



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 again thank the reviewer for their thoughtful comments, which, as the reviewer states, will help ensure that the results are interpreted within the proper context and with sufficient support from the literature. After reflecting on the comments from all three reviewers, we have some additional answers on the reviewer's main comments in addition to the ones we previously posted.

REPLY to 1. We have added additional support to the introduction for the focus on grazing. For example, we have added the sentence “Phytoplankton are thought to be

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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, Liu et al 2021). Any accumulation depends on the imbalance between growth and loss processes, which have been shown to be tightly correlated (Behrenfeld and Boss 2017).” to the fourth paragraph of the introduction. Given the limited availability of observations of grazing, particularly in regions with deep mixed layers in the wintertime, we rely on both models and observations to make the case for the relevance of top-down control in the wintertime. Following the reviewer comment we worked on making our terminology more precise. We have edited the manuscript text throughout to make it clear that the grazing function must increase with prey concentration faster than linearly at low prey concentrations. This is distinct from the grazing function being generally nonlinear and is an important clarification. An additional key point is that the prey concentrations must be low enough that the grazing rate is in the region of the grazing response function where grazing increases superlinearly with prey concentration. If the wintertime conditions were still in the saturated part of either the type II or type III grazing rate function it would not give wintertime accumulation. Figure 2 is meant to summarize the key points and extend the theoretical analysis that was performed near $p = 0$ to the full functions. However, the reviewer comments made us realize that this figure needs to be revised. In our revised manuscript, we will replace the current figure 2 with a comparison of the response of growth and grazing to mixed layer depth. This figure will support our main point that the dependence of the grazing rate on the mixed layer depth (and phytoplankton biomass) is distinct between the grazing functional responses. Although the type II and type III models have different shapes, they have the same number of parameters. This allows us to make a more robust comparison between the two functions when we perform the parameter fitting without biasing the results to one or the other function.

REPLY to 3. The reviewer proposes potential modifications to the model or additional processes that could be included. Viral lysis is indeed an interesting and important process. Our model does not explicitly represent viral lysis but from a mathematical

standpoint viral lysis is often represented using grazing functions similar to the ones we have examined. While inclusion of viral lysis in a similar framework is a potentially compelling follow-up to this study, we do not see an effect of viral lysis reported in the literature that invalidates our key result about the grazing formulation. As for the specifics of the parameter values, the focus of this manuscript is on the functional forms rather than the parameter values. The theoretical analysis is independent of parameter values.

REPLY to 4. In this study we use a simplified model that encompasses a wide range of phytoplankton species in a single phytoplankton type. Therefore, we cannot easily infer the parameters from culture studies. The fitted values for the phytoplankton mortality are within the range of values in Lopez-Sandoval et al 2014, but they vary by an order of magnitude for each functional form. Allowing for this range of variability avoids unnecessarily constraining the population dynamics into an ill-suited model parameter space. Instead, by beginning with the model structure and fitting the parameters, we are able to compare the grazing processes in a way that allows us to best evaluate the influence of model structure. We would like to reiterate a statement made in the previous response because it is a key point about our approach. If we try to fit a model to the observations and show that it cannot match key features of the observations for any parameter values, then we must reject that model. If the model can be tuned to fit the observations, then we can examine the model and parameter values together to assess if the model fits within a reasonable parameter range. In the revised draft, we will more transparently work through this method to place our results in their appropriate context.

REPLY to 5. There are some assumptions of the model, particularly the bulk mixed layer formulation, which may fail at times when mixing is weak or intermittent. In the revised introduction we will include a thorough treatment of phytoplankton growth including the Critical Turbulence Hypothesis (Huisman et al. 1999), positive phototaxis, and the relative importance of biological and physical timescales. This is relevant to

address because the essence of the theoretical contribution is that the relative dependence of growth and grazing on the mixed layer depth determines the response to dilution. The studies cited by the reviewer support the relatively weak dependence of phytoplankton growth compared to grazing on the mixed layer depth. More generally, we wish to reiterate that the contribution of our manuscript is to show that blooms triggered by deepening of a mixed layer and the associated dilution of phytoplankton can develop only for specific grazing functions. This point is treated more extensively in our general comment.

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