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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 #3 for her/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 only outcome that I found did not fit my preconceived understanding on MPB dynamics was that Peringia grazing actually only had a significant effect on very few days over the summer. That is a surprise." "P8 L30 and P15,L1 This is the one area I found surprising, given the number of published accounts of strong inverse correlations between Peringia (Hydrobia) abundance and biomass on NW European mudflats. Particularly when the authors have said in an earlier paragraph that during phase 2 light was limiting, which would make the biomass response even more susceptible to being grazed down? How convinced are the authors that this is a true situation, or is the model not capturing the real impact of grazers during this phase?"

In the model, P. ulvae grazing is considered as limiting in the Results section only when the amount of MPB biomass grazed by P. ulvae is higher than the amount of biomass produced by MPB in the model. As such, a significant effect of grazing is simulated during 12 days in 2008. However, grazing can impact the MPB biomass even when it is not the most limiting term for MPB growth. We show on a new figure (Fig. R4, attached to the answer to referees) the simulated MPB total biomass with and without P. ulvae grazing in the model. It clearly shows that grazing, even if it is not the most limiting term, impacts the MPB dynamics during the whole summer. As suggested in the literature, the MPB biomass is much lower in summer in presence than in the absence of P. ulvae (Sahan et al., 2007; Weerman et al., 2011).

2. "I think the authors need to validate their model using some other data sets, perhaps from some of the other mudflat systems that they have (and are) working on within the Atlantic / Channel seaboard, or resolved at finer temporal scales to demonstrate the robustness of the assumptions under pinning the model. After all, if the model works on one mudflat, it ought to be applicable to other similar systems, and this would really demonstrate its value to others workers in the field."

The lack of validation data was pointed out by the three referees. We agree with this

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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 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

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between 234 and 306 mg Chl a m-2, which is consistent with the concentration simulated by the model in 2008."

Applying the model to other intertidal systems requires year- and site-specific atmospheric and oceanic forcings along with multiparametric data to initiate and validate the model, which is not trivial to set up. However, we agree with the referee that the model portability to other mudflats should be envisaged as it would provide support to the model predicting capacity.

3. "Overall, what are the error terms around the modelled responses? The figures show some significant error terms in the existing field data, but no errors around the model outcomes."

In situ data include replicates at a same sampling time, which permits to compute the standard deviation around the mean. Such an approach is not possible with the model as a unique solution is estimated at each time step by the way of the numerical integration. A numerical model is by nature a mathematical approximation of a true state. As such, it will always depart from a true solution, which is difficult to quantify as it depends on the model complexity and the number of degrees of freedom. Some uncertainty is first introduced in the model through the quality of the atmospheric and oceanic forcings. In addition, the model relies on the choice of mathematical functions and constants, which is based, however, on a theoretical background gathered from observations in the field and/or laboratory. The choice of the parameters values and functions also introduces some uncertainty in the numerical estimates. A way of quantifying this uncertainty and the relevance of a model structure is to perform a sensitivity analysis. We present in the manuscript such an analysis, reinforced by our response to the comment made by the referee #2. It results that the model is sensitive to the choice of the temperature- and light-related constants. More data, including remote sensing data, will be further required to quantitatively assess an error around the model predictions. Nevertheless, the model/data comparison we show in our study and that uses time-limited but time-coincident situ data covering physical (mud temperature) and bio-

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logical (MPB and P. ulvae) variables brings some confidence to a reasonable predictive capability of the coupled model.

4. "P3, L15. “in the light of current knowledge. . ..role still unclear”. I think there is a very extensive set of literature on the roles of abiotic and biotic factors for MPB dynamics, so this statement portrays a false sense of uncertainty. "

We modified the sentence as follows: "The role of each individual abiotic or biotic factor involved in the MPB short term dynamics is well documented (eg. Feuillet-Girard, 1994; Admiraal, 1977; Vieira et al., 2016; Blanchard and Cariou-Le Gall, 1994; Barranguet et al., 1998; Light and Beardall, 2001; Pniewski et al., 2015; Barnett et al., 2015; Blanchard et al., 1997; Cartaxana et al., 2015; Coelho et al., 2009; Weerman et al., 2011; Pinckney et al., 2003; Admiraal et al., 1983; Montagna et al., 1995; Blanchard et al., 2002; Dupuy et al., 2014). However, and in the light of the current knowledge, the quantitative contribution of combined factors in the seasonal MPB dynamics remains uncertain."

