

## ***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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Received and published: 18 September 2018

We gratefully thank referee #2 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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1. "The two short periods of in-situ data are not sufficient to constrain the seasonal cycle. With these data, many other potential modelled seasonal cycles, including constant values (straight lines) could be equally valid results. The authors mention a monthly data set of chlorophyll observations from the same mud flat covering March 1992 to February 1993. A simulation for this period should be included and compared with the observations. The remote-sensing data are not really a substitute for this because they may have their own issues, and in the current manuscript are not the same variable."

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, which is not the case for 1992 and 1993.

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 1st 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<sup>-2</sup>, which is consistent with the concentration simulated by the model in 2008."

With respect to the satellite data, we agree with the referee #2 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 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 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.

2. "The sensitivity analysis leaves me puzzled. Why calculate correlation coefficients which assume linearity if the model equations are clearly non-linear? For which areas of the varied parameter space does the primary production collapse? Why? Why was this subset of parameters selected and not others? Instead of randomised monte-carlo

simulations and questionable statistics, I would think a series of graphs where primary production is plotted as a function of a varied parameter (with others set to reference values) would be much more instructive, or should in the least be used to analyse what happens in the Monte-Carlo simulations. Such an approach could even be used to restrict the range of variation of the parameters such that not so many simulations collapse (if the collapsing simulations occur towards the extremities of the parameter space). These new ranges could then also be critically compared with the ranges reported in the literature."

We took into account the referee #2 comment about the non-linearity in the model between the biological constants and MPB annual production. We performed the same sensitivity analysis but we used the Spearman's correlation coefficient, which is adapted for non-linear relationships. The results of the sensitivity analysis are similar to that from the original version of the manuscript. The model remains mainly sensitive to the temperature parameters related to the MPB growth rate and, to a lesser extent, to the light saturation parameters ( $E_k$ ) and the half saturation constant for light use ( $K_E$ ).

In addition, we took into account the referee #2 comment by varying in the model one biological constant at once in the range of reported values found in the literature. The relationships between the biological constants and the simulated annual MPB production are presented in a new figure (Fig. R2, attached to the answer to referees). It results from the new analysis that the simulated annual MPB production is also mainly sensitive to  $T_{opt}$ ,  $E_k$  et  $K_E$ . In addition, the MPB production collapses when  $T_{opt}$  is higher than 25 °C. As  $T_{max}$  remained constant when  $T_{opt}$  varied, this new analysis highlights the role of  $T_{amp}$  as in the Monte-Carlo analysis. The two analyses hence show very similar results.

3. "Eq. A7 should include  $S(\text{mud\_to\_water})$ . Also, the heating/cooling of the water column should be related to the instantaneous water depth. I can't find this in the equations. Are these just issues with the representation in the manuscript, or is the heat balance model flawed? This should be corrected. " "It is suggested (p. 6, l.

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10) that the mud temperature (fig 4) closely follows the air temperature (fig 3). This is difficult to see. Please include the air temperature in fig 4 for better comparison. "The point above triggers the question if a full mud temperature model is necessary. This question could be easily addressed by driving the microphytobentos model with the air temperature (or air temperature when exposed and water temperature when submerged) and comparing the results with the reference simulation."

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.

Regarding the definition of the total water depth, we agree with referee #2 that the description on how it is considered in the model was not clear in the Appendix section of the original version of the manuscript. In the model, the total water depth is represented as two fractions (set by the alpha coefficient) of the whole water column (i.e. from the top to the sea bed). The alpha coefficient sets the top fraction of the total water depth that is influenced by the atmospheric forcings (i.e. equivalent to the mixed layer depth). The heat balance between water and air is resolved in the model within this top layer while the bottom layer set by the remaining fraction of the total water depth remains at the water temperature computed at the previous time step of the model run. The simulated water temperature of the whole water column results from the mixing between the two layers. We modified the description of the total water depth in the

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model and provide more details in the Appendix A.

With respect to the air and mud temperature relationship, we modified the original sentence (p6, l21) to make it clearer: "The simulated temperature of surface mud followed the seasonal cycle of air temperature (Pearson's  $r = 0.85$ ,  $p < 0.05$ ; Fig. 3d and Fig. 4)." Figure R3 shows the air-mud temperature difference. The mean difference computed from the absolute air-mud differences is  $2.14 \pm 2.3$  °C, which reflects the high differences between the air and mud temperature at the synoptic scale. As a consequence, the air temperature forcing cannot be used to constrain the MPB growth as it departs too much from the simulated mud temperature.

