

Interactive comment on “On biotic and abiotic drivers of the microphytobenthos seasonal cycle in a temperate intertidal mudflat: a modelling study” by Raphaël Savelli et al.

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We gratefully thank referee #1 for his constructive comments with respect to our manuscript. In order to improve the manuscript with respect to these comments, we amended the manuscript as suggested by the referee wherever it was possible.

The modifications made in the manuscript are based on a new model run, which includes the model improvements suggested by the three reviewers. They include the mud temperature model, the *P. ulvae* grazing mathematical formulation and the setting of the mean time spent by a MPB cell at the sediment surface. As a result, the simulated data presented here are modified compared to the initial version of the

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manuscript.

1. "The temperature inhibition value used to achieve this outcome had to be 'tuned' to match the data and the temperature inhibition used for MPB was lower than in previous studies, which was concerning. How sensitive is the annual pattern to this temp? Could you show a run where T_{opt} is ~ 20 C?"

The different microphytobenthic T_{opt} estimation techniques and contrasting in situ versus laboratory conditions explain the range of values reported in the literature (from 20 to 30 °C). In the model run where T_{opt} was set to 20 °C the seasonality of MPB is very similar to that depicted by the model ran with T_{opt} value set to 18 °C. However, while the simulated MPB biomass was maintained during winter 2008-2009 with a T_{opt} value of 18 °C, it vanished with a T_{opt} value of 20 °C. Such a result suggests that at our study site a T_{opt} value of 18 °C allows MPB to cope with cold winter conditions and relatively low mud surface temperatures.

In the discussion section (4.2), additional detrimental effects of high temperature on epipellic diatoms are discussed. Those effects are not considered in laboratory-based estimates of T_{opt} given in Blanchard et al. (1997) because the authors worked with a suspension of MPB cells. In 2008, PAM measurements showed a lower photosynthetic activity in July than in February on the Brouage mudflat (pers. com. S. Lefebvre and J. Lavaud). The authors suggest that micromigrations are lowered by high mud surface temperature (and so by the pore water evaporation and resulting increase of salinity) and that MPB is unable to avoid harmful light conditions at mud surface temperature even lower than 20 °C. MPB cells are therefore photo-inhibited via high temperature-related processes. As photo-inhibition is not accounted for in the Production-Irradiance relationship used in the model, a lower T_{opt} value than the range estimated in the literature is a way to account for the negative feedback of photo-inhibition on the photosynthetic rate triggered by high temperature-related processes within the sediment.

We modified the Discussion section 4.2 (p. 13, l 8-11) to make it clearer:

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" As the detrimental effects of high salinity levels is not explicitly accounted for in the model as a forcing variable, they are implicitly accounted for through temperature-related mechanisms, i.e. a T_{opt} value lower than values reported in the literature (Table 5). Such an approach overestimates the thermo-inhibition process and, as such, promotes low PP rates that implicitly reproduces in the model the detrimental effects of desiccation on the microphytobenthic cells."

2. "Another weakness of the study was that it had a rather limited data set for validation. I am surprised the authors were not able to find a study site with a larger time series of data for grazers and directly measured MPB biomass. "

The lack of validation data was pointed out by the three referees. We agree with this comment. Located 1.7 km from the shore our study site is remote. It is, however, the most studied site in the area but the sampling variables and protocols vary from year-to-year. We hence made the choice to use 2008 data from the French national project VASIREMI as it is unique in the area in terms of space and time coincident in situ measurements of both physical (sediment temperature) and biological (MPB and grazer biomass) variables during two contrasting seasons. In addition, high resolution atmospheric and oceanic forcings required to constrain the model are available for 2008.

To cope with the lack of data, we used two datasets of in situ MPB Chl a concentration available for the same station. The two datasets cover the spring, summer and winter seasons in 2012 and 2013. We added a new Figure (R1, attached to the answer to referees) to show the MPB seasonal cycle in terms of Chl a concentration based on the 2008, 2012 and 2013 data.

We added a new sentence in the Materials and Methods section (2.1.1) as follows: "In addition to the 2008 dataset, we used data of in situ MPB Chl a concentration collected within the 1st cm of sediment at the same station in April 19 – 22, 2012, July 05, 2012, November 14, 2012, February 11, 2013 and April 10, 2013). The sampling protocol is

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fully detailed in Lavergne et al. (2017)."

The new figure (R1, attached to the answer to referees) aims at showing the observed seasonal cycle of MPB Chl a at our study site based on the data available, i.e. a 3-year dataset (2008, 2012, 2013). A new paragraph was added in the Results section (3.2) as follows:

"Two distinct periods were identified from in situ Chl a measurements in the sediment first cm (Fig. R1). The observed seasonal cycle of Chl a was characterised by a spring bloom and by a decrease of Chl a concentration in summer. Given the few available measurements in autumn, the seasonal MPB dynamics at this season remained uncertain. The maximum of Chl a concentration reached during the spring bloom ranged between 234 and 306 mg Chl a m⁻², which is consistent with the concentration simulated by the model in 2008."

