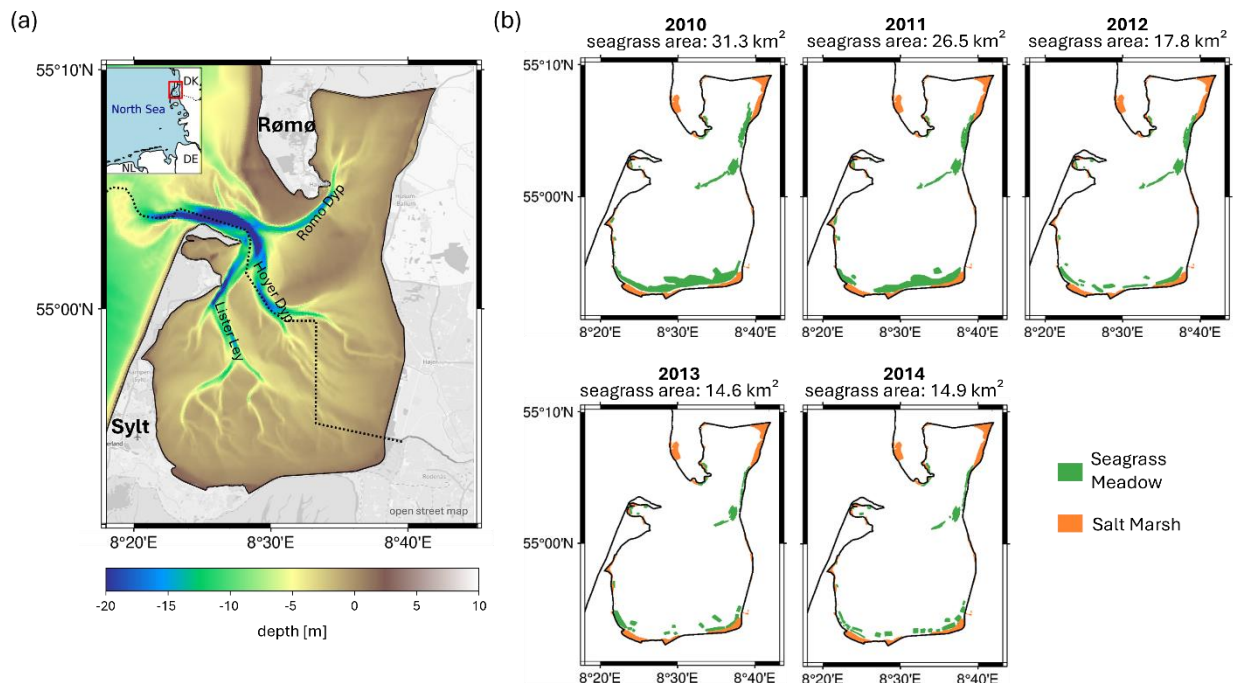
(a5) you estimate an optimal temperature for photosynthetic growth in Table A1. I assume that the word growth is sufficient, and I would prefer the use of references for *Zostera noltii* over those on *Zostera marina* that you have used. And I do think the value of 16 degrees you arrived at from your tuning is pretty low for this intertidal species. Massa et al. (2008, Hydrobiologia) show a pretty flat survival curve up to 37 degrees C, and Perez-Llorens et al (1993 Hydrobiologia 254) show for intertidal narrow-leaved *Z. noltii* that CO₂ uptake is not affected measurably up to a temperature of 30 degr C.

- Our model configuration is based on Leuschner and Reese (1993), who found an optimal temperature for growth of *Z. noltei* at 20°C and a reduction in photosynthesis if the temperature decreased or increased. While 16°C is lower than 20°C, it is sufficiently close to reproduce the patterns of seasonality for this study. Additionally, our hydrodynamic model underestimates the water temperature by approximately 2°C and the temperatures in the seagrass growth model are adjusted accordingly.
- The study by Massa et al (2008) looks at the response of *Z. noltei* to heat shocks over short periods of time. From our understanding, their results fit more for tuning the 'maximum tolerable temperature for photosynthetic growth' than to the optimal temperature for maximum growth rate. Also, our model uses weakly means of temperature for growth, and such temperature shocks are largely smoothed and thus not represented in the model. On the other hand, water temperature in the northern Wadden Sea rarely exceeds 20°C even in summer according to recorded time series in the past. The highest water temperature recorded in the study area (Havneby Havn gauge station, see example in Figure C1) for the simulated period is 23.6°C in 2013 which lasted for only a few days, and temperature remained mostly below 20°C for the rest of time. Therefore, setting a higher temperature for optimal growth would not cause a considerable difference in the simulation results.

My main concern actually is how the model outcome is verified against what happens in the reality of the Rømø-Sylt embayment. In my interpretation the main model outcome has two important aspects (a) the seasonal growth of the seagrass, and (b) the spatial distribution of the lost leaf material across the bay. This seasonal growth is compared or validated with measurements, but the authors remain vague about the origin of these sites 'sparse in time and space', 'multiple local sites' (L199). In my view it is very important to know how much plant material is produced and where in the bay this occurs, but we cannot trace this from the paper in its current form. Particularly the issue 'in space' is critical: where are these beds in the years that are simulated? Is it all the beds that are visible in Fig 1b? Figure 3 shows a seasonality for 5 years, but is this averaged across all pixels with seagrass? In the discussion (L4269) the authors mention there is a notable change in the spatial extent, but this is nowhere made explicit in a table or figure, at least not that I could figure it out.

