

Interactive comment on “An investigation of grazing behaviors that result in winter phytoplankton biomass accumulation” by Mara Freilich et al.

Anonymous Referee #2

Received and published: 5 January 2021

1 General comments

This manuscript aims at explaining the phytoplankton growth rate observed during winter in the ocean mixed layer, when conditions are usually not conducive to biomass accumulation. The work is stimulated by the recent availability of data offered by the BGC-Argo platforms, which are providing unprecedented information on the open ocean microbiome. Positive winter growth rates have been recently identified using Argo floats under sea ice, both in the Arctic and in the Antarctic (Randelhoff et al., 2020; Hague and Vichi, 2020). This is an indication that, even in extreme conditions of light limitations (and likely with minimal predation pressure), phytoplankton have de-
C1

veloped the capacity to grow and accumulate biomass. It is therefore (nowadays) less surprising that this may occur in the winter mixed layer of the North Atlantic Ocean. It is clearly a balance between growth and loss terms, and we are only now - thanks to the new autonomous technologies - starting to understand some of the details of the phytoplanktonic component.

This work is however timely and of relevance for the discussion, but I have some issues with the current manuscript, some of them that I consider quite relevant in order to gain confidence in the presented results. In its current form, I would recommend a thorough revision of the introduction, assumptions and the related methodologies, to ensure that the results are of wider applicability.

1. My first major comment is related to the focus on the grazing formulation in the context of winter biomass accumulation. To emphasize the importance of grazing in tilting the balance of winter phytoplankton development, the authors state that phytoplankton loss is due primarily to grazing and cellular lysis, and secondarily to respiration and natural mortality. Notwithstanding the quite ambiguous definition of “natural mortality”, which should very likely include cellular lysis induced by viruses, they attribute this sentence to Landry and Calbet (2004). I would argue that the cited paper, as well as the twin publication Calbet and Landry (2004), specifically meant to highlight the role of microzooplankton grazing in the microbial food chain, through the analysis of dilution experiments. It is not a generic study on the grazing relationship between phytoplankton and their predators, neither specifically targeting the winter period, which is the focus of this manuscript. I would suggest the authors present their case with more support from the existing literature. I would also recommend the authors to be more rigorous in their use of the concept of linear and nonlinear grazing terms, because I have found their terminology, as well as its use in the presentation of the results, confusing at times. The grazing term of the dynamics is always nonlinear (it is the product of the two state variables P and Z), while the formulation of the grazing rate can

be linear. Apart from some theoretical works in the 80's and early 90's (which can be found in the cited work by Gentleman et al, 2003), there is not one single "state-of-the-art" biogeochemical model that uses a linear formulation for the specific grazing rate (at least to my knowledge. I checked PISCES, BFM, BioEBUS, MEDUSA and a few others and they implement various combinations of hyperbolic functions or Ivlev's. I'm afraid the current wording may mislead the reader to assume that the majority of models uses a linear formulation, and this is why they may fail to show the winter accumulation. Throughout the manuscript I started to realize that maybe the authors intended that the hyperbolic grazing rate function is linear at "low prey concentrations". I concede that this is true for biomass values close to 0, as can be seen with a Taylor series expansion of the term around 0. For any value larger than 0, it however depends on the choice of the grazing saturation factor. My major issue with Sec. 2 results is that the authors made the arbitrary assumption that the Holling type II is equivalent to a linear dependence on phytoplankton concentration, which is only true in the approximation of $P>0$. (Incidentally, please note that it is not always clear which parameters the authors used in Sec. 2, so I would suggest to improve this description). Fig. 2 thus presents a comparison between the Holling type I and Holling type III formulations, without considering Holling type II. The resulting tuned value of parameter p_0 for the Holling type II formulation applied in Sec. 3 is rather large, which forces this grazing rate to be in the linear part of the curve (Fig. 1) for the lowest modelled values of phytoplankton. I am therefore not much confident about the robustness of the results shown in Sec. 3, as I suspect some degree of overfitting led to the observed difference between the two formulations. This comment is further elaborated in point 4 below.

