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Discussions

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

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This study analyzes the importance of considering non-linear functional responses of grazing at low phytoplankton concentrations when modelling plankton dynamics. In particular, the authors point out that including these types of responses is key to reproduce the accumulation of phytoplankton biomass observed in winter in the North Atlantic. The manuscript is well written and the results and conclusions are interesting. However, I have some comments and questions that I think should be addressed in order to be published.

REPLY: We thank the reviewer for their positive assessment of our work.

General comments: 1) If I understood correctly, in the study the phytoplankton specific growth rate decays exponentially with depth due to light absorption with an attenuation coefficient Kd. This would mean that the response of phytoplankton growth to light only depends on the surface irradiance, the Kd, and depth; i.e. depends on the light level at a particular depth. However, it seems that this dependency is modeled as a linear response. If this is the case, please consider that P-I curves have a non-linear form, expressed as a saturating response, or a curve with an optimum due to photoinhibition (see examples in Tian 2006). Although the response might be close to linear in winter due to low irradiance levels, non-linear responses might be important later in the year.

REPLY: It is true that a saturating irradiance model might affect the full annual cycle, especially in the spring-summer. However, the reviewer is correct that we assumed that the response is close to linear during the winter due to low irradiance levels. Since our focus is indeed on the winter period, we have chosen to use the linear function to reduce the number of parameters in the model. Given this focus on the winter period when light levels are low, non-linear dependence of growth on light does not affect our core message. We will discuss this assumption more explicitly when presenting the full annual cycle in the revised manuscript.

2) I could not find in the model how the effect of temperature on growth and grazing rates was introduced. The potential consequences of this effect were not considered in the discussion either. According to Rose and Caron (2007), low temperatures might impact more negatively microzooplankton grazing rates than phytoplankton growth rates (although see Chen et al. 2012), which can allow phytoplankton biomass accumulation in winter. Considering this, could a combination of temperature effect and linear grazing functional response allow a phytoplankton biomass accumulation in winter? Could this combination lead to similar results as those found when applying a grazing response that is non-linear at low phytoplankton concentrations?

REPLY: The reviewer brings up an interesting point regarding correlation between phytoplankton concentrations and temperature. We did not include temperature explicitly in the model, but we do include a section in the discussion about possible effects of other time-dependent terms. If we assume that temperature is approximately proportional to the mixed layer depth and if indeed it only affects grazing rates but not phytoplankton growth rates then we will see that there is an apparent release from grazing as the mixed deepens even when using a linear model. We have chosen to use a simplified model that does not include all potentially relevant factors to make progress towards improved understanding. This comment reveals that additional insights are likely possible using the framework that we have outlined in the manuscript. We focused on grazing because of the support in the literature for this as a potential mechanism for wintertime biomass accumulation (Behrenfeld 2010). There is inconsistent support for temperature dependence of grazing rates that would trigger an accumulation of phytoplankton in winter (Rose and Caron 2007, Lopez-Urrutia 2008, Chen et al 2012). We discuss alternate mechanisms for wintertime biomass accumulation in the paragraph beginning on line 291 and will add additional discussion of temperature effects to that paragraph.

3) Using dilution experiments, Liu et al. (2021) showed that "Holling III function best described the functional response of microzooplankton grazing" and highlighted the importance o this type of response at low phytoplankton concentrations. I think this paper or similar ones based on experimental observations support the results of the current study and should be mentioned in the discussion.

REPLY: Thank you very much for pointing out this recent reference which provides additional experimental constraints on grazing functional responses. We will include a citation to this study, which supports our findings, in the discussion.

Specific comments: About the title: maybe replace "An investigation of" with "Investigating" or "Analyzing."

REPLY: Based on this comment we will simplify the title to "Grazing behavior and winter phytoplankton accumulation"

L18-24: I think at some point here, the Critical Turbulence Hypothesis (Huisman et al. 1999) could be also mentioned as it is a famous and important one.

REPLY: This is a good suggestion. In the revised introduction we will include the critical turbulence hypothesis. When doing so, we will also include references to the recent work on positive phototaxis and the relative importance of biological and physical timescales as mentioned by reviewer #2 (point 5).

L25: I would rather say that the Disturbance Recovery Hypothesis focuses on both phytoplankton growth and loss rates and how they are coupled or decoupled (i.e. on how their equilibrium is disrupted).

REPLY: We have changed this sentence from "An alternative hypothesis proposed by Behrenfeld 2010 focuses on changes in loss rates rather than growth rates." to "An alternative hypothesis proposed by Behrenfeld (2010) focuses on changes in both loss rates and growth rates."

L34: What do you mean with loss at large scales? Please elaborate. Also, I think you could include a reference for this.

