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Interactive comment on "A zooplankton diel vertical migration parameterization for coastal marine ecosystem modeling" *by* Ariadna Celina Nocera et al.

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We address the points below, referee comments are in bold text.

General Evaluation

The authors present a 1-D NPZD model of coastal ecosystems with diel vertical migration (DVM) in zooplankton. DVM is parameterised by an optimal light level and allowed to occur only when food availability is below a certain threshold. A sensitivity analysis is presented showing the relation between DVM and several

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model parameters and boundary conditions. The authors conclude that DVM increases C export and that C export will be severely overestimated without DVM. As may already be clear from the last sentence of the previous paragraph, my main impression from this work is that it has not been thought through very thoroughly. The main model set-up and assumptions appear either rather half-baked or unfounded.

It might be clear to the reviewer but for us, it is not clear how our conclusion led the reviewer to the impression we did not think about the question thoroughly. We are willing to demonstrate our assumptions are neither half-baked nor unfounded.

Another problem I have with this study is that I expect from every model study at least some attempt to compare the model quantitatively with observations, and this has not been done here.

It is true that the purpose of science is to explain and sometimes make predictions about aspects of the observable world. Developing models definitely serves that purpose. However, there are multiple types of useful modeling studies and comparing model results with observations is one among others. The scientific literature is full of examples where some aspects of ecosystem dynamics are discussed only in the *model world*, with only qualitative references to observations. The study of Huisman et al. (2006) published in *Nature* demonstrates that a simple 1D model of primary production in a turbulent stratified ocean can be chaotic, which is one fundamental source of irregularities observed in multiyear records of phytoplankton blooms and associated nutrient distributions. Abraham (1998) is another example of an idealized modeling study exploring how heterogeneity can emerge out of simple ecological happening in a turbulent ocean. These studies are very important for many reasons, especially when the object is of overwhelming complexity, so overwhelming that observing its dynamics can sometimes be impracticable.

The zooplankton component within numerical models is rarely compared against field

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observations because, unlike other parameters such as temperature or Chlorophyll *a*. This might be so because zooplankton observations do not usually have the resolution of the modeled zooplankton variables (temporally or spatially), because they are in different formats or units (species abundance rather than mass expressed in nitrogen units), or because they are inaccessible (Everett et al. 2017). This is something that the scientific community needs to address: gathering modellers and field researchers to work together to better link models and observations. But this is not an essential exercise for the modelling itself.

Also, one of the central assumptions in this model is that DVM occurs only at low food concentrations, but this assumption is only mentioned but not really discussed in terms of how realistic it may be or whether it has been observed. In fact, no evidence is presented for it. While this assumption could make sense below the photic zone, where it could help determining the daytime depth of the zooplankton, I think it is introduced here too simplistically, in a way in which it could also keep the zooplankton very close to the surface. Because of these deficiencies, and I list some more below, I consider this work far below the current state of the art and do not recommend publication.

Here, probably our manuscript was not clear enough, which led the reviewer to think that our model indicates that zooplankton only moves at low food concentrations. The parameterization proposed in the present work refers to a P_{min} value, which does not mean a *low* concentration of phytoplankton, but to a minimum threshold concentration at which the zooplankton responds by migrating. Thus "low" food concentration should mean that there is too little food to support the current predator population, which isn't the case here. As we exposed in the text (Sensitivity analysis section), we examined three threshold values, for three different "food" concentrations, depicting the concentrations found at different stages of phytoplankton succession: before, during and after the bloom, 0.35, 0.7 and 1.4 mmolN m^{-3}, respectively (Schalles 2006).

Pearre (1970, 1973, 1979c) also suggested that hunger was the principal proximal cause of zooplankton migrations to the surface, and that light served principally as a synchronizer between the different species. This statement is taken up in Pearre (2003) and long discussed in his work. This referred work also mentions that in conditions of low food abundance, animals could be found near the surface even in daylight, but eventually, because of the risk of predation they escape to deeper water. In addition, the author states that different species' synchronous migrations would be a special case of vertical migrations initiated by particular, mostly critical, food conditions.

In this sense, low food conditions together with low irradiance values should force migrators to spend more time in surface waters. This is a result shown by our model for winter, when applying the P_{min} concept explained above.

In relation with zooplankton found *near to the surface*, some species have been reported as mostly restricted to the upper layer (< 30 m; Escribano et al. 2012, 2009; Escribano and Hidalgo 2000; Escribano 1998). In addition, modelled copepod distributions in low food conditions showed that the only option to face this situation was to maximize growth (grazing where food is available), resulting in a shallow depth location (Fiksen and Giske 1995).

