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Comment on bg-2021-183

Erik-jan Malta (Referee)

Referee comment on "Modeling the growth and sporulation dynamics of the macroalga *Ulva* in mixed-age populations in cultivation and the formation of green tides" by Uri Obolski et al., Biogeosciences Discuss., https://doi.org/10.5194/bg-2021-183-RC2, 2022

Referee comment to the manuscript bg-2021-183: "Modeling the growth and sporulation dynamics of the macroalga *Ulva* in mixed-age populations in cultivation and the formation of green tides" by Obolski et al.

General comments

Interesting paper simulating potential effects of the effect of sporulation dynamics related to thallus age on biomass build-up of the green macroalga *Ulva* sp. The mechanism and dynamics of sporulation in this macroalgal genus are still largely unraveled. The model presented in the manuscript illustrates their importance both in nature in *Ulva* blooms as in applications such as large scale *Ulva* cultivation – a highly relevant issue nowadays.

In my opinion, the model should be considered as a a theoretical test of the hypothesis that differences in sporulation between differently aged *Ulva* can influence biomass build-up in a population. Growth and thus biomass build-up is influenced by many external factors, starting with temperature, light and nutrient availability that may even lead to periodic patterns (for instance nutrient supply with spring tides, etc.). In addition, due to biomass build-up, algae will experience reduction of light availability due to self-shading, increased competition for nutrients, both directly and due to reduced water flow, increasing pH leading to reduced carbon uptake, etc. that might also generate these patterns, especially when combined with periodic biomass export (as in cultures for examples). This model is too simple to interpret actual data as the authors suggest (lines 201-206), however tempting this may be. Nevertheless, bearing this in mind, in my view the authors convincingly demonstrate the importance of population structure on growth dynamics, especially under articial conditions (cultivation) where other factors such as nutrients are controlled.

Nevertheless, there are still a number of points that require clarification and possibly correction, as it appears to me that there are some points in which the authors contradict

themselves. Starting with the latter, in lines 93-95 it says "Additional studies showed that if the thalli are ageing (i.e. no growth) they become insensitive to the artificially added sporulation inhibitor and release swarmers even in its controlled presence in the growing media (Alsufyani et al., 2017)." In their model, the authors define as old algae "those thalli, which are insensitive to SI and do not produce it." (l. 157-159). In that light I do not understand the explanation of the model outcome offered in l. 180-182: "These findings show that sporulation inhibitor production by a small (20% in our simulations) young population could potentially provide enough inhibitor to prevent the old algae population from biomass loss…" This seems like a contradiction to me – the old algae should be completely insensitive to the inhibitor as the authors stated earlier.

The model has been based on mixtures of two "generations" of algae. Even though they "age" in the model, there is always only two generations. If I understand the model correctly, the new young algal biomass that will arise as a consequence of the sporulation is not accounted for. Although I appreciate the complexity of incorporating this in the model, I think some speculation would be in place on the potential effect of this, as it probably slows down population aging and its negative effects.

Another point of concern are the parameter values selected for the model. The paper does not list a literature or other basis for these values, nor has a sensitivity analyses been performed to assess the effect of changes in them. For instance, if I understand correctly, the degradation constant is the biomass lost, supposedly in part due to sporulation, set at 0.3, or 30% of the biomass at maximum in the oldest age class. This seems quite arbitrary and maybe quite conservative some reference mention complete loss of biomass due to sporulation. What would be the effect if this factor was much higher, for instance 0.9? The same goes for the effect of algae age – are the response equations based on experimental data or are these choices of the modelers?

Specific comments

l. 47 – This merits a reference.

l. 50 – The species mentioned are all filamentous, the *Enteromorpha* morphology. In Europe blooms mainly consist of foliose *Ulva* species. Biomass losses due to sporulation might be less important in those.

l. 67 – I do not agree with this (see also above). For foliose *Ulva* green tides, bloom initiation is thought to origin from vegetative fragments, see Kamermans et al. (1998) Mar Biol 131: 45-51 and other authors.

l. 73 – The Qingdao bloom did not only occur in 2008 but seems to have converted into an annual phenomenon. In addition, although sporulation might be certainly accelerate

growth, the basic requirement for the rapid accumulation is the high nutrient availability.

l. 93 – Has this been demonstrated for other *Ulva* species as well?

l. 104 – Basic understanding of thermodynamics only refers to Zollmann et al. 2018.

l. 113 – This is not necessarily the case for all *Ulva* species. Some, such as *U. ohnoi* in south Spain and Portugal never show sporulation. For other areas, such as the foliose *Ulva* blooms in Brittany, France, and Venice, Italy several authors suggested other causes for biomass degradation. Sporulation can certainly important, but this might be species specific within the genus.

l. 134 – How general is this in *Ulva*, is this process linear, experimental data?

l. 144 – f (I) is monotoning decreasing function? I am not too experienced in modeling so I might be mistaken, but should this not be increasing from 0 to 1 so as to maximise degradation in the oldeste age class?

l. 153 – "We assumed", unless it is based on literature or experimental data this is a setting, not an assumption.

l. 158 – However, due to the sporulation, new t0 generations are constantly formed and even more so in older populations where the rate is maximum. This might dampen the modeled curves.

l. 192 – Again this is not an assumption but a setting.

l. 202 and further – as argued in the general comment, this is highly speculative and might very well be a coincidence. Weekly biomass removal has a number of effects with respect to light and nutrient availability as well in addition to the natural variation in parameters as light and temperature.

l. 207 – Contradictory to earlier statement that older algae are insensitive to sporulation inhibitors.

l. 238 – Again, this seems like a contradiction to me. If old algae are indeed insensitive to sporulation inhibitors, adding them from a certain population age will not have an effect.

l. 252 - At least for some *Ulva* species, not clear how species-specific this is.

Technical corrections

l. 191 – "stimulate" should be "simulate"

Citation Wichard 2015 is lacking in the bibliography.