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Interactive comment on "Quantifying spatiotemporal variability in zooplankton dynamics in the Gulf of Mexico with a physical-biogeochemical model" *by* Taylor A. Shropshire et al.

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GENERAL COMMENTS

This manuscript is a concerted effort to address the fact that zooplankton have historically been under-studied in ecosystem models, which is problematic because of their key role for trophic transfers and biogeochemical cycling. The stated objectives are to develop and validate an existing model (NEMURO) for the Gulf of Mexico (GoM), and then to quantify mesozooplankton diet and secondary production. They describe their rationale for modifiying NEMURO, and assess the effect of these changes. They present model-data comparisons for biomasses and rates of both phytoplankton and

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zooplankton, with misfits mainly related to mesozooplankton grazing and vertical profiles of phytoplankton growth. Their main insights were that herbivory/carnivory differed between mesozooplankton size classes on the shelf, and protists were an important food source in oligotrophic regions. They also estimated that secondary production was an order of magnitude less than new primary production.

The paper, which clearly required a substantial amount of work, is thorough in its undertakings and is written clearly. It makes novel contributions with respect to ecological modeling and GoM functioning. It is useful for other regions, as the authors provided code for their 1D and 3D models, and their Supplemental serves as a great example of decision-making required to configure a model. I recommend its publication, although as described below, some aspects could be fleshed out and some text could be streamlined.

SPECIFIC COMMENTS

1. Model development:

They made 5 structural modifications and changed 25 (but I counted 30 in Table S3) parameter values from the standard NEMURO model. Their modification procedure demonstrates how we can use and gain ecological insight in constructing models (e.g. pg 32 necessary slow leaching of PON to DON),and constitutes an example of best practice. It is a real contribution to our field, that is especially useful for new modelers.

With respect to the modifications: (1) They could arguably have left the SP to LZ connection and just set the SP prey preferences to be very low, but removing it entirely is not objectionable. (2) Replacing quadratic mortality with linear mortality for all biological variables except PZ is a sensible simplification, but should be supported by references to model sensitivity studies about this issue (e.g. Anderson et al., 2015) (3) Now using a "monotonic" ammonium inhibition term, I believe, refers to the fact that some inhibition functions result in nitrogen uptake that decreases as ammonium levels increase as well as exceeding the so-called maximum uptake rate. This has been noted

in the literature and many rational alternatives presented (e.g. Frost & Franzen, 1992, Vallina and Le Que ÌĄre ÌĄ 2008). It would be beneficial to have a sentence explaining what they mean by "monotonic", so that readers appreciate the problem and know to follow them in making the change. (4) Use of the Platt light limitation is commonplace, but it would be useful to state whether the original NEMURO model did or did not include photoinhibition. If it did, it would be helpful to explain why the Platt formulation is considered to be an improvement. (5) Replacing constant C:Chl with variable C:Chl is potentially the most critical of all their changes, since this variable dictates the modeled Chl levels, which are used to compare the model and data. While they do provide the equations in the appendix, a brief overview of how those equations work would be beneficial. Overall, as these are all obvious modifications, the text devoted to this in Sections 2 and 4 could easily be cut down.

2. Model Validation

The model-data comparisons state the different values, but this does not give the reader any sense on whether the differences actually matter. Any text they could add about potential ecological significance of these differences would be helpful.

As noted above, model-data comparison of Chl will be impacted by modeled C:Chl ratios. It would be useful to have a quantitative sense of the model uncertainty related to this model component, At the very least, the issue should be discussed somewhere.

They allege that their biggest model misfit to data is vertical profiles of phytoplankton growth, and were only able to achieve realistic DCMs by tuning multiple parameters. It is not surprising that vertical profiles are challenging to model correctly, as there are many sources of error in the vertical dimension. For example, vertical velocities are always uncertain because they are calculated from the continuity equation, and thus absorb any error in horizontal velocities. This paper's use of a constant vertical mixing coefficient is not representative of higher mixing at surface as compared to interior. Vertical profiles of light depend on attenuation coefficients, which in this model appear

to use Beers's Law, and thus are oversimplifications (e.g. see Anderson et al., 1993, 2015). None of these sources of error are mentioned in the text, but It would be helpful to identify them and therefore guide future investigations.

Their simulation always resulted in modeled DCM being collocated with the maximum growth rate, which is not supported by observations. On pg 34 line 841, they argue that growth rates at a DCM must be high to balance the high mortality at a DCM, a conjecture they based on their (unsupported) assertion that zooplankton abundance covaries with phytoplankton abundance. I question this assertion. Certainly many studies have generated high zooplankton with low phytoplankton and vice versa. Zooplankton abundance depends in part on top-down control (i.e. predators and/or closure scheme), and phytoplankton specific mortality depends on zooplankton abundance as much as it does on grazing. Thus, you could have low phytoplankton growth rates at a DCM and maintain it, because grazing pressure (ingestion X abundance) is not high if zooplankton abundance is low.