The complexity of marine biogeochemical or ecological models can be organized along two major axes, the biogeochemical or ecological complexity and the physical complexity (Gruber and Doney 2018). In this context, the plankton model implemented here presents a biogeochemical approach close to the highest complexity levels (as it is a NPZD including a bacterial loop). Although rather simple, the NPZD model considers several nonlinear interactions, zooplankton playing a pivotal role. As the model is quite cheap in terms of computation, this allowed us to perform sensitivity tests on the different threshold values or on the intensity of the zooplankton vertical velocity (more than 1500 simulations were performed). Regarding the physical complexity of the ocean, GOTM allows for a representation of a one dimensional ocean that allows for the understanding of a coupled food web model. Both together provide a good representation for upper ocean ecology focused on lower trophic levels. In summary, we consider our approach as a good compromise for tackling a ecological question of plankton ecology in a well constrained physical (oceanographic) framework.

Specific points

Abstract, line 3: "... most zooplankton species." DVM occurs in many but probably not most species, e.g., it is not known for many microzooplankton species.

We have changed the word "*most* zooplankton species" by "*exhibited by a large number* of zooplankton species". Our assertion is true for mesozooplankton (particularly copepods) for which DVM is widespread (Ringelberg 2010), but we will change it to avoid confusion.

P. 2, line 5: "The efficiency 5 of the biological carbon pump is regulated by zooplankton and micronekton vertical migration ..." Surely, other processes and phenomena also affect the efficiency of the biological C pump. For example, sinking of phytoplankton and aggregates and their stoichiometry.

Referee #2 also suggested to add more details about the biological carbon pump (BCP), although the objective of this work is to emphasize the role that zooplankton vertical migration plays in this phenomenon and not the process itself. We have modified this paragraph and added more details about others components of the BCP that could affect the carbon export to depth in the water column before reaching the bottom and being sequestered in the sea floor.

The new paragraph states: "The efficiency of the biological carbon pump within coastal regions involves a series of carbon transformations (Fennel et al. 2018). These processes include the production of organic matter from inorganic carbon by phytoplankton, its consumption by primary consumers (zooplankton), the sedimentation of carcasses and dead organisms, as well as the formation of marine aggregates (Honjo et al. 2014). At the same time, it is argued by many studies that the active swimming of zooplankton and micronekton regulates and even facilitates the carbon export (Bianchi et al. 2013, Steinberg et al. 2000, Steinberg et al. 2002, Tutasi and Escribano 2020). Zooplankton, apart from transferring energy to higher trophic levels, plays a central role in the active transport of dissolved and particulate organic matter to depth (Ducklow et al. 2001). The production of feces is particularly efficient for exporting carbon to the ocean's floor as fecal pellets sink fast, in the order of 1-10^2 meters per day. The rate and timing at which they are produced is thus an important factor modulating the efficiency of the carbon sedimentation (Turner 2015)."

P. 7, line 30: "parameter space" It remains unclear how many parameters the model has, and why the ones examined here were selected.

In order to clarify this aspect, we decided to incorporate an Appendix section where all the model parameters are defined, which a recall from Burchard et al. (2006). The same list of parameters are used in the present study. The specific parameters presented in Table 1 are those that have been modified, added with our DVM parameterization, and varied in the sensitivity analysis.

P. 8, line 23: "rC:N = 7 mmolC mmolN " Further above the authors give two C:N ratios for phytoplankton and zooplankton, citing Redfield (1958) (who did not distinguish between phytoplankton and zooplankton). So this is inconsistent with the model set up and could lead to a mass balance violation. It is not clear whether the model was checked for mass conservation.

We thank the reviewer for pointing out that mistake. The text was changed to be in accordance with the description given in section 2.2 Biogeochemical model. We removed this citation and we included two others that are best suited for this, namely Fasham et al. (1990) and Anderson (1994). The model was checked for mass conservation, which will be stated explicitly in the text.

P. 8, lines 26-27: "... a non-realistic benthic zooplankton community ..." A benthic community is not necessarily unrealistic, although it is of course not zooplank-

ton, as long as it undergoes no (vertical) motions. This seems to be the case in the simulations without DVM.

