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Interactive comment on "CITRATE 1.0: Phytoplankton continuous trait-distribution model with one-dimensional physical transport applied to the Northwest Pacific" *by* Bingzhang Chen and S. Lan Smith

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Reviewer #3 This manuscript presents a newly developed model based on an emergent trait-based approach to simulate phytoplankton traits (size) and associated diversity according to environment factors. The authors chose to construct an adaptative dynamics models that employs moment closure to allow continuous distribution of traits and limit the number of variables. Indeed, the model simulates the characteristics of phytoplankton community in terms of total biomass and mean size while the diversity is approximated by the variance in size. Some important processes for phytoplankton

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growth, corresponding to physiological adaptation to light and variable C:N ratio are also incorporated. As such, the model described in this paper is of valuable contribution to the scientific understanding of the plankton diversity which has become a central issue of marine ecosystem management. The manuscript is well-written and gives a general overview on the ability of the model to simulate size-structured distribution of phytoplankton in various environmental conditions using two contrasted stations of the Northwest Pacific. However, I have some questions concerning the methodology which has been applied and whether/how this work can be generalized to other stations or a broader oceanic region (e.g. in the context of 3D modeling setup). Indeed, I am not familiar with the use of DRAM-type algorithm to adjust model's parameters value to observational data and it took some time to me to understand exactly the method that is implemented in this study. Therefore, a more detailed description of what is exactly done by the parameters optimization algorithm and how this will be used to apply the model to other regions would be very useful to help the reader to understand the concept behind this model. It would thus significantly raise the likely impact of this paper. I recommend these questions, detailed in the 'general comments' section below, to be addressed before the manuscript could be considered to be published in 'Geoscientific Model Development'. Some minor and more specific comments are also included at the end of this document.

General comments: 1- Technically, the proposed model setup uses a DRAM algorithm to adjust the targeted parameters values and minimize the differences between model outputs and observational data based on two available dataset for contrasted stations of the Northwest Pacific. In the discussion section (p. 21, l. 3-7), the authors argue that this model would be 'easy to couple with 3D global or regional ocean models' (see also page 5, lines 6-8). As far as I understand, the idea would be to use the single set of parameters which has been found in this study (i.e. the one which gives the highest likelihood with regards to observational data for both stations) to run the model in other oceanic regions (otherwise, I do not see how the method can be applied to large oceanic system while seeking for a single set of parameters that would lead to the

best fit to observational data over the considered region). This point is not specify in the manuscript. Could you please add further thoughts on that in your discussion section and describe the preconised method to apply this model to larger oceanic regions?

[Response] This is a good point that we had not explained with sufficient clarity in the previous manuscript. Yes, our intention is to use the single set of parameter values, obtained by fitting the model to the data from the two observation stations, as an initial estimate of parameter values for 3D simulations. As a test of the feasibility of this approach we present an example in which we use the parameter values optimized from the two stations K2 and S1 to model another independent station (the well known station ALOHA) in the North Pacific (Results section 3.5). Although the results are not as satisfactory as we wished, the parameter values obtained in the present study nevertheless provide a useful initial estimate for modeling other stations and for 3D applications. We propose for later studies to combine the "transport matrix" technique with DRAM or other parameter optimization techniques to calibrate 3D models in the discussion (Sect. 4.2.5).

2- In the introduction section (p. 4, l. 16-17), you write that 'relatively few continuous trait-based models have been validated against oceanic observations'. The comparison that is done in results section 3.3 (p. 13-14) does not constitute a 'validation analysis' as you are using the same observational data to contrain the model's parameters and to 'validate' the results. Indeed, the specific aim of the method which is used in this study is to provide the best fit between model outputs and measured data. Therefore, the main outcome of this study is actually the parameters set you obtained after running an ensemble of 10 000 simulations. A validation analysis should involve totally independent data for model parameterization and for validation and could only be carried out if you have runned the model for a different region using the same set of parameters. Here again, a more explicit description of the aim of your method (i.e. seting up a set of parameters which can be subsequently used to run the model in other regions ?) would have been useful to avoid the confusion.