2. Another major issue I have with this manuscript is the apparent naivety in the biogeochemistry formulation and the related terminology. With all due respect, the sentences in line 65 and line 209 would have made me reject the manuscript

C3

immediately, since there is no carbon content in any dissolved inorganic nutrient and nitrogen pool cannot be described in units of carbon. I truly believe in the value of theoretical simplified models, and therefore I may interpret what the authors meant with these statements (this is why in mathematical modelling there is a tendency to use non-dimensional formulations). Nonetheless it is a major mistake that would confuse the non-modeller, and it is found throughout the manuscript. This actually invalidates any use of other nutrient-related parameters taken from the literature (because they are usually in units of nitrogen or with multiple "currencies"), unless the authors state in advance what is the stoichiometric relationship between nutrients and carbon in their compartments and adjust the values accordingly. For instance, they refer to the nitrate half-saturation constant used by Moore et al. (2001), but in their appendix A this value is in mmol/m³. I would recommend the authors to present their formulations using the appropriate units for the generic nutrient, eventually adopting the use of constant stoichiometric ratios if needed.

3. The authors make the statement that loss terms other than grazing are of lower orders, but I argued in point 1 above that this is a not fully justified statement. I would thus recommend to explain more in detail their choices for the model formulation. For instance, does phytoplankton mortality parameterize respiration and viral lysis? This is a rather important concept, since this parameter has been considered freely tunable (see my point 3 below). I would also argue that the authors have not given much attention to the choice of the zooplankton closure formulation. Is there a specific reason for not using a linear mortality as indicated by Edwards and Yool (2000)? This is briefly mentioned at line 155 but without context it is difficult to appreciate its role. The disturbance-recovery hypothesis would also affect zooplankton mortality rates, which I understand was the authors' interpretation since they treated this parameter as freely tunable. However, if this parameter is re-tuned when the mathematical term is changed, then it is difficult

C4

to assess the outcome. In addition, the authors do not always explain the use of certain mathematical notations. For instance, they use material derivatives in eq. (1) but make no assumptions as to why they are used and eventually turned into partial derivatives in eq. (2).

4. Another major point is linked to assuming the phytoplankton mortality constant (d_p) dependent on the mathematical form of the grazing rate. If this loss term is meant to parameterise phytoplankton mortality other than grazing, should not this be treated as independent of zooplankton and hence belonging to the fixed set of parameters in Table 1? This is a first-order loss term, which is usually interpreted as basal (or biomass-related) metabolic losses. It may indeed also include viral lysis, although in this case it should be density-dependent (see the excellent review in Mateus, 2017). I would recommend the authors to repeat their experiments assuming a constant value for this specific loss term and simply attributing it to basal respiration, which is the more plausible metabolic rate. It is not completely clear to me if the parameters calibrated in Table 1 have been used for the theoretical analysis presented in Sec. 2 and Fig. 2. Edwards and Yool (2000) gave clear indication that the role of parameters is often more important than the choice of the mathematical formulations, and it should be demonstrated that it is not the case here. In relation to Sec. 3, what would be very important, is to ensure that the overwintering phytoplankton biomass is the same in both the experiments, and that all parameters but the ones related to grazing terms are fixed. I do not agree much with the statement that this is an unknown (and thus freely-tunable) term. They can find a range of values in Lopez-Sandoval et al. (2014; between 9 and 22). At line 139 the authors state that mortality time scales are 10 times the scale of division rates. This is an unclear and unsupported statement (division rate can be made equivalent to a carbon fixation, or production, rate using some algebra, but I think the authors should compare like with like). The paper cited above reports it to be about 10