3. "Given the importance of the physical model, it was also disappointing that there was very little temperature data, which is very easy to collect. The limited data available also seemed to disagree in pattern and magnitude a lot more than I would have regarded as acceptable for a physical parameter."

We took into account the referees #1 and #2 comments regarding the sediment temperature model. Based on Guarini et al. (1997) and Phizacklae (1987), we modified the physical model by setting a rapid equilibrium between mud surface temperature and the temperature of the overlying water layer, i.e. the simulated mud surface temperature is now set to water temperature during immersion periods. In the new model run, the root mean squared error (RMSE) between the observed and simulated MST values for the two 2008 periods (RMSE=1.81 °C) is reduced twice compared to the previous model run (RMSE=3.98 °C). In addition, the Pearson's correlation coefficient is higher in the new model run ($r=0.93$) compared to the previous model run ($r=0.76$). The referees comments helped to significantly improve the model capability to simulate the MST.

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4. "In the conclusions and perspectives part of the manuscript, it then goes on to say resuspension is not included in the model. Could the authors please clarify what the generic loss term is?"

We agree with referees #1 and #3 that the resuspension process is not explicitly detailed in the manuscript. As there are no data available of current velocity on the sea bed in 2008 at our study station, we did not infer on hydrodynamically-related resuspension processes of MPB. In the model, we assumed a constant rate of MPB cells resuspended during immersion periods. During immersion periods, the generic loss term (vF , 0.003 h^{-1}) includes the chronic resuspension and MPB senescence processes. During emersion periods, the loss term is lower (mF , 0.001 h^{-1}) as it only represents the MPB senescence.

5. "I also suggest the discussion of resuspension be included earlier on in the discussion, rather than being raised right at the end. I would also like to see this discussion expanded a little. At present, it really only addresses possible PP by MPB during resuspension, it does not address how much MPB might be exported. The possible resuspension and export of MPB should be discussed and omission from the model justified."

We agree with referee #1 that some text on how much MPB might be exported and on the justifications about our mathematical formulation were lacking in the discussion. In the original version of the manuscript, we included this part in the perspectives section, because we currently work on the MPB resuspension mechanisms and related physical processes to be further included in the model. The referee #1 comment was hence taken into account by adding some text in the Results and Discussion sections.

The Results section was modified as follows: "In the model, the linear loss terms applied to the MPB biomass simulated within the 1st cm translated into a yearly averaged resuspension of $1.7 \pm 0.3\%$ of the averaged MPB biomass in the 1st cm of sediment during high tides. Over the year, 25 % of the simulated MPB production during low

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tides was resuspended, which corresponded to a total annual resuspension of 31.6 g C m^{-2} ."

The Discussion section was modified as follows: "The short-term daily dynamics of MPB is regulated by resuspension events (Blanchard et al., 2002). The intensity of resuspension of MPB into the water column can be either chronic or catastrophic according to the flow velocity and the sediment stabilization (Marrioti and Fagherrazzi, 2012). Catastrophic events can locally resuspend all the MPB biomass as the resuspended sediment layer is thicker than the vertical distribution of MPB biomass (Marrioti and Fagherrazzi, 2012). The repeated occurrences of such events over several days can shape the seasonal cycle of MPB by lowering the biomass of photosynthetically competent MPB. In their model, Guarini et al., (2008) introduced a chronic resuspension of all the MPB biomass remaining in the biofilm when tidal floods occurred. In their parametrization, the MPB biomass remains at the sediment surface according to a mean time spent at the surface (equivalent to τ in our study). In our model, the chronic resuspension of MPB biomass is formulated by a linear loss term of the MPB biomass within the first cm (0.002 h^{-1}). In the absence of MPB biomass deposition, the total simulated MPB biomass which is resuspended into the water column represents 25% of the simulated benthic MPB annual production. Such a value supports the fact that benthic MPB production contributes significantly to the pelagic food web (Perissinotto et al., 2003; Krumme et al., 2008). In the light of the work of Marrioti and Fagherrazzi (2012), resuspension and deposition are key mechanisms that need to be related to fauna bioturbation, sediment characteristics (e.g. nature and stabilization) and hydrodynamics (Marrioti and Fagherrazzi, 2012). Such an approach requires the availability of waves and current data to estimate the bed shear stress and modulate the intensity of resuspension (from chronic to catastrophic events), which are not available at our study site for 2008."