[Response] Yes, we totally agree. We have changed the word “validate” to “calibrate”. We indeed attempted to validate the optimized model against independent datasets at station ALOHA. And we have emphasized our goal is “CITRATE is intended to be a starting model for later incorporation into three-dimensional (3D) general ocean circulation models (GCMs) and for further development of more comprehensive trait-based models” at the end of Introduction.

3- How do you convert the mean size and size variance into four size classes fraction? I guess the calculation is done by comparing the occurrence of each size classes from the size distribution (Gaussian distribution of the log biovolume) other time (e.g. seasonal average in fig. 8 and 9?) but this is unclear. Could you please specify the method that has been used in your method section?

[Response] Yes. We have added the method to calculate the four size classes of Chl based on phytoplankton biomass (in terms of nitrogen), mean size, and size variance (after Eq. 11d in Sect. 2.2). Actually, because we assumed lognormal distribution for phytoplankton cell volume, the Chl distribution is no longer a lognormal distribution (because the modeled chlorophyll to carbon ratio depends on cell volume). In order to obtain accurate estimates of the chl distribution, we had to discretize the phytoplankton size spectra to numerically estimate the fractions of size fractionated Chl.

4- In the introduction section, you say that functional groups (PFT) models, representing a defined and limited number of plankton types, generally ’underestimate local diversity’. You argue p.3, l. 24-26 that the main reason for that is their inability to resolve the trait space combined with their failure of representing the appropriate mechanism sustaining high level of diversity. Although these considerations are correct, I think they are not specific to aggregated models but can also apply to the model presented here. Indeed, as you point out in the discussion section, you choose to consider the size as master trait but ignore some other major traits (temperature optima, mixotrophy, grazing resistance etc.) which may also vary among planktonic organisms of same size and enable coexistence by achieving similar fitness between different adaptation

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strategies (i.e. mechanisms for sustaining diversity). In that sense, I would say that the two techniques have a similar bias of taking into account a limited number of traits and mechanisms to explain the huge plankton diversity. Please modify the introduction to consider this point. Moreover, another difference between the two methods is that the measure of diversity that is provided by moment-closure models corresponds to a relative measure of diversity (variance in size in this case) which only allow a relative and comparative analysis of the phytoplankton diversity (in time and space) but does not provide any absolute measure of diversity (number of taxons or species) to compare with observational data.

[Response] As admitted in the Discussion, we agree that our approach also suffers from lacking some of the important functional traits so that it also underestimates diversity. We also note in Sect. 4.2.1 that a promising approach might be to combine the discrete functional group approach with the continuous trait approach, to include the merits of both approaches. We have added the following text in the Introduction: "Although this approach might overlook some other important traits that are not related to size and thereby underestimate trait diversity to some extent, it serves as a starting point for later development of more comprehensive diversity models that can include more traits or be integrated with the discrete functional group approach."

Indeed, the diversity metrics of our model cannot be directly comparable to the classic definition of "Richness" as the reviewer mentioned. Maybe other metrics like the Shannon-Wiener index that consider species evenness can be better compared to the trait variance we used in our approach. These metrics can be also calculated from observational data (e.g. size-fractionated Chl.). We have added "The trait variance, treated as a tracer in the model, serves as a measure of trait diversity, although it cannot be simply equated to species richness but may be converted to other diversity metrics like the Shannon-Wiener index (Quintana et al., 2008). The diversity of functional traits is arguably a better diversity index than species richness to relate to ecosystem functioning (Loreau et al., 2001)." in page 4.

p. 4, l. 9, you argue that 'the factors controlling diversity can be directly quantified and better understood' with the continuous trait-based models. This sentence is not unclear. Could you specify how and why are the factors (which factors?) controlling diversity better characterized using the latter method ?