C5

5. The dilution hypothesis is one of the possible explanations for winter accumulation of primary producer biomass, however this is based on the assumptions that light limitation is preclusive of any photon assimilation. Even if I did not expect the authors to be aware of the very recent papers on phytoplankton phenology cited above, I would have expected this work to give a more proper consideration to the role of light as a driver of phytoplankton growth. Not all the assumptions are justified, and particularly how the various processes have been averaged in the bulk mixed layer model. The authors added an implicit treatment of patchiness due to the entrainment of phytoplankton-depleted water from the deeper ocean, but ignored and did not discuss the inhomogeneity of growth due to the exponential decay of light in the mixed layer. This implies that the authors assume that the average phytoplankton growth is determined by the average light, thus assuming negligible that the Sverdrup himself suggested that growth may take place even with strong turbulence if the phytoplankton displays a positive phototaxis. This problem has been treated extensively in Paparella and Vichi (2020), both considering cases in which the biological rates are quicker than the physical scales and the opposite, which is the main founding assumption done by Sverdrup and also made by the authors. In both cases, it has
6. Finally, I'm afraid the authors gave a somewhat biased interpretation of the discussion about the Sverdrup model and instrumentally presented it to reinforce their argumentations. It is now widely accepted that the Sverdrup model is a conceptual mathematical formulation that helped to promote the quantitative study of the ocean microbiome, in an era when marine biogeochemistry was still a branch of descriptive biology. This is clearly illustrated in the cited paper by Fischer et al, and even more in the special issue of the ICES journal edited by Sathyendranath et al. (2015). Citing from the abstract, this set of papers celebrates an elegant and powerful hypothesis that has had long-lasting influence. Sverdrup clearly intended to describe the April-May period and not the winter accumulation, and

C6

therefore it should not be used as an alternative hypothesis for the winter case. It is also important to remark that none of the current biogeochemical models make predictions based on the Sverdrup hypothesis. As such, this is more to be seen as an emergent property, rather than an explanatory mechanism. I have thus been quite surprised to see that the authors made their own revisit of the Sverdrup model in Sec. 2.1, attributing their interpretation to the original formulation. Sverdrup introduced just a first-order loss term and then, eventually, made a few considerations about the role of grazing, showing that the data available at that time were in agreement with his postulation. It is the authors' interpretation to attribute this constant loss term to grazing, and it should be made very clear. I would particularly recommend removing it from the title of sec. 2.1 because it would be rather misleading to those readers who are less familiar with the original paper.

2 Specific comments

L143 Concentration L152 (and L155-157) A decrease in MLD would likely enhance growth terms more than the grazing losses (see point 5 above). Since episodes of re-stratification are actually frequent in the ocean (e.g. Smith et al., 2016), this assumption may not hold even during fully mixed conditions. L177 Please indicate which equation set is being used here L183 More details are needed to explain the modelling of the nutrient concentration and how this has been constrained according to observations. The use of a generic nutrient variable is sensible in Sec. 2, but here, because of the connection with the specific BGC-Argo measurements, it is important to clarify which nutrient is being used and how it has been assessed in terms of seasonal cycle. The floats do not measure nitrate, but other historical data can be used. L191 Biology has been demonstrated to be patchier than physics in the North Atlantic (e.g. Mahadevan and Campbell, 2002). Please consider this in your discussion. L192-193. There are