5. "Figure 5 is an important figure. It needs to be made clear in the legend that this refers to S*. Why when the NVDI signal varies by over 100% in the course of the year, does the S* value only vary by at most 6-7%. Though the “pattern” looks the same (what is the correlation or correspondence between the two annual cycles?), the order of magnitude of change does not. How can this be, when they are assumed to be measuring the same thing?"

With respect to the satellite data, we agree with the referee #3 that the remotely-sensed NDVI and simulated Chl a concentration data cannot be quantitatively compared as they are not the same variable. However, the Spearman’s correlation coefficient between the NDVI and the simulated Chl a concentration in the biofilm is 0.58 ($p < 0.05$). The NDVI/simulated Chl a relationship is therefore qualitatively reliable and can inform on the MPB seasonality. At a constant Chl a concentration, the Chl a pigments would absorb more light in summer than in winter because of the package effect. The

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remotely-sensed NDVI would hence be expected to be higher in summer than in winter for a same biomass. However, based on field measurements, the NDVI is observed to be higher in winter (March) than in summer suggesting that the package effect of the Chl a pigments has no influence on the NDVI seasonality.

Furthermore, the simulated biofilm saturates quickly in terms of biomass at the sediment surface. Such a pattern therefore tempers short terms variations of the MPB dynamics at the sediment surface retrieved by the NDVI.

6. "P7, L9 onwards. The variable Ts is dependent on overall biomass, but then the outcomes of this seem counter-intuitive to what we know about biofilms and cell micro-cycling. Cells appear to spend the time they need at the surface to photosynthesise and accumulate enough carbon, while minimising their risk of photodamage. So each cell spending 54 minutes at the surface during January and August, while only 12 minutes in April, appears to be an outcome of an underlying assumption about biomass, rather than an understanding about diatom photophysiology and behaviour?"

The mathematical formulation was chosen to introduce an effect of carrying capacity in the simulated MPB dynamics. However, we agree with the referee #3 that, in terms of photophysiology and light requirements for the photosynthesis and inorganic carbon fixation, the mathematical formulation used in the model is counter-intuitive. To that respect, we replaced the initial mathematical formulation of Ts by the one from Guarini et al., (2008), which assumes a constant Ts value (Ts=1 h) over the year.

7. "P7, L20, clarify if this is the assumed intrinsic growth rate?

The simulated growth rate is not the intrinsic growth rate. It is obtained from the product between the simulated production rate in mg C mg Chl a-1 h-1 and the simulated Chla:C ratio to get the production rate in mg Chl a mg Chl a-1 h-1 or h-1. As such, the simulated growth rate does not include loss terms and is hence a gross growth rate. The sentence was hence modified as follows: "The annual mean of the MPB gross growth rate simulated within the biofilm was 0.25 $\pm$ 0.07 d -1 with a range of values

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between 0.05 d -1 and 0.41 d -1 ."

8. "P8, L14 onwards. This section appears to be saying that during the summer periods, the biofilms are light limited, because there are longer days? If this just a mathematical artefact? After all, an individual cell only needs some many quanta of light to meet its photosynthetic requirements, and with variable migration, lower biomass and longer days, why would individual cells be light limited? "

We agree that individual cells are supposed to meet their photosynthetic requirements more easily in summer than in winter. In the model, the simulated light limitation takes into account the effect of low tides occurrence over the daytime periods (i.e. variable light levels) and the temperature conditions (i.e. optimal or not compared to the temperature optimum for MPB growth).

On the first hand, light is limiting in the model during daytime emersion periods in summer when the daytime emersion periods occur early/late in the daytime period during neap tides. The simulated MPB migrates towards the sediment surface but is exposed to low light levels during dawn and dusk compared to spring tides conditions when the emersion periods occur in the middle of the day at high light levels.