The original version of the biogeochemical model we use here is based on the seminal work of Fasham et al. (1990), who aimed at representing the nitrogen cycle and plankton dynamics in a depth-integrated mixed layer sitting on top of a nitrogen reservoir. Kuhn and Radach (1997) coupled this model to a one-dimensional physical model, aimed at representing the pelagic planktonic ecosystem. This idea was later followed by Burchard et al. (2006) who applied the model in a realistic scenario. However, none of these works focused on zooplankton. One key aspect of the model is that zooplankton is able to graze on phytoplankton, detritus and bacteria. When detritus sink and accumulates on the seabed, zooplankton growth rate can become significant producing unrealistic zooplankton concentrations near the bottom. This is of course an artefact that has gone unnoticed in these studies, simply because it was not the focus of the paper. To avoid the growth of such zooplankton, other strategies can be employed, like removing detritus as soon as they reach the seabed, simulating carbon sequestration in sediments. When adding DVM, this "benthic zooplankton" growth can't happen anymore, which provides a mechanistic way to avoid this unrealistic phenomenon. An example of this was shown in Figure 4a.

To further clarify this, we propose replacing Figure 3 of our original manuscript by Figure 1 shown in this reply, where DVM is schematized in relation with the physical setting. The proposed caption would be : "Schematic illustration of the diel vertical migration in the context of a stratified marine environment. The left panel shows the relevant parts of the water column between the sea surface and the seabed. Wind forces turbulent mixing from the sea surface down to the pycnocline. The interior layer is characterized by low diffusivity ($K_z = 10^{-5}$ m s^{-2}) and the benthic layer is where detritus accumulates. Without DVM (central panel), zooplankton grows wherever there is food, which is predominantly phytoplankton in the euphotic layer, and detritus that accumulate near the seabed. With DVM (right panel), zooplankton swims toward a

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preferred light level, sometimes fighting against turbulence, with occasional pauses wherever phytoplankton is sufficiently abundant. One consequence of DVM is that it never ventures below a certain depth and can't develop near the seabed."

P. 9, lines 25–26: "When turbulent diffusivity is low enough, zooplankton aggregate into narrow patches (Fig. 4c and f), while if it is strong enough, it will be mixed homogeneously (Fig. 4b and e)." It is not clear that this is what is going on between Fig. 4b and e. Both panels look very similar, with zooplankton being concentrated near the optimal isolume.

We recognize that panels *b* and *e* look very similar. We wanted to explore the differences between constant wind scenarios with one where the wind forcing is realistically variable in time. What results show (Fig. 4 but also Figures 6 to 8) is that there aren't much differences between the constant high wind scenario and the chosen variable wind scenario. What's to remember though is that realistic values of turbulent diffusivities can be dilute zooplankton even though it swims up to 320m d^{-1}. In response to Referee #2, we added some quantitative analysis about what diffusivity can overcome what swimming speed.

We've decided to change panels in Figure 4 and present in the revised manuscript the numerical experiments listed in Table 2 to give more clarity to the Results Section (following Referee #2 comment).

P. 11, line 3–4: "a more or less abrupt transition happening around a critical grazing rate that we call gmax, from no migratory behavior (Ω = 0) towards a stronger, more clearly defined one (Ω > 0)." I think this sentence highlights a major problem of this ms. The model makes a very strong assumption, namely that DVM stops once a certain amount of food is available, and no evidence is presented for this assumption. Then major conclusions are drawn based on this assumption. This is an example for such conclusions. The effect of the maximal grazing rate is solely due to this assumption because it determines whether the

zooplankton can graze down their food below the critical level allowing for DVM.

We agree that the hypothesis that DVM is affected by food availability is a strong one and that we did not properly supported it. In his review, Pearre (2013) discusses the hunger/satiation hypothesis as a possible driver for vertical migration and cite multiple studies carried out over the past century that mention this effect, which is nonetheless very hard to confirm experimentally. The work by Bianchi et al. (2013), that we now describe in greater detail, uses that hypothesis in their DVM parameterization. We do not believe this assumption to be a major problem in our approach. We instead feel that including it as a possible driver and exploring its effect by way of a sensitivity analysis (the value of P_{min} is varied) can be valuable to determine how such a mechanism can impact a light-driven DVM parameterization. One result that comes out of this is that the resulting vertical excursions depend on how fast can zooplankton feed, decrease the local food stock,here represented by the maximum grazing rate g_{max}, and proceed to migrate again.

