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

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We thank the reviewer for their thorough and thoughtful comments. We have made revisions and clarifications where appropriate, as outlined below. We have included the reviewer comments in this response and respond in line. The reviewer comments are in italics.

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 developed 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.

This manuscript focuses on the mechanisms underlying the wintertime biomass accumulation, which has previously been reported from autonomous observations. We have added the recent references to the introduction.

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.

We have rephrased this sentence to now read "Phytoplankton are thought to be tightly controlled by grazing and loss processes within the microbial food web (Landry and Calbet 2004, Calbet and Landry 2004, Strom et al 2007, Evans et al 2012, Prowe et al 2012). Any accumulation depends on the imbalance between growth and loss processes, the magnitudes of which are correlated to each other (Behrenfeld and Boss 2017)." We have also added additional citations to observational programs that observed that top down control is important, although given observational limitations at high latitudes that are addressed in the introduction, these are not wintertime observations. However, we have also included a citation to modeling work that also reveals the importance of top down control.

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.

The reviewer has made the valuable comment that the wording about the types of non-

linearity that can promote wintertime biomass accumulation should be more precise. We have edited the manuscript text to make it clear that rather than merely nonlinear grazing at low prey concentrations, a grazing function must increase with prey concentration faster than linearly at low prey concentrations. In mathematical terms, the second derivative of the grazing function with respect to phytoplankton should be positive as p goes to zero. We have included this analysis in section 2. This excludes the type of saturating nonlinearity that is present in a type II functional response. We have made this more clear in the abstract, in the results section (changing "non-linear" to "superlinear"). Discussion changed "there must be non-linearity in the interaction between the zooplankton and the phytoplankton at low phytoplankton concentrations" to "the grazing rate as a function of phytoplankton concentration must decrease faster than linearly" Changed "a nonlinear coupling between phytoplankton and zooplankton" to "the reduction in grazing rate".

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.

Fig 2 presents a comparison between the Holling type I, II, and III formulations. The low phytoplankton approximation of the functional forms used in section 2 is not used in Fig 2. The full functional forms are used over a wide range of phytoplankton concentrations. It is evident from this figure that the sublinear change in grazing rate at moderate phytoplankton concentrations that is present in both the Holling type II and III formulations does not have the same effect as the faster than linear change in grazing rate at low concentrations. As shown in this figure, the simplifications in section 2 allow us to expose the dependence of grazing on the mixed layer depth at low phytoplankton concentrations more clearly without missing any important dependence of grazing

rates on the mixed layer depth at large phytoplankton concentrations. The analysis in section 2 is independent of any parameters.

The resulting tuned value of parameter p0 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.

The value of p0 used here (15 mg C/m^3) is within the range of the equivalent parameter used in previous work e.g. 20 μmol C/L Aumont et al 2015 Table 1b (PISCES), 20 mg C/m^3 Laufkotter et al 2015 Table 6 (PELAGOS). The Holling type II formulation has two linear parts, the part that increases linearly with phytoplankton concentration at low phytoplankton concentration and the part that is nearly constant with phytoplankton concentration at high phytoplankton concentration. The highest degree of nonlinearity is between those extremes but this nonlinearity is slower than linear and so does not reduce the grazing as the mixed layer deepens. With regards to the overfitting, we would like to point out that the analysis in section 2 is independent of the parameter values. We have approached this question from the perspective of model structure and elaborate on that approach in response to point 4.

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

We thank the reviewer for pointing out the ways in which this model formulation was not clear. The currency of the model is indeed nutrients. We have now reported the values as they are given in the literature and all terms in the nutrient equation are in nitrogen units. We have added a clarification sentence that comparison to the observations is done in carbon units. "Phytoplankton biomass is compared to the observations in carbon units and conversions between nitrogen and carbon units are performed using a Redfield ratio of 16:106."

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).

The point about the importance of viruses is an important and was also mentioned by the other reviewer. We have now clarified that our model does not include viruses, but the effect of viruses is likely similar to the grazing functions that we have examined. We have added the following sentences to the section introducing the model. "The grazing function represents a density-dependent mortality process. Other mortality processes such as viruses may also be density-dependent and could be studied in a similar manner but are not included in this analysis (Weitz et al 2015, Mateus 2017). Some of the

conclusions may be applicable to other density-dependent mortality processes."

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 to assess the outcome.

We have chosen a quadratic mortality because it represents predation processes on zooplankton. This seems appropriate given the focusing of this article on density dependent processes. The results of Edwards and Yool 2000 do not provide convincing evidence that a linear mortality term is superior to a quadratic zooplankton mortality term. However, the reviewer is correct that dilution does affect zooplankton mortality in addition to zooplankton growth. This is discussed on lines 158-164. The focus of this manuscript is on the functional forms rather than the parameter values, as is explained in response to point 4.

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).

We have corrected this error and now use material derivatives throughout.

4. Another major point is linked to assuming the phytoplankton mortality constant (dp) 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).