- We would like to clarify that, to avoid deviation from observations, the growth of seagrass in the model is restricted to the observed distribution for each year, which are indeed shown in Figure 1b. We added clarification of this to L228-230 (track changes version) : '*Seagrass growth, hydro- and morphodynamics are simulated for five years (2010-2014). The seagrass growth is restricted to the observed meadow areas to avoid model deviation (Fig. 1b).*' This is why only the seasonality is validated against observations, and not the spatial extent.

- We also added information on the meadow area to Fig 1b and increased the size of the individual plots for better visibility.



Updated Figure 1: Map of the Sylt-Rømø Bay. (a) Topography of the bay. The grey dotted line is the border between Germany and Denmark. (b) Location of seagrass meadows and saltmarshes in the Sylt-Rømø Bay from 2010-2014. The observational data for seagrass meadows can be accessed at [LKN.SH Nationalparkverwaltung \(2024\)](#) and the observational data for saltmarshes are provided at [Datahuis Wadden \(2023\)](#).

- We added further information for the observed values of seagrass properties to L240 (track changes version): ‘The seasonal change of shoot biomass, shoot density and root biomass was validated against measurements of *Z. Noltei* meadows located near Sylt, taken from six major meadows of different growth density from 2021-2023 (personal communication with Dr. Tobias Dolch).’
- The model results in Fig. 3 are averaged over all computational cells covered by seagrass. We added this information to the figure description.

So how is the model outcome actually verified with field observations? I only find a qualitative ‘are well within the range’. With so much effort on constructing a complex model, I would have expected an observed-predicted plot, not only of standing stock or shoot density, but also of spatial extent. Maybe the latter was not possible, but then the basis of POC production and then redistribution across the bay as well as local and further away burial is unconvincing. I suggest the authors particularly clarify this issue in their revision, include the annual variation in spatial extent of the seagrass beds as well as POC transport and burial and are clear about possible weaknesses. Verification of seagrass-derived POC burial may be a trifle more difficult, but could be assessed against sediment

organic matter, where hotspots of accumulation as suggested by fig 4 may well correspond to areas with higher sediment organic matter.

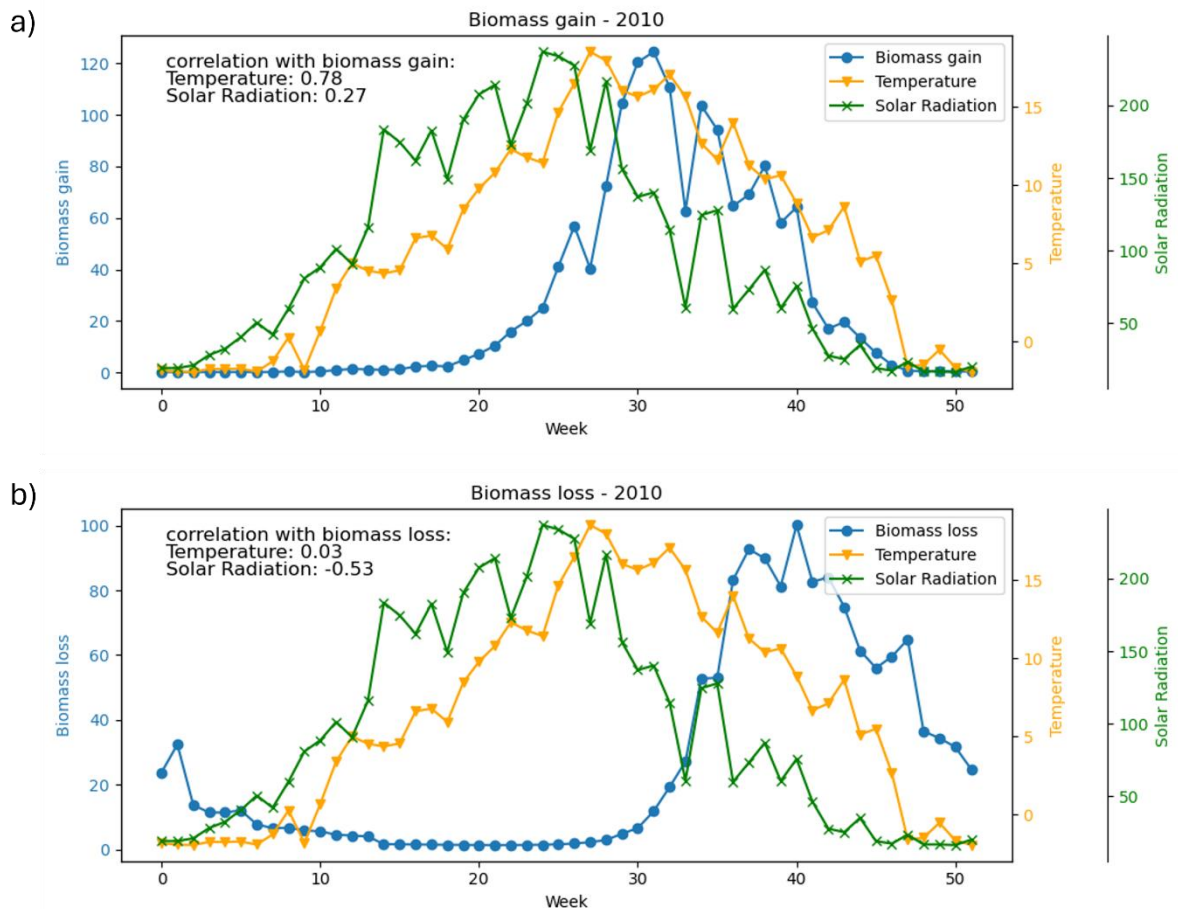
- As explained in previous response, the spatial extent of seagrass meadows is not modelled in this study but prescribed based on the observations to avoid model deviation. We clarified this in L228 (track changes version): *“Seagrass growth, hydro- and morphodynamics are simulated for five years (2010-2014). The seagrass growth is restricted to the observed meadow areas to avoid model deviation (Fig. 1b).”*

An alternative validation of the seagrass model could have been done separately on a stand that has better data coverage, before it was linked to the hydro-morphological part of the modelling workflow.