They found that grazing by small mesozooplankton was overestimated, whereas grazing by large mesozooplankton was underestimated, both by a factor of about 2 (pg. 22 and pg 33). I am skeptical about their explanation that this is due to modeled grazing reflecting functional groups as opposed to size classes, especially given that the two groups' biomasses were reasonably simulated. It seems far more rational to assume the problem lies with the characterization of grazing, especially since grazing formulations are known to be highly uncertain, particularly when considering ingestion of multiple prey types. Although they did assess the effect of changes to the maximum grazing rate, they do not appear to have examined the effect of the two other grazing parameters (Ivlev coefficient and threshold), which is surprising given that these parameters would be expected to vary among taxa, and their NEMURO modifications were motivated by the "significant taxonomic differences that found between mesozooplankton communities and their prey in the GoM and the North Pacific". They also don't appear to have examined the effect of altering the mathematical form of the functional

response. I am not advocating that they conduct a slew of further sensitivity studies at this point (indeed, that could warrant its own publication), but I do think they should devote some text to describing issues with their modeled grazing, and the challenges of getting it right and the consequences of getting it wrong. Again, this will serve to encourage future studies of ways to better represent this critical process, and to test the effect of different candidate formulations.

3. Parameter Sensitivity

Sections 3.4 and S5 are dedicated to what they call their "Parameter Sensitivity" study. This is not a sensitivity study in the traditional sense, which assess the robustness of a model output to variations in parameters (e.g. +/- 10%). Rather it is more an examination of how the model output changes if some subset of the original NEMURO formulations/values were used. It is not obvious what the reader was supposed to learn from this comparison beyond what was already presented with the parameter tuning. It didn't help that there was no text to clarify Table S3 or that the Taylor/Target diagrams that were hard to see and were also not described in the text. I think this analysis could easily be removed without any loss to the paper. If the authors feel differently, I strongly recommend that they revise these sections to make the value of the comparison clear. I also suggest changing the name of the section to something more representative of what is covered (e.g. "Ecological Effect of NEMURO modifications")

4. Simulated mesozooplankton diet

Their use of trophic level was a clever way to summarize zooplankton diet information. However, their findings that, on the shelf, LZ is more herbivorous and PZ is more carnivorous, and that protists are more important diet source in oligotrophic are not unexpected since they prescribed their model to have that output. For example, LZ grazing has no terms for interference by other prey, i.e. any consumption of SZ does not reduce ingestion of LP. In contrast, PZ has 3-fold higher grazing rate on LZ, as well as ingestion of zooplankton interfering with ingestion of phytoplankton. Given that

diet was a fundamental aspect of their study, I think it would behoove them to add text about what these grazing functional responses are assuming with respect to prey preferences (e.g. see Gentleman et al., 2003).

5. Simulated secondary production

Despite this being a stated objective, secondary production was only given a paragraph in the text, and is not mentioned in the discussion/conclusions. This is a missed opportunity to gain some more insight into the GoM function. If the authors don't want to flesh out the analysis, I suggest removing it from the objectives and possibly also from the results.

TECHNICAL CORRECTIONS

In Methods, on pg 9 of manuscript say 3 observational benchmarks, but in S3 pg 3 say and list 5.

In S3 pg 6, should give units for alpha.

I realize writing parameter tables and equations can be challenging to proofread, but in my surface examination I noted some typos and would recommend authors carefully review. e.g. –Supp pg 11, KSi says ammonium half saturation constant, should say Silica –pg 18 under Limitation terms, two eqns for GL_SP2SZ, one should be for GP_LP2SZ

Table S3 would be improved if the percentage difference was listed

Intro (pg 3) missing point that mesozooplankton also exert top down pressure on protists, which indirectly affects phytoplankton biomass

Methods (pg 6) Steele and Frost, 1977 not good reference here, as very detailed grazing formulation uncharacteristic of early NPZ. Better reference is Steele, 1974.

Methods (pg 13) Note that this size-based definition for small zooplankton includes early stages of mesozooplankton, which may sometimes be prey, but generally mature

to mesozooplankton (i.e. there is a mismatch between the data and model characterizations). You may want to note this in the text, as that could contribute to model-data differences.

Methods (pg 15) Line 398 accent on second Decima

Results (pg 18). Table 1 does not appear to be related to data/model comparison, or validation. Should this perhaps be removed or at least moved to a separate section? If it is retained, it would be worth pointing out the interesting result that the max in the oligotrophic regions is less than the min on shelf.

Supp: RLP in Table S2 not highlighted as changed but different value, same as tauSP2SZ

Discussion pg 36. State that protists are often missing from models, despite their importance. However, many modern ecosystem models have both microzooplankton and mesozooplankton components. It would be worthwhile to reference some of these other models, as well as the substantial body of work related to appropriate ways to model them, esp. for mixotrophs (see Flynn and Mitra).

The last two sentences of the conclusions are not really conclusions, they are more future work and could be moved to the discussion or removed.