We have set bounds on the parameter values that can result from the parameter fitting to ensure that the values are within the previously reported range of population-level loss rates. However, because this is an oversimplified model that encompasses a wide diversity in a single phytoplankton type, we cannot know the parameters exactly. The best we can do is fit the parameters to the available data. Our approach in this manuscript is to start with the model structure rather than the model parameters. If we try to fit a model to the observations and show that it cannot match the key features of the observations, then we must reject the model. If the model does fit, on the other hand, then we can examine the model with parameter values and assess if the model fits within a reasonable parameter range. The mathematical analysis in section 2 is independent of the parameter values and therefore shows that certain grazing functions cannot result in wintertime biomass accumulation under the other model assumptions given here regardless of the parameter values. However, the parameters have the same significance as in Table 1.

At line 139 the authors state that mortality time scales are 10 times the scale of divi-

sion 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

We have added additional support about the importance of grazing: "However the assumption is likely inappropriate for most blooms where grazing is a main source of mortality immediately prior to bloom formation (Calbet and Landry 2004, Irigoien et al 2005)."

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

In the float profiles used in this analysis we do not see a strong vertical dependence of chlorophyll in the mixed layer. Therefore, we assume that the biological variables are sufficiently well-mixed to justify the use of the zero-dimensional bulk mixed layer model and neglect 1-D effects. This is a simplification that yields relevant insights but which

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necessarily does not capture all relevant aspects of the system.

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 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 revisitation 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.

We have removed "Sverdrup" from the title of section 2.1 and replaced it with "critical depth hypothesis". We have also changed the text in this section to distinguish between Sverdrup 1953 and the critical depth hypothesis. This section does not claim that Sverdrup was wrong, but merely incomplete. In the spring when conditions change rapidly the critical depth hypothesis and Sverdrup 1953's conclusions are probably accurate. However, there are some limitations, as we state "While the critical depth

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hypothesis has become the most widely accepted framework to interpret the onset of spring blooms–but there are growing objections (Behrenfeld 2010)–it is not very useful to make quantitative predictions. The criterion requires knowledge of the grazing rate at the end of winter before bloom onset, which is very difficult to measure."

2 Specific comments L143 Concentration

Thank you. We have corrected this typo.

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 restratification are actually frequent in the ocean (e.g. Smith et al., 2016), this assumption may not hold even during fully mixed conditions.

We selected float data that does not include lateral restratification (line 190) to avoid those effects. The statements on the cited lines refer to the specific model presented in this section and are not general statements about phytoplankton growth and physiology.

L177 Please indicate which equation set is being used here

We have added "equation" to the equation reference on line 180 to make it clear which equation is being used.

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.

The nutrient concentrations have not been constrained to observations. This is an idealized model and as subsequent sections explain we fit the model to phytoplankton accumulation rates only, with no assessment of fit to nutrients or zooplankton. We are

able to convey the key points about the dependence of grazing dynamics on the mixed layer depth without explicitly fitting the model to nutrients.

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.

We have changed "regions" in this sentence to "trajectories", which is more precise. We have also added citations to Mahadevan et al 2012 and Karimpour et al 2018 to the previous sentence. We have discussed some of the vertical velocity processes that cause patchy productivity in the North Atlantic "Finally, there is evidence that wintertime growth can be triggered by mixed layer instabilities that occasionally restratify the mixed layer during the winter and thus increase the light available for phytoplankton (Karimpour et al 2018). However this cannot be the unique explanation, because float observations presented in Mignot et al (2018) and reviewed here show many examples of wintertime accumulation where these mixed layer dynamics did not seem to apply."

L192-193. There are 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.

These time series are available and we have added a reference to where they can be found. "These individual float trajectories are plotted in the appendix of (Mignot et al 2018)."

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.

We have corrected this oversight.

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?)

We have clarified by writing in the previous sentence "where t1 is the calendar day of. . ."

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.

We have consolidated the presentation of the parameter fitting to a single paragraph and added additional details. The parameter fitting algorithm is well-suited for both linear and non-linear problems. The optimal solution is found iteratively within the whole parameter space rather than one parameter at a time. We performed a sensitivity analysis by changing the initial parameter combinations within the range of reasonable parameters.

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.

Yes, equation 12 was used to estimate this rate, which is a biomass accumulation rate. The concentration is decreasing because the mixed layer is deepening. Although the biomass is increasing, the concentration is still decreasing because the dilution effect outpaces the accumulation effect.

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.

We have revised this sentence to read "We demonstrated that the grazing rate as a function of phytoplankton concentration must decrease faster than linearly at low phytoplankton concentrations in order to release the phytoplankton from grazing pressure."

L294-295 Light dependence was made less influential by assumption (see point 6 above). Please rephrase.

We have rephrased from "light availability" to "maximum insolation" to be more clear about what is meant here. The change in mixed layer depth is the main effect on light modification of growth.