Finally on the model performance, since light availability at the canopy is such a crucial aspect, personally I would have greatly preferred to see (a) how this light climate did vary across and between years, and how this then affected the seasonal shoot density or aboveground biomass curves; and (b) how it worked through the model work flow.

- We added a section to Appendix A, showing exemplary for the year 2010 how temperature and solar radiation influence the biomass loss and gain rates in the model (L:605-608 track changes version):

‘The growth of the seagrass is mostly driven by the temperature (figure A2a). During the main growth season, variations in solar radiation also noticeably influence the growth rate, especially during weeks with low solar radiation. For the biomass loss (figure A2b) the influence of both solar radiation and temperature is less prominent. The seasonality of the biomass loss is mostly driven by the seasonal loss terms summarized in the loss function f_{age} .’

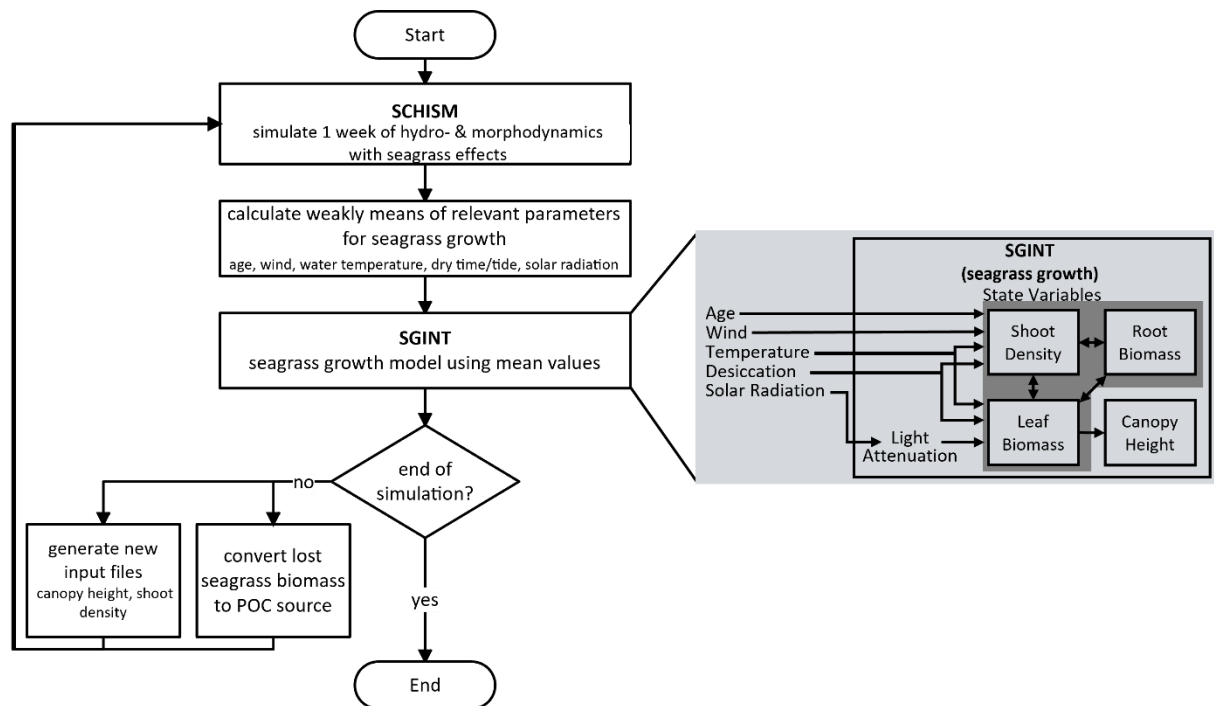


- **Figure A2:** (a) Mean biomass gain together with weekly mean temperature and solar radiation used for forcing the seagrass model for 2010. (b) The same for biomass loss.

The last paragraph of the introduction suggests that the model explicitly resolves the bio-physical interactions between seagrass and .. environments', and when searching for a hypothesis, research question or objective, I find that the authors 'seek to fill the gap in quantitative research of carbon sequestration potential of seagrass meadows in the Wadden Sea'. Does the paper meet these two expectations? Regarding the former, I must say I cannot find how they modelled the effect of the seagrass on the hydromorphology, I can only see a oneway influence of hydrodynamics on seagrass growth and then POC transport. I would appreciate to see how, or if, they modelled the effect of the seagrass on the hydrodynamics. Regarding the latter, I would propose a slight rephrasing including the word 'intertidal', for example like 'quantify the annual fluxes and fate of carbon produced by intertidal seagrass in a Wadden Sea bight', but then I would say the authors have reached their objective. Figure 7 gives us a complete annual budget that includes the different export terms, and in its form for me is convincing. One might wish the inclusion of other primary producers in the budget, but that was not the study objective so that is fine.