On the other hand, the simulated light limitation during daytime emersion periods in summer also relies on the simulated mud surface temperature. Despite favourable light levels during daytime emersion periods, the simulated mud surface temperature can be close to the temperature optimum for MPB growth and can hence promote microphytobenthic growth in relatively low light conditions.

The text was modified as follows: "In phase 2, light was the most limiting factor (60%, Table 2). The increasing daytime duration allowed MPB to grow on two daytime emersion periods at the beginning and at the end of the daytime period during neap tides. However, the simulated MPB is exposed to relatively low light levels during dawn and dusk compared to spring tides conditions, when the emersion periods occur in the middle of the day at relatively high light levels."

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9. "P13, L6, see Steele et al. Biofouling 30, 987 – 998 for a detailed study of EPS and desiccation on diatom photosynthetic capacity

We thank the referee #3 for the reference. The positive effects of EPS on diatoms is much more developed than in the previous cited reference. We hence replaced it by that of Steele et al. (2014).

10. "P18, L3. What happens if a resuspension element is included in the model (Dupuy et al gives 3%, Blanchard et al 2006, in In J. Kromkamp [ed.], Functioning of microphytobenthos in estuaries: Proceedings of the microphytobenthos symposium, Amsterdam, The Netherlands, August 2003. Royal Netherlands Academy of Arts and Sciences, and Hanlon et al. 2006 Limnol. Oceanogr. 51: 79-93, provide other values, and de Jonge and van Beusekom (op. cit) provide some critical wind speeds)?"

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.

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 first cm translated into a yearly averaged

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resuspension of 1.7 $\pm$ 0.3% of the averaged MPB biomass in the sediment 1st cm during high tides. Over the year, 25 % of the simulated MPB production during low 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 tau 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. "

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

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 (Topt); b) the temperature maximum for MPB growth (Tmax); c) the light saturation parameter (Ek); d) the half-saturation constant for light use (KE); e) the optimal temperature for grazing (ToptZ); f) the shape parameter of the temperature related grazing (alphaZ). 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

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surface temperature (°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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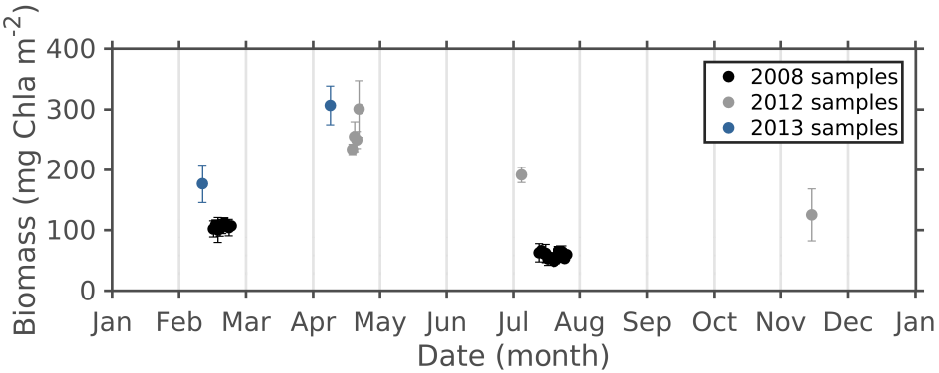

Fig. 1.