C7

not many figures in this manuscript. I would thus suggest the authors to add some more information on the floats that have been used, and possibly provide a table with their identification numbers. It would be valuable to see the individual timeseries, to appreciate the phenological variability prior to their standardization. L199,L202, and others. I would recommend the authors to be consistent in their terminology. There is a tendency to consider the term accumulation and growth as synonyms, however, there can be accumulation without growth. L205 I would need some more explanation here. According to the description, I was expecting a non-dimensional axis and not calendar days. If the model was not rescaled, what are the t1 and t2 values for the model (and actually, having two different model formulations, which one was chosen?) L217 I understand that this is more of a personal choice, but I think there is value in introducing the methodology at the beginning of the paper. The parameter fitting procedure is now interrupting the presentation of the results. Also, the actual description of the optimization procedure is shown later at lines 224-227. Many of my major issues are related to the possible influence of overfitting that may have biased the results, and I think the authors should make an effort to demonstrate that this is not the case. I am not much familiar with this methodology and therefore it would be useful to know if the parameters have been tested one-at-a-time and what kind of sensitivity analysis was performed. L231-232. Please indicate if eq. (12) was used to estimate this rate. I struggle to understand why the rate is positive but concentration keeps decreasing. L273-276 My concerns on this statement are expressed in the major points above. The degree of nonlinearity of the Holling type II formulation depends on the value of the parameter, which is tuned differently in the two experiments, as well as the basal loss rates. The response of zooplankton would largely depend on the extant biomass during winter, which is quite different in the two simulations. L294-295 Light dependence was made less influential by assumption (see point 6 above). Please rephrase.

C8

3 References

Calbet, A., Landry, M.R., 2004. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnology and Oceanography* 49, 51–57. <https://doi.org/10.4319/lo.2004.49.1.0051>

Edwards, A.M., Yool, A., 2000. The role of higher predation in plankton population models. *Journal of Plankton Research* 22, 1085–1112. <https://doi.org/10.1093/plankt/22.6.1085>

Hague, M. and Vichi, M., 2020. Southern Ocean BGC-Argo Detect Under Ice Phytoplankton Growth Before Sea Ice Retreat, *Biogeosciences Discuss.* [preprint, accepted for publication in *Biogeosciences*], <https://doi.org/10.5194/bg-2020-257>

López-Sandoval, D.C., Rodríguez-Ramos, T., Cermeño, P., Sobrino, C., Marañón, E., 2014. Photosynthesis and respiration in marine phytoplankton: Relationship with cell size, taxonomic affiliation, and growth phase. *Journal of Experimental Marine Biology and Ecology* 457, 151–159. <https://doi.org/10.1016/j.jembe.2014.04.013>

Mahadevan, A., Campbell, J., 2002. Biogeochemical patchiness at the sea surface. *Geophysical Research Letters* 29, 1926.

May, R.M., 2004. Uses and Abuses of Mathematics in Biology. *Science* 303, 790–793. <https://doi.org/10.1126/science.1094442>

Mateus, M.D., 2017. Bridging the Gap between Knowing and Modeling Viruses in Marine Systems—An Upcoming Frontier. *Front. Mar. Sci.* 3. <https://doi.org/10.3389/fmars.2016.00284>

Paparella, F., Vichi, M., 2020. Stirring, Mixing, Growing: Microscale Processes Change Larger Scale Phytoplankton Dynamics. *Front. Mar. Sci.* 7. <https://doi.org/10.3389/fmars.2020.00654>

C9

Randellhoff, A., Lacour, L., Marec, C., Leymarie, E., Lagunas, J., Xing, X., Darnis, G., Penkerc'h, C., Sampei, M., Fortier, L., D'Ortenzio, F., Claustre, H., Babin, M., 2020. Arctic mid-winter phytoplankton growth revealed by autonomous profilers. *Science Advances* 6, eabc2678. <https://doi.org/10.1126/sciadv.abc2678>

Sathyendranath, S., Ji, R., Browman, H.I., 2015. Revisiting Sverdrup's critical depth hypothesis. *ICES J Mar Sci* 72, 1892–1896. <https://doi.org/10.1093/icesjms/fsv110>

Smith, K.M., Hamlington, P.E., Fox-Kemper, B., 2016. Effects of submesoscale turbulence on ocean tracers. *Journal of Geophysical Research: Oceans* 121, 908–933. <https://doi.org/10.1002/2015JC011089>

Interactive comment on *Biogeosciences Discuss.*, <https://doi.org/10.5194/bg-2020-444>, 2020.

C10