4. "I'm puzzled by the few sharp peaks in ingestion. Is this realistic behaviour or an artifact of the model? If the latter, could it be related to the exponent in Eq B11, which can change sign depending on the temperature? This seems odd from a mathematical perspective. Was this kind of behaviour of the equation envisaged/included in the range of values considered in the publication in which this relationship was proposed?"

Referees #2 and #3 pointed out possible issues regarding the simulated ingestion rate of *P. ulvae*. In order to improve the ingestion rate simulated in the model when the simulated mud surface temperature exceeds the optimal temperature for grazing, we formulated the ingestion-temperature relationship according to a Holling type III sigmoid mathematical function (see Gentleman et al., 2003), which accounts for the effect of mud temperature. The new equation is described in the Appendix:

"The individual ingestion rate IR (ng Chl a ind<sup>-1</sup> h<sup>-1</sup>) of *P. ulvae* is calculated using a Holling type III sigmoid mathematical function accounting for the effect of mud temperature T (°C):

$$IR = IR_{max} * (T^{\alpha Z} / (T^{\alpha Z} + ((T_{optZ} + 10)/2)^{\alpha Z})) * H(S - 0.5),$$

where  $T_{optZ}$  (°C) is the optimal temperature for grazing.  $IR_{max}$  is the maximal observed individual ingestion rate.  $\alpha Z$  (no unit) is a curvature parameter. The right

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part is a heaviside function H related to the biomass in the biofilm.

The maximal individual ingestion rate  $IR_{max}$  ( $\text{ng Chl a ind}^{-1} \text{ h}^{-1}$ ) is calculated according to the formulation of Haubois et al. (2005) for adult snails. It depends on the total MPB biomass:

$$IR = 0.015 \times (F + S)^{1.72}$$

The Chl a uptake rate is converted into carbon unit according to the C:Chl a ratio described previously. The term  $(F + S)$  is expressed in  $\mu\text{g g dry sed}^{-1}$ . The biomass expressed in  $\text{mg Chl a m}^{-2}$  is converted into  $\mu\text{g g dry sed}^{-1}$  as follows:  $[\text{Chl a}] (\mu\text{g g dry sed}^{-1}) = [\text{Chl a}]^{1.2605} (\text{mg Chl a m}^{-2}) / \rho_{\text{S}} * \text{thickness}_{\text{sed}}$ ,

where  $\rho_{\text{S}}$  is the sediment bulk density in  $\text{g l}^{-1}$  and  $\text{thickness}_{\text{sed}}$  is the sediment thickness i.e. 1 cm. The Chl a concentration is scaled by the exponent 1.2605 in order to reach a maximal observed ingestion rate of  $385 \text{ ng Chl a ind}^{-1} \text{ h}^{-1}$  (Coehlo et al., 2011) when the Chl a concentration converges towards a maximal observed value ( $300 \text{ mg Chl a m}^{-2}$ , Guarini (1998))."

With the new grazing formulation, an increase of the simulated mud surface temperature towards the optimal temperature for grazing results into an increase of the ingestion rate until it reaches a plateau at its maximal value. This maximal value is determined by the simulated MPB biomass within the first cm of sediment according to the relationship of Haubois et al., (2005). In contrast with the original model run, the new grazing mathematical function dampens the sharp peaks of ingestion and, as such, is more realistic with respect to previous works (Blanchard et al., 2000; Haubois et al., 2005; Pascal et al., 2008).

5. "p. 7, l. 30-p. 8, l. 2. 4xsignificant. I disagree. These differences are not significant, because the model mean is within the confidence interval of the observations."

In the manuscript, we give the  $\text{mean} \pm \text{standard deviation}$ . The data distributions are skewed and asymmetric. This is the reason why we used an appropriate non-

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parametric test (i.e. Mann-Whitney) instead of the confidence interval. The non-parametric analysis tests the means taking into account the skewness and asymmetry of the data.

6. "p. 8, light limitation. The definition is confusing. Also during the night, light is the limiting factor. Please use the full 24 hr period, not just daylight hours to represent this."

As mentioned by the referee #2, MPB is also light-limited during the night in the model. However, as the MPB production occurs only during the daytime emersion periods, we computed the limitation terms that constrain primary production only during the daytime emersion periods.

7. "Discussion. The authors provide a substantial number of numeric comparisons with published results throughout the discussion. This information is very difficult to digest in this way. Please compile a table of all these data/values/references, and present as part of the results."

We agree with the referee #2 comment. To make the discussion clearer, we included a new table in the Results section.