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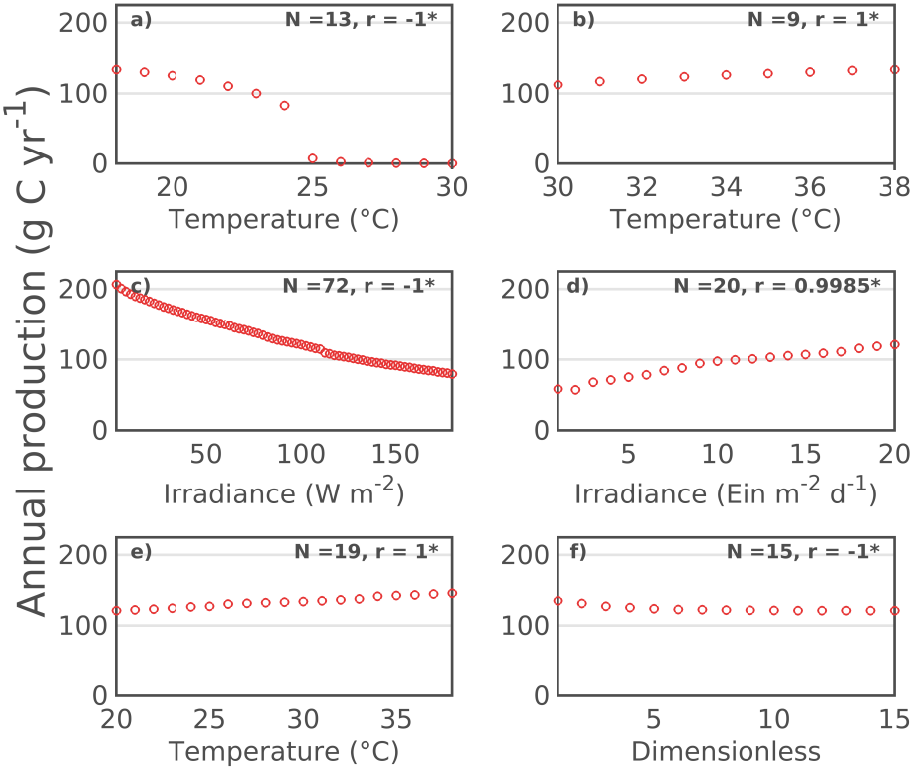

Fig. 2.

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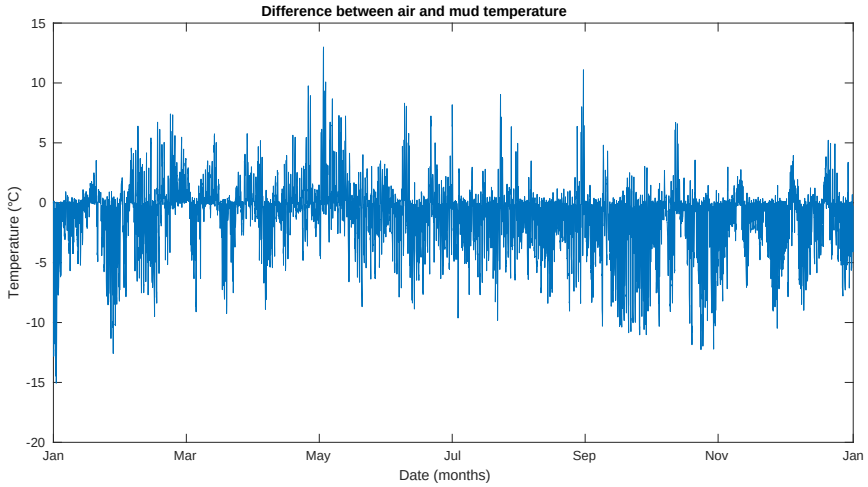

Fig. 3.

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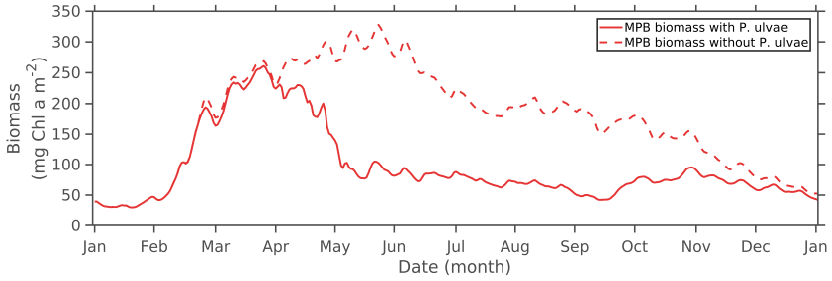

Fig. 4.

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