

Peer review

Paper: Mohr et al – Limited blue carbon potential of intertidal seagrass meadows in the Wadden Sea – a case study in a tidal basin

For: EGUSPHERE / Biogeosciences

Jan Vermaat, March 5, 2026

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.

Moderate/major issues

- (a) 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.

(a2) The function f_{expAG} 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 f_{expAG} 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.

(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.

(a4) L419 Your I_k estimate is from Kohlemeier (2016), this reference is absent in the refile. It 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 $\text{plm } 5 \text{ E/m}^2/\text{d}$ from our fig 3a for leaf RGR), which converts to $\text{plm } 12\text{-}15 \text{ W/m}^2 \text{ PAR}$. 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.

(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.

(b) 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 (L169) 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.

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.

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.

(c) 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 thee 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.

Minor Issues

L 11 insert 'intertidal' before seagrass

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.

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).

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 ..'.

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 works needs to be cited here when Wadden Sea *Zostera noltii* dynamics are modelled.

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 Potoroglou 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>

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.

L61 include 'intertidal' before seagrass

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.

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 Eems 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?

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

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.

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?

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.

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.

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 aboveground material. Jacobs et al (1981) present photographs of feeding gaps.

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.

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

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.

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.

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

L238 heterology = variation

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%?

L254 'is in' = 'ends up in'

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

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?

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

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

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.

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.

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

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.

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

L471: check to remove the capitals from marina and noltii

L475 Tab 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.

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

==