6. "Is it possible the loss of biomass is just resuspension on a few windy days?"

Bed shear stress induced by physical factors (i.e. current and wave orbital velocities,

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bed roughness) and sediment stabilization control the resuspension of sediment and associated MPB (Tolhurst et al., 2003). Dupuy et al. (2014) showed that benthic diatoms are resuspended at a friction velocity of 3 cm s⁻¹. This critical friction velocity for diatoms resuspension can be lower than the tidal current velocity without the action of wind during spring tides on sheltered mudflats according to the simulations of Le Hir et al., (2000). In addition, the impact of grazing activity by benthic deposit feeders has to be considered. Bioturbation generates a fluff layer of sediment-organic matrix, which is resuspended at a lower critical friction velocity (1 cm s⁻¹ for *P. ulvae* bioturbated fluff layer; Orvain et al., 2004). Chronic resuspension of MPB cells can therefore occur with no wind, as shown by Guarini et al. (2008). Furthermore, waves and winds interact with tidal currents. When considering an angle between the waves and the current direction for the bed shear stress calculation (Soulsby, 1997), the wave forcing can be antagonistic, synergetic or neutral on the current bed shear stress according to the tidal and the wave conditions. Resuspension can hence occur without any action of winds.

7. "The manuscript was generally well written and the ideas well constructed. There were a few spelling and grammatical issues. I have noted a few below, but it would be easiest for the authors to use a spell checker to find these."

Spelling and grammatical issues have been checked according to the referee comment.

8. "Pg 4 l19. Could clarify a little better that (1st cm) means 1st cm of sediment."

It has been changed by (1st cm of sediment).

9. "Pg 8 line 32 onwards. This is a little confusing. first it is stated that grazing is mostly limiting, then it says days where MPB biomass consumed was larger than that produced occurred only 8.7% of the time."

The sentence is confusing. Considering the modification made on the grazing formulation in the model, the results are now different from the original version of the manuscript. Grazing is now mostly significant during phase 1. The sentence was mod-

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ified as follows:

"The top-down control by *P. ulvae* occurred mostly during phase 1, when the ingested MPB biomass exceeded the MPB PP during 7% of the time (Fig. 9b)."

10. "Pg 15 line 13. This implies a very high growth efficiency (13.63/15.8). Can this be correct? Or do they graze other food sources too?"

The initial sentence is confusing: "The combined effect of grazing and thermo-inhibition translates into 22 % (5.9 g C) of the simulated annual MPB PP channelled towards *P. ulvae* gross secondary production. The simulated *P. ulvae* gross secondary production is 27 g C m⁻² y⁻¹".

On the 5.9 g C grazed by *P. ulvae* during events of combined grazing and thermo-inhibition only 55% (assimilation rate γ , Annexe B) was assimilated by *P. ulvae*, which corresponds to 3.2 g C. The sentence was hence modified as follows:

"The combined effect of grazing and thermo-inhibition translates into 22 % (5.9 g C) of the simulated annual MPB PP channelled towards the *P. ulvae* compartment before assimilation and gross secondary production. The simulated annual *P. ulvae* gross secondary production is 27 g C m⁻² y⁻¹."

11. "Figure 5. I don't understand why there is a small plot (original data) for biomass. If this is from the model, it should be more continuous? Or perhaps you have only extracted the same days as the NDVI data? Why not show all the data?"

For the model/satellite comparison, the MPB biomass simulated in the biofilm was extracted for the same days than the NDVI data. In order to filter both NDVI and simulated MPB biomass data, the resulting time series were first regularised to obtain regular time intervals between all points. Small plots were hence showed to illustrate the shape of the original time series before the numerical treatment. The figure and the caption were improved according to the comment of referee #2 to make it clearer (small plots were removed and the extracted points were overlaid on the main plots).

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12. "Figure 9b. Caption could specify days dominated by grazing pressure when temperature is greater than grazing optimum ($T > T_{optZ}$). I found this a little hard to understand at first."

The information given in the legend was included and detailed in the figure caption to make it clearer.

Captions of attached figures:

Fig. R1: Daily averaged in situ MPB biomass sampled in the sediment 1st cm at the study station on the Brouage mudflat in 2008 (black full dots), 2012 (grey full dots) and 2013 (blue full dots). Error bars correspond to the standard deviation.

Fig. R2: Univariate sensitivity analysis of the simulated MPB annual production to: a) the temperature optimum for MPB growth (T_{opt}); b) the temperature maximum for MPB growth (T_{max}); c) the light saturation parameter (E_k); d) the half-saturation constant for light use (K_E); e) the optimal temperature for grazing (T_{optZ}); f) the shape parameter of the temperature related grazing (α_Z). r is the Spearman's correlation coefficient (asterisk inform when $p < 0.05$) and N is the number of tested values for each biological constant.