- The vegetation in the model influences the hydrodynamics and therefore the morphodynamics, as described in L142 (track changes version): 'The impact of

vegetation such as seagrass on hydrodynamics is implemented through a modification of the momentum equation by introducing an additional drag term and by expanding the turbulent kinetic energy equation with an additional source of turbulence (Zhang et al., 2020). These additional terms depend on the vegetation properties including shoot density N , canopy height h_{can} and stem/leaf diameter D , as well as a vegetation-dependent drag term C_D . The seagrass properties are updated after each timestep (7 days) in the seagrass model. We adjusted L121 (track changes version) to clarify this: ‘The map of seagrass properties is updated based on the simulation results from the seagrass model, which is used for the hydro-morphodynamic model to simulate seagrass-mediated currents and sediment dynamics for the next round (i.e. 7 days).’ We also updated Fig. 2 to better illustrate the iterations between the hydro-morphodynamic model and the seagrass model:



Updated Figure 2: Flow chart of the modelling process, including a schematic overview of the intertidal seagrass model SGINT.

- We have also added intertidal to better define the aim according to the suggestion (L65, track-change version): ‘In this study, we seek to fill the gap in quantitative research of carbon sequestration potential of intertidal seagrass meadows in the Wadden Sea.’

Minor Issues

L 11 insert ‘intertidal’ before seagrass

- Added ‘intertidal’

L29, 32 (and possibly elsewhere) I would prefer to use 'sediments' for the collected aggregates and particles at the bottom of the sea instead of 'soils'. I would like to reserve the word soil for terrestrial soils that have been subject to soil formation processes such as weathering, but I may be a bit old-fashioned.

- We agree with the suggestion of the reviewer and changed the occurrences in the manuscript accordingly.

L37 *Zostera Marina*: please check the spelling and typography: *Zostera marina*. Also the paper uses both *Zostera noltii* (my preference, and that of the monograph by Moeslund et al, 2023, Aquatic plants of Northern and Central Europe including Britain and Ireland, Princeton UP) and *Z. noltei* (the preference of others).

- We corrected all instances of *noltii* to *noltei* and also made sure the spelling is correct everywhere in the text. We decided to use *noltei*, since this is the spelling most commonly used in the references we cited.

L42 'heterological': what does that mean? I had to look it up and found 'not of shared origin'. I suggest a simpler phrasing of 'necessitates process-understanding of heterological carbon cycling in seagrass ecosystems' like for example 'necessitates understanding of the different processes involved in carbon cycling ..'.

- Adjusted as suggested

L46 the importance of direct grazing on *Zostera noltii* leaves, shoots and rhizomes in the Wadden Sea was already studied by Jacobs et al. (1981, AQBOT 10). Their findings were later corroborated by our work in SW Netherlands, but importantly, I think this work needs to be cited here when Wadden Sea *Zostera noltii* dynamics are modelled.

- This is definitely a relevant reference, thank you for making us aware of it. We have cited it at the suggested place.

L57 Oppelt et al is a key reference to justify the current work, but the reference is incomplete in the REFLIST and cannot be traced. Also the Potouroglou reference is hard to trace. Is it a MSC or PhD thesis? A doi would have been useful. Google helped me: Potouroglou, M., 2017. Assessing the role of intertidal seagrasses as coastal carbon sinks in Scotland. PhD Thesis, Edinburgh Napier University. Retrieved from <http://researchrepository.napier.ac.uk/Output/975386>

- the oppelt reference refers to this report: https://www.nabu.de/imperia/md/content/nabude/meeresschutz/240126_nabu_nordsee-kohlenstoff_projektdokumentation.pdf (accessed 16.03.2026). We have updated the reference list accordingly.
- We have also updated the reference for Potouroglou (2017)

L58 'large uncertainties' I agree that any transfer of quantitative numbers to populate a growth model across latitudes can be problematic and may be cause of both uncertainty and bias. Possibly more bias than random uncertainty. Consider to rewrite.

- Rephrased to '*This may induce bias and subsequently large uncertainties when the rates are directly transferred to the Wadden Sea*' as suggested.

L61 include 'intertidal' before seagrass

- Adjusted as suggested

L76: how much of the bay is intertidal? And does that area set the maximum extent for the *Z. noltii* beds? It looks like these are limited to the upper intertidal from your maps, but I miss a (brief) description of the tidal zonation.

- We have added information on the intertidal flat area in L81 (track changes version): '*The bay has an area of approximately 410 km² with intertidal flats occupying ~45% of the area (Konyssova et al., 2025).*'
- We added information on the tidal zonation to L93 (track changes version): '*The seagrass meadows are located in the upper intertidal zone, preferentially along the leeside of the islands, and the core area of the meadows has remained stable since the 1930s.*'

L85 'making it one of the most studied areas...'. In my view this is an unnecessary statement. If I look back on how much earlier literature is available on e-g the Ems estuary or the Western Wadden Sea the Sylt Rømø basin is indeed one of several very well published areas, but why should that be interesting to your audience?

- Indeed, we have changed L88 (track changes version) to: '*Several studies on hydrodynamics and sediment transport have been carried out in this basin (de Beer et al., 2005; Fofonova et al., 2019; Kappenberg et al., 1998; Konyssova et al., 2025; de la Vega et al., 2018; Mohr et al., 2025; Pejrup et al., 1997).*'

L92 a link to a source appears missing 'error etc'

- fixed

L93-96. First of course I am happy that one of my papers is indeed cited, but I take liberty to suggest two corrections of the description given here. First: We showed that a low density of single shoots has survived the winter and resumes first leaf growth (this is not sprouting I would say), then branching and then also flowering. In our estuary, a side branch of the Eastern Scheldt, which is not part of the Wadden Sea, this seasonality is governed by light availability. Katja Philippart found the same pattern in the Dutch Wadden Sea on the flats off Terschelling. Second, I think leaf loss is a continuous process, so I would not support the

statement that ‘most leaves that have not been grazed are shed by December’. Leaf life span is limited throughout the year. We also showed that shoot size declines and shoot mortality continues through the low light season. This is a matter of re-phrasing, not a major objection.