P. 13, lines 7–8: ***This indicator [export] is consistently larger when*** g_{max}***< 1.0 d***$^{-1}$ ***in all experiments*** **These are the same conditions where DVM is suppressed, so this is the foundation for the conclusion that C export can be severely overestimated without DVM. But apparently this does not fit with the authors' view of DVM as a process favouring export, so they provide both, resulting in a self-contradictory conclusions section.**

The sentence *This indicator [export] is consistently larger when* g_{max}*< 1.0 d*$^{-1}$ *in all experiments* is in the Results section and describes what is happening in Figure 8 and indeed, as we mentioned in the text, reflect *all* experiments under this condition only. When g_{max} is increased beyond that value that we called $g^{\star}_{\mathsf{max}}$, we can see that C export increases for the model without DVM as well as when w_{max} takes large values. What we want to conclude from this is that the grazing rate is a key parameter influencing carbon export estimation.

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On the other hand, the sentence *Carbon export can be severely overestimated without DVM* is mentioned in the Discussion section, but it wasn't a conclusion derived from our study. In this paragraph, we were pointing out the importance of including DVM into ecosystem dynamics to calculate carbon budget and we referred to this, but we didn't include the references which stand for it.

Here is the modified paragraph we propose: "Furthermore, in models without DVM, permanent phytoplankton-zooplankton match greatly influences pelago-benthic coupling. Carbon export is an issue of great importance in determining the role of the ocean in global change related processes,such as increasing anthropogenic CO_2 and its consequence on reducing sea pH, and this amount can significantly differ when DVM is considered in the system (Aita et al. 2003, Gorgues et al. 2019, Hansen and Visser 2016, Morales 1999, Tutasi and Escribano 2020). As a result of this new fractional interaction in space and time,as we show in the present study, carbon export to depth also varies. The fraction of phytoplankton that is not consumed by zooplankton becomes part of the detritus found in the water column, where it can also be grazed by zooplankton (though in a lower proportion/preference than phytoplankton) but eventually settles towards deeper layers. While it is known that DVM favors carbon sequestration (Ringelberg 2010; Turner 2002, 2015), few studies include it and consider its effects on the potential carbon sequestration at the sea bottom. The different cases presented here illustrate this fact, but further studies in different configurations are needed to better understand its importance and constrain its representation."

Please also note the supplement to this comment:
https://www.biogeosciences-discuss.net/bg-2020-10/bg-2020-10-AC1-supplement.pdf

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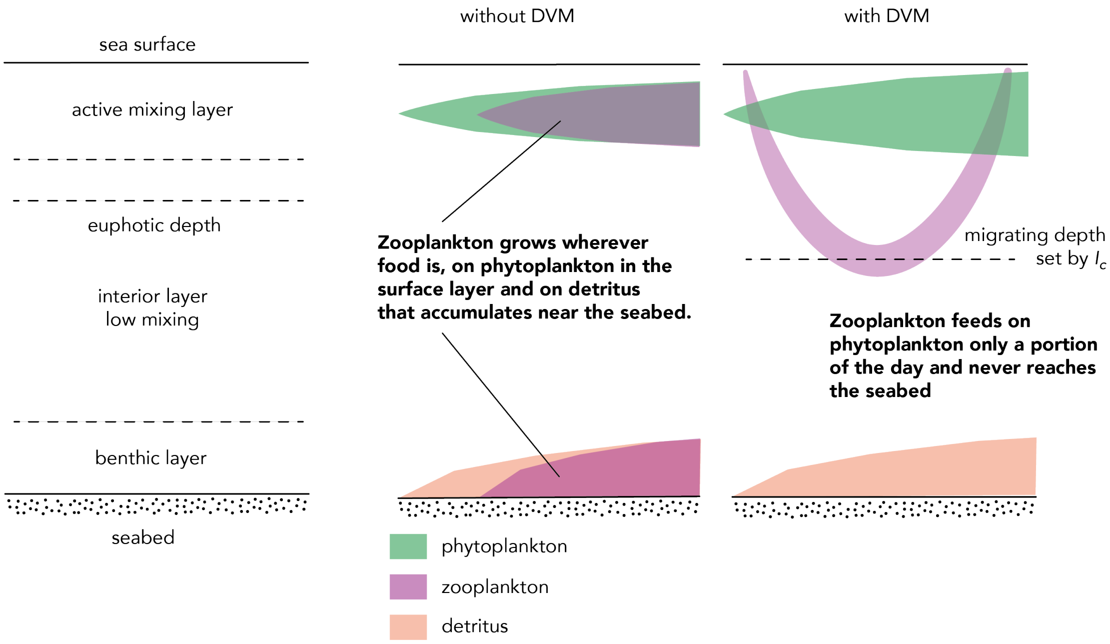

Fig. 1. Schematic illustration of the diel vertical migration in the context of a stratified marine environment.

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