8. "Table 1. I'm not sure if figures are allowed within a table - check journal requirements. This table doesn't seem to contain new information compared with the text (appendix B1). Ensure there is no duplication (delete table?)."

We agree with the referee comment that the differential equations appear both in the Appendix B and within Table 1. Nevertheless, Table 1 provides a clear and synthetic view of the simulated ecological processes that may provide the reader a rapid understanding of the model. In turn, the Appendix B section provides more details on the mathematical functions used in the differential equations shown in Table 1. The journal editorial support confirmed that figures can be inserted within a table.

9. "Appendix B1.  $dZ/dt$  is identical in the three cases. Please print only once. Also B4 is identical to B2 except for the formulation for  $\tau$  - find an alternative way to present

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this without duplication."

In each case, the differential equations are mathematically and numerically linked to each others as each scalar refers to other scalars. This is why they must be all shown in each presented case to help the reader clearly understand how the biomass flows between the model compartments. In addition, it permits the reader to focus on one case independently of the others.

10. "p. 1, l. 14. export flux: from, to? "

The sentence was modified as follows: "The model ability to infer on biotic and abiotic mechanisms driving the seasonal MPB dynamics could open the door to a new assessment of the export flux of biogenic matter from the coast to the open ocean and, more generally, of the contribution of productive intertidal biofilms to the coastal carbon cycle."

11. "p. 4, l. 7. The reference to fig 3 occurs before the first ref to fig 2. Swap figures."

The two figures were swapped.

12. "p. 5, l. 31. This sentence is unclear. "

To make it clearer, the sentence was modified as follows: "The variable  $S_{\text{chl}}$  represents the S compartment that incorporated the S instantaneous production of biomass, which was directly transferred to the F compartment ( $\text{mg chl a m}^{-2}$ )."

13. "p. 6, l. 13. This sentence is unclear. "

The sentence was modified as follows: "We performed a sensitivity analysis to quantify how simultaneous variations of key biological constants might impact the simulated MPB production. "

14. "p. 6, l. 15. First use, write out the names of the variables. Why these - there are many others (Table A3)?"

The names of the constants was added: "A Monte-Carlo fixed sampling method (Hammersley and Handscomb, 1964) was used to randomly select values of the temperature optimum for photosynthesis ( $T_{opt}$ ), the temperature maximum for photosynthesis ( $T_{max}$ ), the optimal temperature for grazing ( $T_{optZ}$ ), the shape parameter of the temperature related grazing ( $\alpha_Z$ ), the light saturation parameter ( $E_k$ ) and the half-saturation constant for light use ( $K_E$ ) within observed ranges (Table 3)."

We selected these biological constants, because they are direct inputs in the mathematical functions that enter in the calculation of the simulated MPB production rate and *P. ulvae* ingestion rate. Other biological parameters as beta and pbMAX were not included in the sensitivity analysis since they vary seasonally in the model.

15. "p. 6, l. 23-24. This sentence is unclear. "

By seasonal amplitude we mean the difference between the maximum value and the minimum value for the time period considered.

The sentence was modified as follows: "The amplitude (i.e. the difference between the maximum and the minimum value) of the simulated mud temperature was higher in summer-fall ( $32.1\text{ }^{\circ}\text{C}$ ) than in winter-spring ( $18.1\text{ }^{\circ}\text{C}$ ). "

16. "Fig 5. Label graphs. Also plot 'original data' in the main figure for better comparison. Rephrase caption to make it clear what these original data are. "

We overlaid the original data on the two panel of the figure. The figure caption was modified as follows: "Seasonal cycle of the 2008: a) Normalized difference vegetation index (NDVI) and b) simulated daily maximum of the MPB biomass in the biofilm. Original extracted data (black circles) are overlaid. The black full lines represent the original extracted data regularized and filtered with running medians (window size = 7). NDVI is calculated at the pixel corresponding to the study site. Phases are determined according to the amplitude of the sign change of the second order derivative."

17. "p. 7. l. 2-5. Fall bloom. This seems less evident in the 'original data'? Is that true

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and if so why? "

In fall, less satellite scenes were available than in spring and summer. Nevertheless, NDVI estimates retrieved in fall showed higher values in autumn than in late summer suggesting a moderate fall bloom. Such a pattern is also simulated by the model. In addition, such a fall bloom is also evidenced in Fig. 6a by the simulated MPB biomass within the sediment first cm.