REPLY: By "at large scales" here we mean that in situ observations are needed for measuring zooplankton distributions and grazing rates. This is in contrast to the widespread autonomous measurements of nutrients, light, and chlorophyll concentration. This wording is confusing and we will change it to "for a whole population".

L36: Loss due to grazing also depends on temperature and probably on other environmental factors (see for instance Chen et al. 2012).

REPLY: We will revise this sentence to clarify that we did not mean that loss due to grazing depends exclusively on phytoplankton and zooplankton concentration, but we focus on that particular dependence because its significance has not been fully appreciated.

L40: It sounds like it is only possible to quantify this interaction through mathematical models. What about dilution experiments for example? It would be clearer if you say that it can be modeled through a mathematical relationship.

REPLY: As the reviewer suggests, we will change “quantified” to “modeled”

Fig. 2: What are the units of the axes? Also, I am a bit confused about what the contour colors represent. At the beginning of the figure caption, it says that colors represent grazing rates and in the next sentence, it seems that colors represent the rate of change in biomass. Additionally, in the case of Holling type III, for each phytoplankton concentration, rather than a decrease in the grazing rate with deeper mixed layer depths, there is first an increase and then a decrease (i.e. It seems that there is an optimal mixed layer depth for grazing rates at each phytoplankton biomass). Finally, I think the last sentences of the caption should be better written. Decreases and increases do not occur at a particular level but rather when moving along a particular axis (see for example “This occurs at low values of phytoplankton biomass and deep mixed layers” or “At high biomass there is also a decrease in grazing rate). At a particular combination of mixed layer depth and phytoplankton biomass can occur larger/est or lower/est grazing rates.

REPLY: Both this and the other reviewers have highlighted ways in which figure 2 is unclear. Rather than just updating the caption, in the revision we will improve the clarity of this figure to better make the main point that the dependence of the grazing rate on the mixed layer depth (and phytoplankton biomass) differs for the various grazing functional responses. To answer the specific question of the reviewer, the axis units are meters for mixed layer depth and mg C per meter squared for biomass.

L 214: Reference for Kd = 0.05 m-1?

REPLY: The reference for this is Organelli et al 2017, which presents a global map of

attenuation coefficients from Argo floats. This value is also computed for the set of floats used in this manuscript in Mignot et al 2018. These references will be given in the revised manuscript.

L 219-202: Maybe include a reference to Fig 3 saying between which days this peak is found.

REPLY: We have added a reference to Fig 3.

Fig. 3: There are too many lines in the gray grid. Select just a few for the x and y axes. Why the grazing rate is not another panel? The axis labels are too small. In the units of the axis labels, erase the space before the exponent and separate mg and C. I’d add a vertical thicker line on day 1 to make it clear that the plots do not start on day 1. The thin black line from day 315 to day 5 is very difficult to see and can be confused with the thicker black line. Maybe use another color (blue?) and maybe make it dash.

REPLY: In the revised version we will improve the clarity of this figure

L 238-239: Is it discussed whether the dp inferred by type III is more realistic? This could be supported with references.

REPLY: These values are problematic to compare for different grazing formulations because the linear mortality includes different processes if the grazing is parameterized differently. One process that is included in the linear mortality is phytoplankton respiration. Phytoplankton respiration rates from in situ observations and incubation experiments fall within the range of these linear mortality rate estimations from the parameter fitting (Lopez-Sandoval et al 2014, Briggs et al 2018). We will add this discussion and these references to the manuscript.

Briggs, N., GuÃřmundsson, K., Cetinić, I., D’Asaro, E., Rehm, E., Lee, C., & Perry, M. J. (2018). A multi-method autonomous assessment of primary productivity and export efficiency in the springtime North Atlantic. Biogeosciences, 15(14), 4515-4532.

L246: clarify which period is the end of winter by adding in parentheses which day/s of the year (or period in days of the year).

REPLY: We have specified the days: 320-365 and continuing to 1-75.

Fig. 4: Separate mg and C in the axis labels. Why for one of the curves there is a labeled dot for day 135 and in the other for 130? If there is not a clear justification, use the same day for better comparison.

REPLY: Different days were labeled to reduce the cluttering on the figure but we will instead use the same day for comparison.

L294-295: Why does light little influence on wintertime biomass accumulation? Does not an increase in light through the seasonal cycle increase phytoplankton specific growth rates and contribute to the decoupling with their grazers?

REPLY: It is true that light has an influence on the annual cycle, but the phenomenon of wintertime biomass accumulation does not arise from the annual cycle in light. The light is decreasing or low during the winter. Moreover, the changes in light are the same with the two functional responses.

Technical corrections L133: modify reference as "(Behrenfeld, 2010)" and maybe introduce it as "(see for example Behrenfeld, 2010)".

REPLY: We have made the suggested modification.

L136: Comma after "However".

REPLY: We have made this correction

L343: very "difficult" to quantify?

REPLY: Yes. We have added this missing word

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