- Thank you for the comments. We have rephrased L102 (track changes version) to:
‘The seagrass in the Wadden Sea is also featured by a strong annual growth cycle. After winter, shoot density is low and growth resumes in spring when conditions (e.g. light and temperature) become favorable. The meadows reach their maximum extent and shoot density in August. The growth of leaves slows down by the end of August, and massive grazing by migratory birds starts in September, leading to a strong decline in shoot density. The loss of leaves continues throughout the winter, while most roots and rhizomes underground remain (Philippart, 1995; Vermaat and Verhagen, 1996).’

L100. Although I greatly appreciate the usefulness of the colorful part 8a) of figure 1, my grasp of the extent of the seagrass beds would be helped if the five plots in part (b) would be larger. Also, does the between-year pattern correspond with what Dolch et al (2013) report?

- We have adjusted the size of the figures according to your suggestion (see above)
- The extent of the meadows we illustrate here is from the aerial mapping dataset (acquired by surveyors on an airplane that draw the seagrass meadows they see on a map) available from LKN.SH Nationalparkverwaltung (2024) and used in Dolch et al. (2013). Though the analysis in Dolch et al (2013) is made based on aerial photographs, they made a comparison with the mapping data and found a high degree of similarity between the two methods (~1% difference in seagrass cover).

L106. A one-week time step. From a plant growth perspective, with RGR at about 0.05 d^{-1} , potential shoot life spans beyond half a year and the lunar tidal cycle moving approximately monthly, this time step to me seems reasonable. But the authors do not justify their choice, and I did not find a start and end to the simulation period.

- A paragraph describing the selection of the time step is now added to section 3.5 Model setup: *‘The timestep of the hydrodynamic model is 2 minutes and the seagrass model is evoked every 7 days. Net relative leaf growth rate in *Z. noltei* typically ranges from -0.05 d^{-1} to 0.05 d^{-1} (Philippart, 1995), implying relatively small changes in biomass over one week. Thus the temporal update of seagrass properties every 7 days is sufficient to capture variability in temperature, light and inundation time, even though some short-term extreme events might not be fully captured. To figure out the uncertainty related to short-term extremes, shorter timesteps (1 day, 4*

days) were tested but did not lead to a notable improvement in model performance while the computational cost increased considerably.'

- A paragraph on the simulation period has been also added to the section 3.5 Model setup: *'The simulation period is 2010 – 2014. The hydro- and morphodynamics are modelled successively, while the seagrass model is reset at the beginning of each year to account for the changing extent of the seagrass meadows observed in the respective year. For the tracking of the seagrass debris released from the meadows in 2014, the first four months of 2015 were also modelled.'*

L118: How large is the unstructured horizontal grid actually? Does it span the whole bay? This is likely, but not explained. Then the variation in insolation, wind and temperature can be substantial between years but the paper does not mention this here. Also a reference to Appendix C should be given here or in section 3.1 as this appendix gives some of the necessary answers, but we also have to find some in the companion paper by Mohr et al 2025. I would greatly appreciate a concise but more complete description of the two models in the current paper..

- Thank you for the suggestions. The model domain is now described in section 3.5 Model setup: *'The model domain consists of the entire Sylt-Rømø Bay, as well as the adjoining part of the North Sea off the coasts of the islands of Sylt and Rømø. The grid resolution gradually increases from 500 m at the open boundary in the offshore area to 100 m inside the bay.'*
- L118 refers to the SCHISM model in general. To make this clearer, we have modified this sentence (L133 track-change version) to: *'[...], a 3D hydrodynamic model based on unstructured horizontal grids and hybrid s-z vertical coordinates.'*

L156: I would rather rephrase this point of leaf loss, based on our findings in the Zandkreek, I would say that the rhizome networks disintegrate 'especially in autumn', whilst leaf loss is a far more continuous process. Also, my personal observations on the grubbing by brent geese and wigeon suggested these animals were feeding in a sloppy way, so this might indeed have caused a substantial loss of above ground material. Jacobs et al (1981) present photographs of feeding gaps.

- Thank you for this valuable insight. We modified the sentence, it now reads *'Loss of seagrass biomass in Z. noltei occurs when leaves are torn off either by wind, currents or during grazing'* (track changes version: L181)

L164 Harwell & Orth (2010 Ecology) demonstrated substantial medium-distance dispersal of floating fragments of *Zostera marina* clones – at least 34 km. This could be a paper worthwhile citing, I see no reason why a similar pattern would be possible for *Z. noltii* in this

comparatively small and sheltered bay system. Evidence from Dolch et al (2013) suggests that indeed successful expansion by *Z. noltii* has occurred in this Rømø-Sylt bay.