18. "Figure 9. The white colour is missing from the legends. For graph b, there is no grey. Is this actually the case or an issue with the figure? It seems that in graph b,  $T_{opt}$  was plotted, not  $T_{opt\_z}$ ?"

Panels a and b represent the time periods during which either mud surface temperature or grazing is the most limiting term for MPB growth in the model. While on panel a the time periods in white represent the light limitation periods, they correspond in panel b to periods during which grazing is non-limiting.

The new figure based on results of the improved model run now presents grey colour.

To make it clearer, the figure caption was modified as follows: "Seasonal cycle of the MPB biomass (green full line), and time occurrence and duration of the daily limiting term in 2008: a) time periods when MPB is limited by mud temperature, b) time periods when MPB is limited by grazing. Mud temperature data are averaged over the daytime emersion period. The dashed vertical lines delimit the 3 phases shown in Fig. 5. The red colour on vertical bars indicates a match between temperature- and grazing-limited time periods."

19. "p. 9, l. 17. key: why are these 'key' (and how is that defined)?"

We selected these biological constants, because they are direct inputs in the mathematical functions that enter in the calculation of the simulated MPB production rate and *P. ulvae* ingestion rate. We modified the sentence as follows: "A total of 10000 model runs (N) was performed, in which a set of biological constants ( $T_{opt}$ ,  $T_{max}$ ,  $T_{optZ}$ , al-

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phaZ, Ek and KE) were randomly selected within reported observed ranges (Table 3). These biological constants were chosen, because they are direct inputs in the mathematical functions that enter in the calculation of the simulated MPB production rate and *P. ulvae* ingestion rate."

20. "p. 12, l. 29. Here, a section starts on salinity (it's not entirely clear to me where this ends). This is the first mention of salinity, and as far as I understand salinity is not represented in the model. So this paragraph seems a bit out of place. Either delete, or argue why salinity was not included in the model in Methods, and then move this bit to a separate heading in the discussion.

Even if the salinity is not explicitly represented as a forcing variable in the physical model, we discussed the detrimental effect on the MPB cells and growth rate of high salinity levels induced by a strong heating of the mud surface and subsequent high temperatures. This is the reason why this part is developed in the Discussion section 4.2 on the role of mud surface temperature on MPB.

We modified the end of this paragraph (p. 13, l 8-11) to make it clearer:

" 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."

21. "p. 30, l. 31-35. This contradicts statements in Results."

If this comment refers to p. 14 l. 31-35, *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

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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).

22. "Figure 8. Why does the vertical axis start at 5? The plot seems to suggest that this truncates the data in mid-summer? "

The vertical axis was extended to range from 0 to 23h.

23. "emersion (is it emergence?) and immersion are easily confused, please use exposure and submergence."

We understand that the two terms can be easily confused. However, they are commonly accepted and widely used and accepted amongst the community (e.g. Admiral and Peletier, 1980; Underwood and Kromkamp, 1999).

24. Figure 1. the font size used for latitude and longitude may be too small.

The font size was increased.

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 ( $\alpha_Z$ ).  $r$  is the Spearman's correlation coefficient

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(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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Interactive comment on Biogeosciences Discuss., <https://doi.org/10.5194/bg-2018-325>, 2018.

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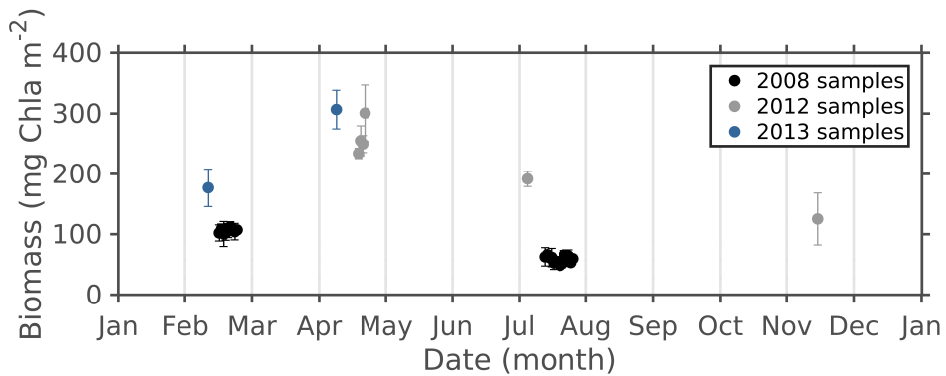


Fig. 1.