[Response] We meant that from the equations of moment closure, the factors controlling diversity can be directly quantified and better understood because the diversity itself is a tracer, and the sinks (e.g. the second derivative of growth rate indicating resource competition) and sources (e.g. the trait diffusion terms indicating the effects of mutation) are given explicitly. We have revised the sentence to "Thus, the continuous trait-based model has the advantage that the factors controlling diversity can be directly quantified and better understood because the sources (e.g. speciation or immigration) and sinks (e.g. resource competition) for diversity are specified explicitly." to make it clearer.

Specific comments: Please put 'et al' in italic while citing referenced publications throughout the manuscript. [Response] Thanks for the comment. But it seems that the GMD format does not require to put 'et al' in italic.

Model description P5 L12: Add the unit of P [Response] Added.

P5 L18: Figure 1: What is the inset in the box on the top left (with probability axis)? Please add a description in the figure caption. [Response] We have added a description in the figure caption.

P5 L22: Please provide more explanations on the role of the trait diffusion parameter [Response] Yes, we have added a sentence "u is the trait diffusion parameter, which describes the probability of the parental size l(i) changing to adjacent size values l(i–1) or l(i+1) in offspring cells (Merico et al., 2014)." after Eq. 7c.

P6 L7-11: Please provide the references for the growth dependences to light, nutrient concentration and temperature. [Response] We have added a sentence "Following

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previous studies (Flynn, 2003; Geider et al., 1997; Follows et al., 2007; Chen and Laws, 2017)," before this sentence.

P6 L17: Eq. (5A) should be Eq. (4A) [Response] Thanks for pointing it out. We have corrected it (now Eq. (10A)).

Section 2: I would suggest to separate the description of the biogeochemical equations (section 2.2) and the 1D implementation (section 2.3). Therefore the paragraph l. 9-13 on page 7 should be moved to the section 2.3 and the name of the section 2.2 should mention only 'Biogeochemical model (nutrient, zooplankton etc.)' [Response] We have followed the suggestion to separate the description of the ecosystem model (now section 2.1) from that of the 1D implementation (now section 2.4).

P7 L13: The sentence 'the 1D model contains only biological tracers' is unclear. It should be replaced by 'the biological model is runned offline' or something similar

[Response] We have rewritten the sentence to "For computational efficiency, instead of explicitly solving the complete moment, temperature, and salinity equations, we imported the physics variables that are directly relevant to the ecological processes from external data products.".

P8 L5: Please replace 'water depth' by 'the depth of the water column depth'. [Response] We have changed it to "z is the depth of the model grid (m)".

P8 L11: Please verify the equation for detritus (- -). [Response] Sorry, it was a typo in the previous version. We have corrected the detritus equation.

P9 L12-14: Do you assume that the surface mixed layer has a depth of 100 m? (the explanation for the use of the threshold of Kv > 10-3 m2.s-1 is unclear). [Response] Yes. We just tried to use a simple calculation to demonstrate why we use the threshold of Kv > 10-3 m2 s-1.

Why do you use a different parameterization for the MLD calculation for phytoplankton growth and MLD showed on fig. 2 from observational data (page 12, line 15)?

[Response] This is a good question. The definition of MLD based on observed temperature and salinity profiles is because there were no observational data for vertical eddy diffusivity (Kv). In the model, since we have the Kv from 3D model outputs but do not have salinity variables, it is best to define MLD based on Kv.

P11 L8: 'and both model'? Please check the sentence. [Response] Sorry, it was a typo (although we do not know why it appeared). We have deleted them.

Fig. 2 caption: Add the description of the white scatter plots (MLD) in the legend. Change ': : :at station S1. (f-i) The same for station K2' [Response] Description of MLD added. The figures indices also corrected.

Fig. 2: Check x-axis thick labels (subplots b, c, f and g). [Response] Sorry, we did not find problems with x-axis thick labels.

Fig. 3: Add x-axis labels. [Response] Added.

Results In general, there is some discussion points that are included in the results section and that should rather be discussed in section 4.