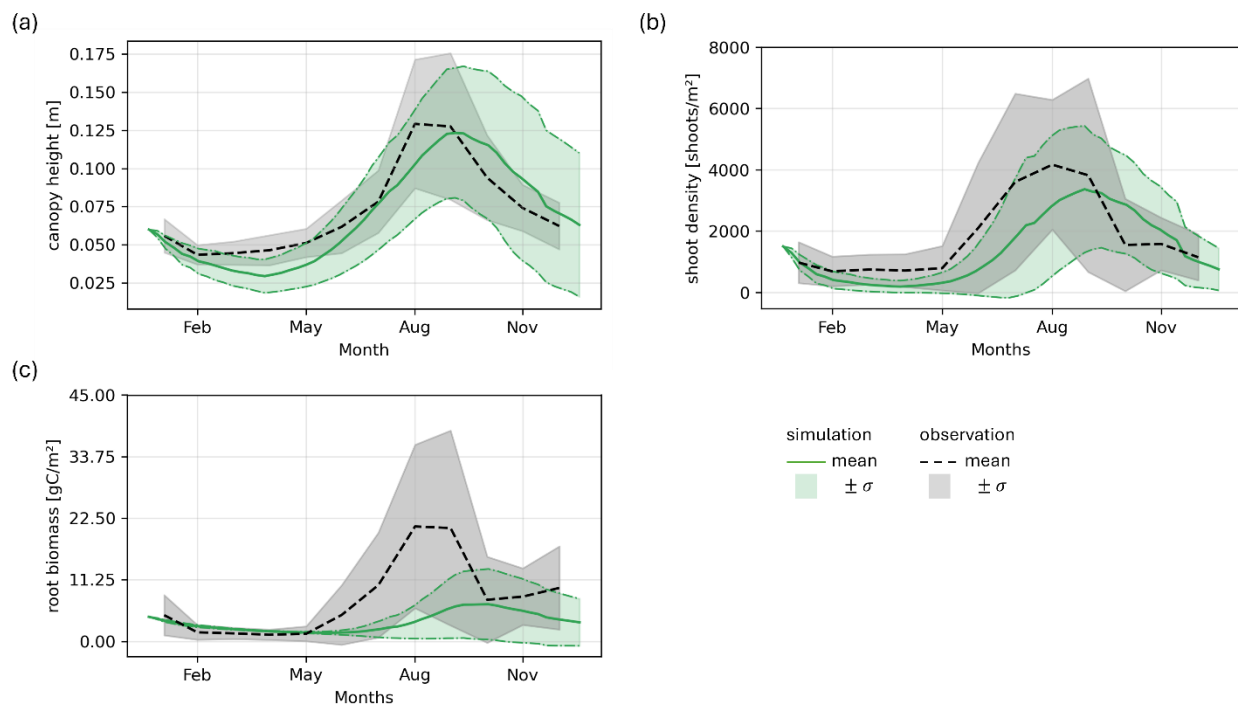
- Thank you. This is a helpful reference that we added to the cited papers

L208: the Vermaat observations were NOT from the Wadden Sea but from the Zandkreek in SW Netherlands.

- Thank you for pointing this out! We have corrected L250 (track changes version) to: *'[...] general seasonal trend that was observed in root biomass of seagrass meadows in the Netherlands (Philippart, 1995; Vermaat et al., 1987; Vermaat and Verhagen, 1996).'*

L214: On figure 3: please use a large font for the axes, and less 'major ticks' for the verticals; and please reduce all these 5 years also to only a mean and SE or STD, the latter possibly also as shaded area, just like the range of observations indicated – now the figure is undecipherable spaghetti, certainly for color-blinds like me.

- We adjusted the size and the number of ticks in the plots, as well as reduced the observations for the different years to a single mean value with standard deviation and hope that the cleaner layout helps with understanding the figure:



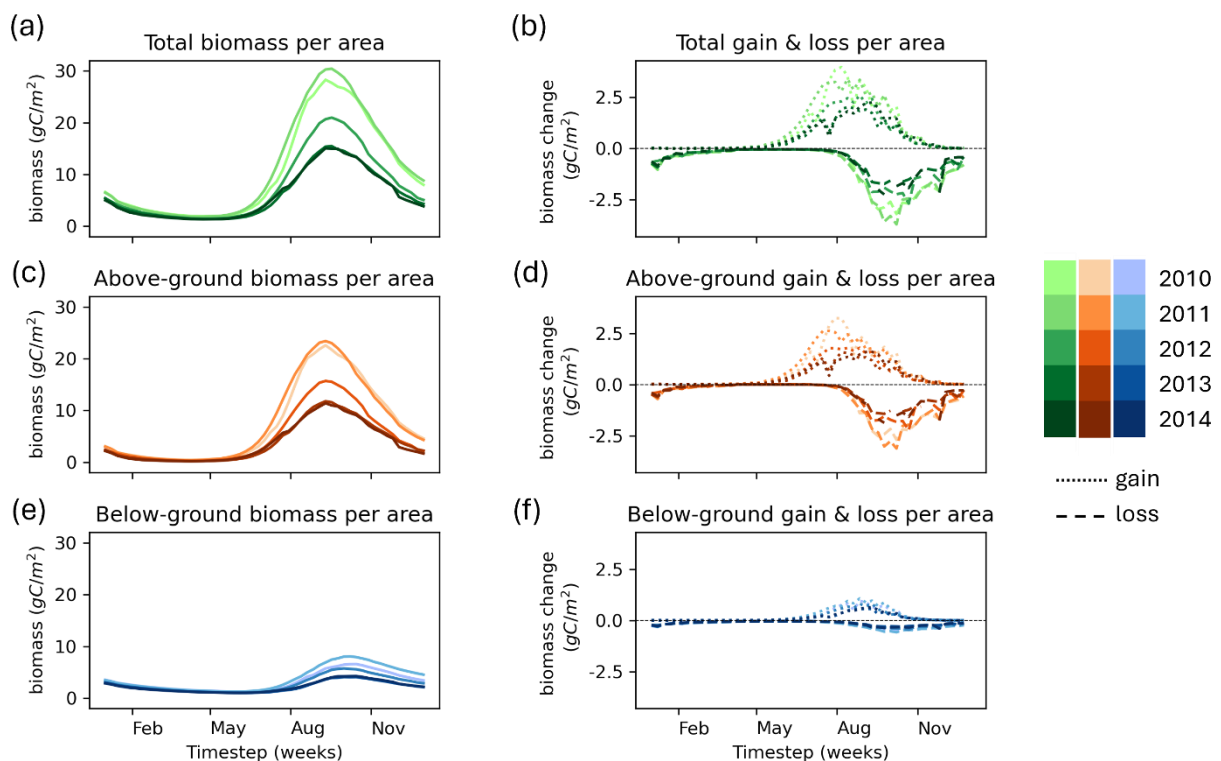
Updated Figure 3: Comparison of observations and model results of (a) seagrass canopy height, (b) shoot density and (c) root biomass. The plots show the mean values and the range between $\pm$ standard deviation σ . The model results are averaged over all computational cells with seagrass. The observation data of the root biomass are derived from the above ground biomass, using the ratio found in between above and below ground biomass in the Netherlands (Philippart, 1995; Vermaat et al., 1987; Vermaat and Verhagen, 1996).