Fig. R3: Difference between the observed air temperature and the simulated mud surface temperature ($^{\circ}\text{C}$) in 2008.

Fig. R4: Seasonal cycle of the MPB simulated biomass in the 1st cm of sediment in the presence (red full line) and in the absence of *P. ulvae* (red dashed line) in 2008.

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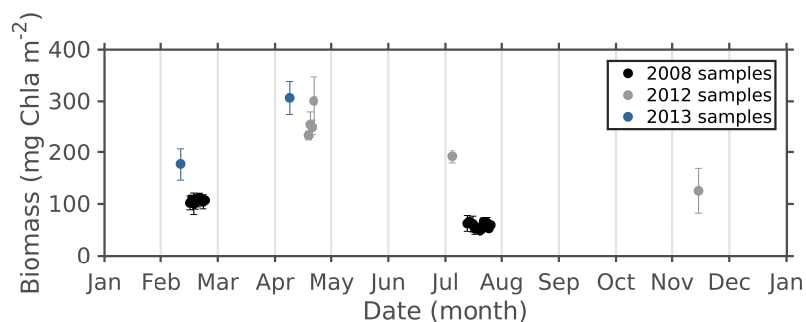


Fig. 1.

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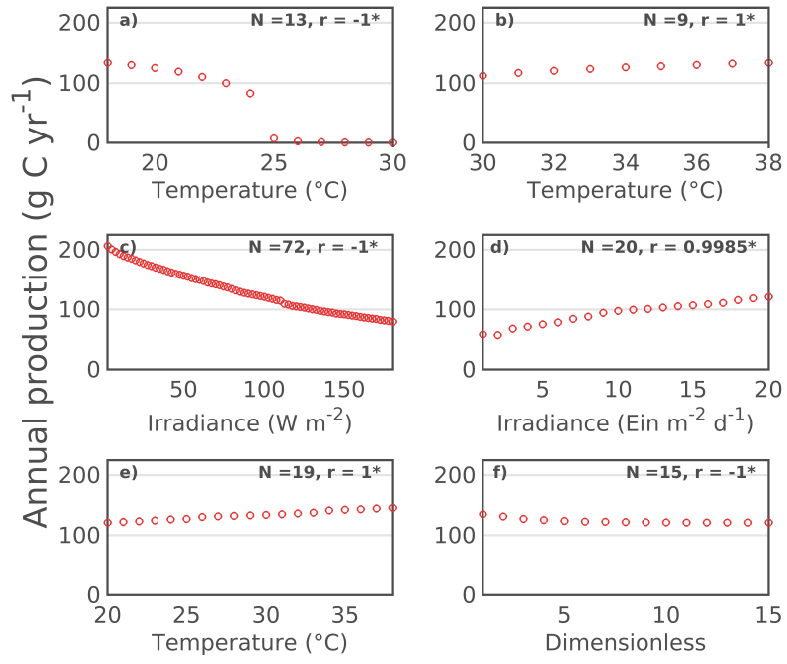


Fig. 2.

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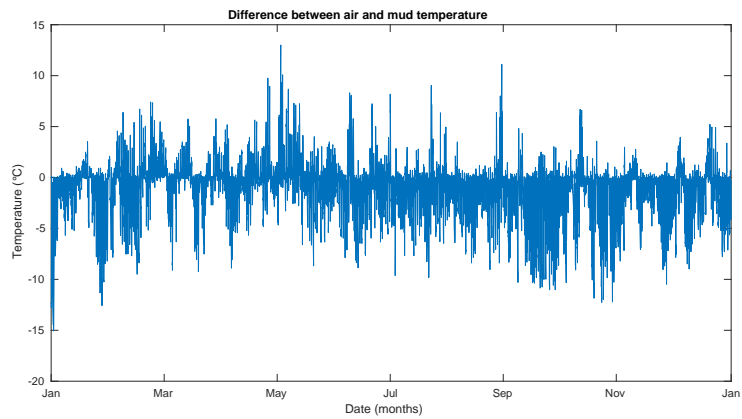


Fig. 3.

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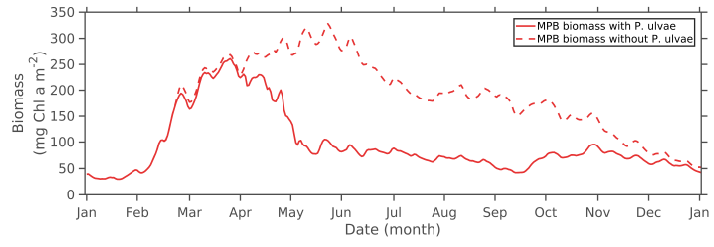


Fig. 4.