P12 L18-25: This section describes the physical forcing and does not concern a result of the simulation. I would suggest to move this part in section 2.3 (method). [Response] Yes, it is true. But we think that acquiring physics forcing is also an important component of our modeling work and the physics background should be counted as results although they are not direct results from simulation. So we feel it should better to be put in the results instead of in the method.

P12 L23: 'with the model estimates of MLD consistent with those measured from in situ temperature and salinity profiles': it is not clear what you are comparing exactly. (Please also add a reference to the figure showing that. What are white scatter plots on fig. 2 b and f?). [Response] As explained above, we were comparing the MLDs from CTD profiles of temp. and salinity with from modeled profiles of Kv. We have added a reference to the figure ("Fig. 2b,f,j") showing this and also descriptions of white scatter

boxes in the figure caption.

Fig. 4 caption: Remove the 's' in 'log-likelihood'. Replace (b-j) by (b-i) [Response] Removed.

P13 L6: The SSqE of the smallest size fraction (fig. 4, q) also increases with time at S1 [Response] Yes. But in the new simulation results, SSqE of the smallest size fraction decreases with time at S1.

P13 L9: The figure 5 is not commented in the text. Please add a sentence to describe the trend. [Response] Added in the second paragraph of Sect. 3.2.

P13 L 11-16: The discussion on the value of the trait diffusion parameter should appear in the discussion section. [Response] We feel that this interpretation on the value of the trait diffusion parameter should immediately follow the results to make the logic smooth and so that readers will easily be able to understand. We have changed the sentence to "The optimized u value was much higher than in Acevedo-Trejos et al. (2016). Reducing u to 0.05 yielded worse fits to the size-fractionated chlorophyll since lower size variance failed to capture the observed size scatter. It also relates to the limitation of the model that has to assume a lognormal distribution of size (see Sect. 4.2.1). However, an abnormally high u could drive the model to unstable conditions in which the size variance kept increasing.". In the Discussion section, we did not present details concerning the parameter values.

Fig. 6 and 8 captions: Complete the caption with the position of the different variables. [Response] Completed.

P13 L20: 'the higher surface concentrations' [Response] Yes. Changed to "the higher surface concentrations of DIN during winter than summer".

P13 L22-24: Isn't it in apparent contradiction with the fact that you argued that the modeled MLD is in agreement with observational data (page 12, line 23)? [Response] Yes, this disappears with the new simulation results.

P13 L22-24: discussion [Response] This part has been removed during revision.

P14 L5: The observational data on the size fractions are relatively noisy. Could you please provide more details on how these data were obtained (sampling methods, size measurments, sampling frequency) in section 2.5? At station K2, the size distribution in unclear in data and the model overestimate the proportion of 3-10 _m size class. At station S1, observational data show the dominance of smaller cells but do not show the vertical structure of the size distribution that is simulated by the model with smaller cells at the surface. Please add a comment on this.

[Response] We have added a description of how the data of size fractions were obtained. The data did show some seasonal and vertical patterns, and we have described the patterns of the data and comparisons between data and model in Sect. 3.3.

P14 L7-9: 'At station S1'. Do you mean station 'K2'? [Response] We meant at S1. However, we have removed this sentence because there was indeed some vertical pattern at S1 if one looks really carefully.

P14 L10: discussion [Response] We have moved this sentence to Sect. 3.2 because we feel that the comment of light limitation on large cell size should immediately follow the description of optimized αI.

P14 L19: 'following stratification which occurs earlier in S1 than K2' [Response] Yes, we have added 'which occurs earlier in S1 than K2'.

P14 L24: Show a figure of Chl/C ratio [Response] The figure of Chl:C ratio shown in Fig. 10 and 11.

Fig. 10, g: High growth rate at the surface at K2 despite low TIN and low Chl a concentrations? [Response] With the new simulation results, high Chl and growth rate occur at the same timing at surface at K2.

P15 L5-6: discussion [Response] This sentence has been removed during revision.

P15 L24 – P16 L4: discussion [Response] We have either moved the text to discussion or deleted it during revision.