L215: I would appreciate a rounding off to whole numbers so that you do not suggest unjustified precision or accuracy: 17 plm 5 is much more convincing to me than 16.8 plm 5.4. This holds for the whole paper.

- While we recognize the concerns of the reviewer, we decided for the current precision of the numbers in the manuscript since rounding off all values would deviate from simulation results, in some places significantly. We considered rounding off the values in places where it does not lead to a significant deviation from the simulation results, but decided to keep the precision uniform throughout the manuscript, to avoid the implication that some values have a higher precision than others.

L225 this figure 4 is not very clear, and at least part of it should be merged with figure 3.

- We prefer to separate figure 3 and 4 since they are used for different purposes: figure 3 is used for analyzing the performance of the seagrass model, while figure 4 is used as a basis for the discussion of carbon sequestration related to the biomass. To avoid confusion, we have modified figure 4 to make it easier to understand:



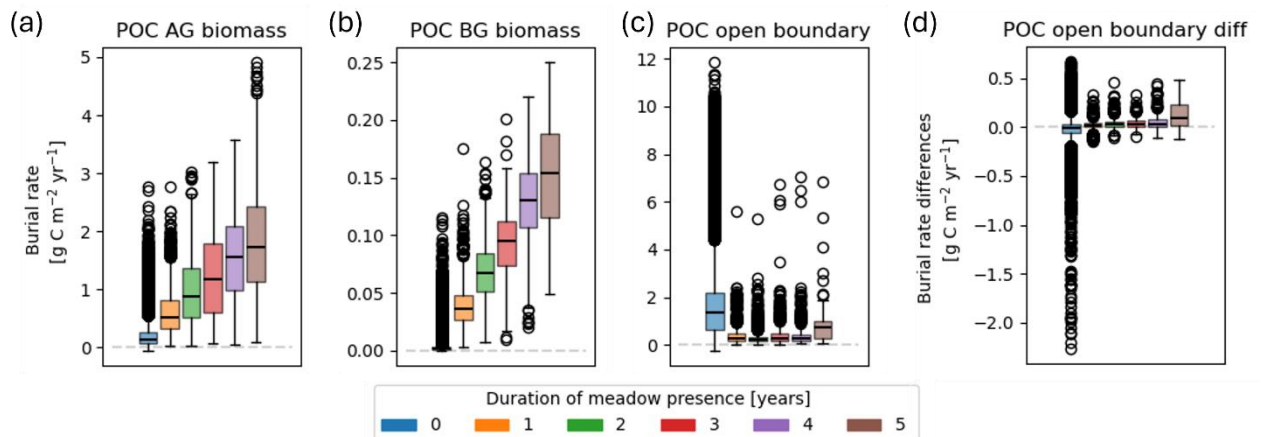
Updated Figure 2: Development of (a) total, (c) above-ground, and (e) below-ground biomass and (b) total, (d) above ground, and (f) below-ground gain and loss of biomass throughout the year, for 2010 to 2014

L238 heterology = variation

- Adopted in manuscript

L245 Figure axis and caption for figure 5: Sequestration: I would maybe rather call it burial?
 ‘Normal spread’ I would guess these are quartiles, so 25% and 75%?

- This aligns with the comments from another reviewer. We have rechecked the manuscript thoroughly to disentangle the different terminology to carbon cycling in the manuscript.
- The normal spread indeed refers to quartiles. We have added this in the figure description



- Updated Figure 3: Boxplots of (a-c) annual burial rates on tidal flats for different POC sources, averaged over five years of simulation time and sorted by years with seagrass cover, and (d) difference in the annual burial rates compared to simulations without seagrass, for allochthonous POC from the open boundary. The boxplots show the median and quartiles for the burial rates on the model grid; dots denote outliers from the spread.