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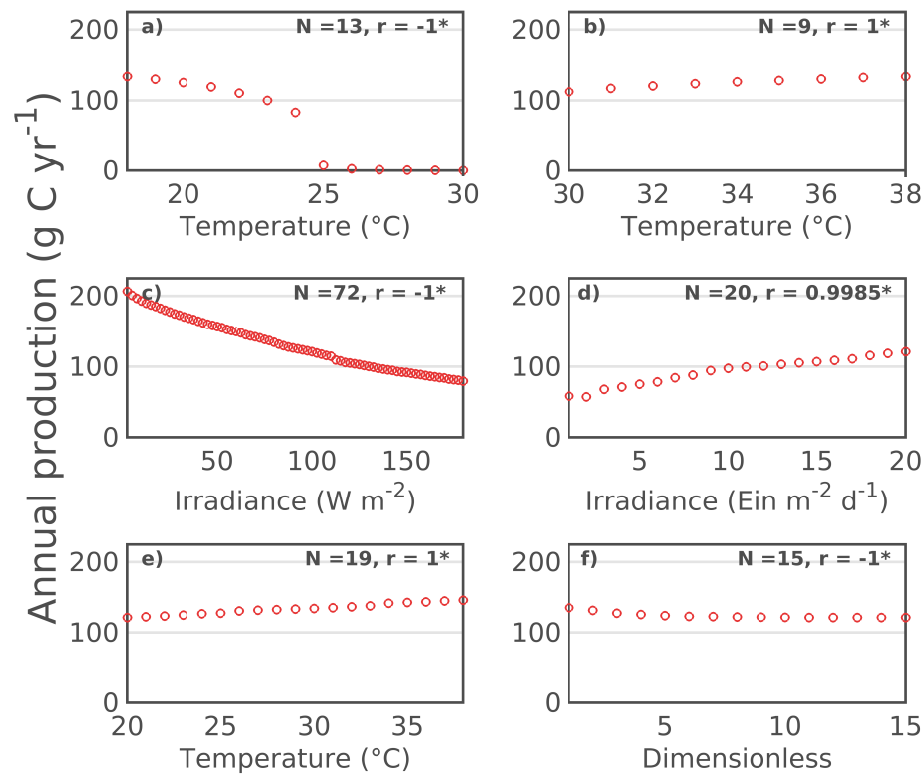


Fig. 2.

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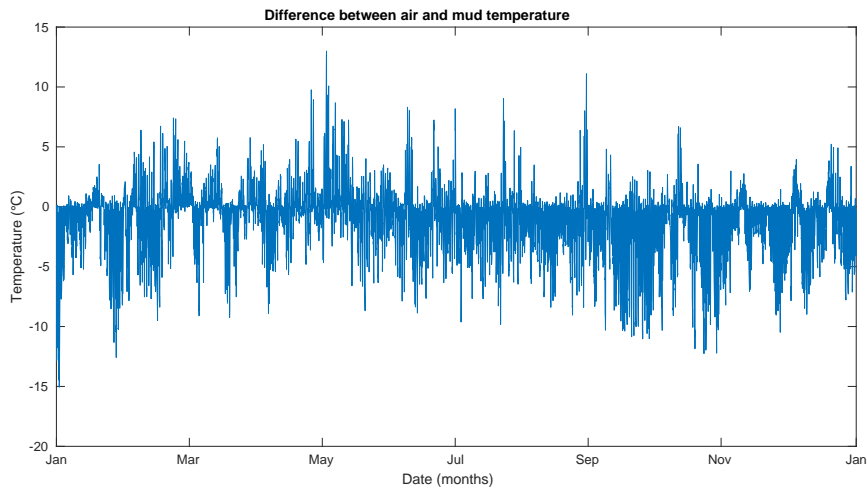


Fig. 3.

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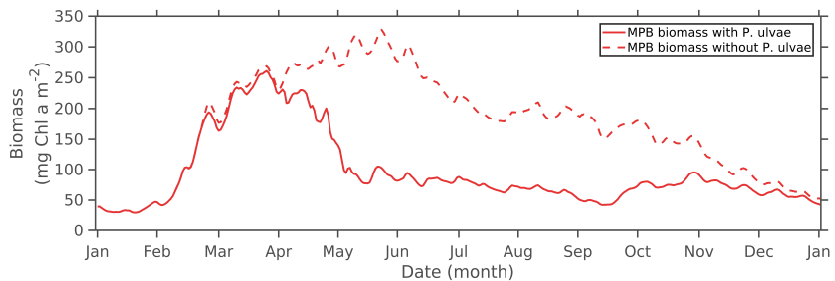


Fig. 4.

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