P16 L3: The ‘dynamic equilibrium theory proposed by Huston is only briefly mentionned (see also page 17, l, 1-2). This hypothesis implies that, under non-equilibrium conditions, the outcomes of the competition depend on the timescale of the competitive displacement and the relative rate of change in competitive abilities of each competing species. This point should be further developed and discussed according to your results on diversity in the discussion part of the manuscript. [Response] This is a good point. We have added discussions on the ‘dynamic equilibrium theory’ in Sect. 4.1.1: “Using ‘adaptive dynamics’, it is easier to quantify competition intensity (and other ecological quantities), which makes it easier to test ecological theories such as Huston’s “general hypothesis of species diversity” (Huston, 1979). For example, the absolute magnitude of (dˆ2 μ(I))/(dIˆ2) correlates positively with μ (Fig. 13), indicating that higher growth rates induced greater resource competition. This agrees well with the “dynamic equilibrium theory”. Huston (1979) emphasized that in natural environments where equilibrium is rarely achieved, growth rates play a greater role in determining diversity than do steady state competitive abilities as typically quantified by R* values (Tilman, 1982; Litchman et al., 2007). This is because when environmental conditions favour fast growth, it takes less time for the dominant species to predominate, and diversity decreases. The positive correlation between the absolute value of (dˆ2 μ(I))/(dIˆ2) and μ is a mathematical manifestation of the verbal argument in Huston (1979). ”

P16 L6-9: As I said above, the role of the trait diffusion in maintaining diversity and the way it is used in the model is a bit tricky to understand. You could perhaps add a paragraph in the method section to clarify this point which is then only discussed briefly page 17, lines 10-14. [Response] We have expanded the explanations on trait diffusion in Sect. 2.2: “u is the trait diffusion parameter, which describes the probability of the parental size I(i) changing to adjacent size values I(i–1) or I(i+1) in offspring cells (Merico et al., 2014).” Also in Sect. 3.4:

“Second, the contributions from the second derivatives of growth and trait diffusion (dominated by 2uμ(l) with the contributions from (dˆ4 μ(l))/(dlˆ4) being minor; Eq. 7c) were the two largest terms, which usually offset against each other. The values of (dˆ2 μ(l))/(dlˆ2) were always negative in all times at both stations, suggesting that without “trait diffusion”, size variance would decrease toward zero (Eq. 7c). This highlights the importance of trait diffusion (which can be interpreted as genetic mutation or trans-generational phenotypic plasticity) to sustain diversity. The values of (dˆ2 μ(l))/(dlˆ2) were more negative when growth rates were higher and it is the margin of these two terms that (partially) drove the changes of size variance. For example, in early April of S1, the decrease of size variance was induced by a more negative (dˆ2 μ(l))/(dlˆ2) (see also Fig. 11h). Similar situations also occurred at the end of December.” also in Sect. 4.1.1: “The incorporation of trait diffusion originally developed for continuous trait-based models (Merico et al., 2014) also provides a mechanism similar to speciation (or mutation) for sustaining diversity, linking ecological and evolutionary processes (Rosenzweig, 1995). The increasing effect of trait diffusion with growth rate is consistent with the Metabolic Theory of Ecology that metabolic rates, closely coupled with growth rates and generation time, are expected to correlate with mutation rates and affect speciation (Allen et al., 2006; Dowle et al., 2013). Our results have shown that it can be the largest term to balance competitive exclusion (Fig. 13). Without considering this mechanism, diversity could be underestimated in productive waters due to strong competition. This could also contribute to the latitudinal diversity gradient since in tropical regions (ectothermic) organisms tend to growth fast (i.e. short generation time) due to high temperature and therefore have high mutation and speciation rates (Rohde, 1992; Allen et al., 2006; Dowle et al., 2013). ”

Discussion P17 L22-27: There is no figures showing the N:C and Chl: C ratio patterns at the two stations. [Response] We have added the figures showing the N:C and Chl: C ratios at the two stations in Fig. 10 and 11.