L254 ‘is in’ = ‘ends up in’

- Adopted in the manuscript

L263 figure 6. What was the release date so day 1? The start of the growing season, day dgrow (day 100 table A1, early April), or day 260 (dloss, late Sept if I guess right) that you set as a start of massive leaf loss? Explain here

- The seagrass debris is released continuously at 6-hour intervals at each location where loss of biomass occurs. We have added this information to the caption of figure 6: ‘Seagrass debris is released continuously at 6-hour intervals throughout the simulation at the locations where loss of seagrass biomass occurs for the respective timestep.’ and in section 3.4 ‘tracking of seagrass debris’ L188 (track changes version) ‘Particles representing seagrass leaves are released every 6 hours during the simulation at locations where loss of seagrass biomass occurs due to aging, wind scouring or shedding.’

L267 how much carbon is actually produced by phytoplankton and microphytobenthos? I assume floating mats of macro-algae were not very abundant and periphyton on the seagrass is ignored?

- We did not model phytoplankton or microphytobenthos, since our analysis focusses on the seagrass-originated carbon. We included allochthonous particulate organic carbon (POC) from the open boundary in the North Sea associated with primary production, to see if seagrass meadows are able to modify sedimentation of this external POC. We are aware that this adds a major uncertainty to the model results in terms of the magnitude and relative importance for the buried POC beneath seagrass meadows. Therefore, we have discussed this in section 5.4 Limitations and further research needs.

L272 Insert 'Our modelling outcomes suggest that a fraction etc etc

- Adapted in manuscript as suggested

L295: I like figure 7. Maybe a bit many numbers and fluxes (consider to drop the per m² fluxes as well as the standard errors /standard deviations from the % to create a bit more clarity and overview?) And I would add the area of seagrass and the area of unvegetated mudflats in the caption

- We removed the per m² fluxes from the plots to enhance the readability of the figure. Since the uncertainties for some of the values are quite high compared to the absolute values, dropping them would implicate a false sense of certainty of the results. We added the area of the seagrass meadows to the figure caption. The area of unvegetated mudflats is not relevant for this figure, since the mudflats are not considered separately from the subtidal sediments in this analysis.

L300: you make a big point of the issue that your estimates are lower than those previous ones reported by authority reports and then you stress methodological issues. I would say, they are still within one order of magnitude, and I would probably rather compare with intertidal *Z. noltii* literature, like Martins et al (2022, Ecosystems). Also, I am quite aware of the Wadden Sea as a unique tidal ecosystem, but for example this Ria Formosa (Martins and many others) or the Baye d'Arcachon (Auby & Labourg, 1996, J Sea Res 35) are also highly dynamic etc. That is not the main point, or it should not be. I would focus on the plausible main underlying driver of a rather low carbon burial within intertidal *Z. noltii*. And if you ask me this is (a) the fairly low annual input of seagrass material (the Philippine meadows I worked in have easily 1 kg DW/m²), and (b) the long period in the year with very little seagrass cover or growth.

- Thank you for the helpful comments. The section 5.2 Carbon Sequestration in the Wadden Sea focuses on previous estimates in the Wadden Sea and the comparison to other habitats especially in the German Wadden Sea. The comparison to other regions, such as the Ria Formosa (Martins et al, 2022) is now included in the following section 5.3 according to your suggestions, as well as a remark on the long period with low seagrass cover

L344. For me this whole section on limitations and future research needs can be greatly reduced. I do not feel I am informed of something new or interesting. This may of course be my fault.

- While we acknowledge that the limitations and future research needs are quite straight forward, we included them so that less knowledgeable readers see where uncertainties arise in the model and issues to address in future studies.

L375. In Vermaat & Verhagen (1996) I actually needed self-shading during low tide to explain the observed pattern.

- Self-shading should indeed not be ignored. While we did not explicitly emphasize this term in the model description, we do consider some of its effects on the growth of the seagrass which is represented in the growth limitation by above ground biomass (Eq. A10).

L395 Here you conclude 28% of leaf material is lost as large debris– You separate the loss of finer leaf fragments from larger debris fragments, which likely are several shoots on a rhizome large. But actually this is a continuum. Indeed throughout the growing season the leaf tops are sloughed (or even clipped off, as they were in Mauretania by burrowing fiddler crabs), but some larger material also disappears during summer. So would it matter if you pooled the two POC pools and let them be distributed together over the bay? Now you treat them separately.

- The difference between the two pools is the way they are added to the model. The fine part of above ground biomass is added to the POC in the water column, while the below ground biomass is added to the POC in the sediments. The large debris is calculated separately from both. We acknowledge that they are a continuum and that larger debris continues to disintegrate when being transported. However, we haven't included the disintegration process during transport of the large debris in the model since we are not aware of any field data that can be used to formulate the process. It represents another future research need in modeling, and we have added in the discussion (track changes version L416).

L415 the fraction goes to root and rhizomes. Rhizomes are the larger fraction of the two is my (documented) experience.

- We have modified this sentence to '[...] *is routed to the below ground biomass*' since we do not distinguish between roots and rhizomes in the biomass calculation.

L471: check to remove the capitals from marina and noltii

- Adjusted in manuscript

L475 Tabe A1: you use W/m² as light unit. I would prefer mol or Einstein er m² per day. Watt is Joule per second and that is an instantaneous flux, for the plant I would actually be most interested in the total light received within a daylight period, at the canopy. I am not sure how you estimated this light availability.

- The light unit W/m² is used by the original hydro-morphodynamic model that links the atmospheric forcing (e.g. solar radiation) to light intensity in water. For consistency between the models, we did not change this unit.

Reflist: let someone read all the spelling once more carefully, there is several minor issues there as well.

- Thank you. We went over the reflist again to make sure the spelling is correct.

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