P18 L3: ‘Instead, we employ : : :’: The word ‘instead’ seems unappropriate as you

mention a very different process than in the previous sentence: the trade-offs between maximal growth rate and nutrient affinity in the phytoplankton is not related to the size-dependence of the grazing by predators. [Response] Here actually we meant different mechanisms to control phytoplankton mean size. These two mechanisms are the two most plausible mechanisms (one from bottom-up and the other from top-down) that may affect phytoplankton size structure. We have modified the text to : "We have provided both bottom-up and top-down mechanisms to affect the size structure of phytoplankton in CITRATE 1.0. First, we employ an observation-based unimodal relationship between maximal growth rate and size to give the nanophytoplankton the advantage under nutrient-replete conditions (Chen and Liu, 2010, 2011; Marañón et al., 2013), thus allowing a trade-off between nutrient affinity and maximal growth rate within the pico- and nano-size range."

As you mention l. 17-19, the role of grazing in shaping phytoplankton community has been shown to be crucial. In order to take into account a various palatability of phytoplankton for zooplankton feeding according to the cell size, the model should ideally involved a larger number of predator size classes (and/or, at least, an additional mesozooplankton size class) which would lead to much more complexity in the model. In addition to the predator-prey size-ratio, the predators' feeding mode (Mariani et al., 2013) and the formulation that is used to constrain the herbivorous impact on primary producers community composition are also very important. Please add the information on what kind of predation function you are using in your model in 'Model description'. Also, this points should be mentionned in the discussion section (add other references such as Anderson et al., 2010 ; Prowe et al., 2012).

[Response] We admit that zooplankton feeding including predator-prey size ratio and feeding mode is indeed an important process shaping phytoplankton size structure. We have added a mesozooplankton compartment to allow more subtle effects on phytoplankton size structure and later development of more sophisticated models. However, our parameterizations do not allow zooplankton grazing to play a significant role

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in affecting phytoplankton size structure because 1) we do not have sufficient data to constrain the zooplankton parameters and 2) following the principle of Occam's Razor, if bottom-up factors alone can well simulate the patterns of phytoplankton size structure (we feel the bottom-up factors play the dominant role in oligotrophic oceans while top-down factors might be important in coastal waters). Therefore, we feel it unnecessary to add more complications at this time.

We have given the grazing function (Holling-Type III) in the section of 'Model description'. But as we have argued, it is not necessary for our model to contain too many details of zooplankton grazing such as feeding mode without sufficient data.

P20 L12: 'other mecanisms such as vertical migration': I am not sure that vertical migration is a very common process in small phytoplankton populations that are found at the surface of subtropical waters during the summer. What about the nutrient limitation terms? What should be the half-saturation constants for nitrogen/phosphorus uptake in the 1-3 _m size class found in observationnal data?

[Response] Vertical migration is certainly not a common process in small phytoplankton populations. However, some have found that very large phytoplankton that can perform vertical migration in the subtropical oceans (e.g. Villareal et al. Nature 1999; Villareal J. Phycol. 2004). It has been claimed that this vertical migration might be significant for new production and it seems a fair mechanism to provide nutrients to the surface waters.

For the nutrient terms, first we need to clarify that the half-saturation constants for GROWTH (Km) used in the Monod equation should be much smaller than those for nutrient uptake (Ks; Laws Ann. Rev. Mar. Sci. 2013). Experimental measurements for Km are scarce, but generally have very low values, much lower than those used in the model (Laws et al. J. Phycol. 2011). However, we do not believe that using a very small Km will solve the problem because phytoplankton growth has to be limited by nutrient, and in any case the growth rate in surface waters will be lower than at

depth closer to the nutricline. In any case, we do not know any measurements on half-saturation constants of 1-3 μm phytoplankton at our stations.

Please also note the supplement to this comment:
https://www.geosci-model-dev-discuss.net/gmd-2017-104/gmd-2017-104-AC5-supplement.pdf

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