

Interactive comment on “Isotope data improve the predictive capabilities of a marine biogeochemical model” by T. Van Engeland et al.

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Author’s final comment

We thank the referees for their constructive input. The referees found that our modelling study was performed in a technically sound way and that the technical aspects were well communicated. However, they also raised two important concerns. We agree with the concerns of the referees that our main message was not well communicated, and the “disconnect between the different sections” of the manuscript. Furthermore, the referees questioned whether the current manuscript (MS) could stand alone independent from the companion paper of De Kluijver et al. (also this issue). This second comment is largely elicited because our main message (which is different from that of De Kluijver et al.) was not clear enough.

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1. Clarifying our message:

As indicated in the project description, one of the ambitions within EPOCA (European Project of Ocean Acidification) was to integrate modelling and experimental efforts; Workpackage 9 provided this interface. A lack of modeller-experimentalist interaction has been signalled by several authors over the last decade (see for instance Vallino, 2000; Flynn, 2005), and proves a difficult issue to tackle. Clearly, modellers need data and experimentally derived ecosystem information to design, drive and calibrate their models. However, it may not be clear to experimentalists why they should provide all this information, since there seems to be no direct return from generic models.

The primary goal of this MS was to show how modeling meosocsm experiments can provide added value to experimentalists as well, i.e. by providing information on the impact of uncertainty in the data and experiment (i.e. lack of data, and unexplained variability) on experimental results.

This was here accomplished by analysing an isotope-resolved ecosystem model, specifically designed for the pelagic mesocosm experiments of EPOCA. Because of our main focus on a non-modeller public we decided to focus on a clear and elaborate treatment of the calibration procedures. To improve the outcome of large-scale mesocosm, it is desirable that an experimentalist has an idea of the capabilities and limitations of the model and subsequent model analyses, given their own efforts in data collection (which are enormous in the case of large mesocosm experiments like those of EPOCA). Model assumptions and choices on process equations are only briefly touched upon and largely based on the available experimental data. Model complexity is here only treated as an implication of data availability to avoid too much confusing technical details.

2. Independence of the two companion manuscripts:

Clearly, the angle of this MS is NOT an analysis of the experimental results in order to increase our knowledge on the effects of CO₂ perturbations on pelagic carbon cycling.

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This is reserved for the companion paper of De Kluijver et al. (also this issue). Our study investigates the uncertainty in the model output that originates from uncertainty in the data. More specifically, it focusses on the role of isotope tracer data in directly constraining carbon flows between ecosystem components. It is complementary to the MS by De Kluijver et al. (this issue), but at the same time, takes the analyses a step further by addressing particular assumptions from the model against a background of available data. These additional analyses serve an illustrative purpose and show how direct feedback can be given by a modeller on the experiment. For brevity, our study was based on the data from the control treatments only.

We acknowledge that the MS falls short in communicating our goals, and we will make appropriate adjustments to better convey our message. Sections have been added to the discussion to summarize our findings and the feedback to experimentalists. Three additional figures were added, which are also given here.

A. Specific replies to comments from referee 1:

1. The referee considers the plankton model rather simplistic (in contrast to the state-of-the-art calibration methods).

Reply: It is clear from our results that even this simple model is overparametrised. Essentially, all model decisions (process equations, forcings, parameter fixation) prior to the final analyses put a conditionality on the latter. This is now better communicated. Model complexity is discussed in light of data availability.

2. The referee focuses on two conclusions, which she/he finds rather trivial (a.) or unsupported by the main text (b.).

a.) Referee: “The conclusion that additional observations can help constraining more parameters is really commonplace...”

Reply: True, but our study not only provides an objective assessment of this statement, it also neatly demonstrates how these additional data provide better constraints.

In addition, suggestions for improvement are given. Another conclusion is not “more complexity is better”, but rather “If we want to make our models more realistic (or rather more detailed), data acquisition has to follow”. This was already put forward by Anderson and Gentleman (2012). We will make this observation more explicit in the MS.

b.) Referee: “... the conclusions about using modelling to assess experimental uncertainties do not appear substantiated by the main text of the MS.”

Reply: Our analysis methods quantify the amount of uncertainty in the model-derived fluxes that originates from imperfect data. In contrast, experimentalists consider the data and (implicit) assumptions to be perfect, and, based on this will derive perfect flux estimates. For instance, typically experimentally-derived fluxes only consider the compartments directly involved, disregarding the (indirect) impact on other compartments. A mass-balanced mathematical model does include these indirect effects. We have clarified this in the MS.

3. Focus of the paper is problematic:

a.) overparameterisation and model calibration

Reply: cf. “1. our message” (above)

b.) Referee: “The authors stress the kind of additional data they use, which is 13C data, but then do not make much of this.”

Reply: The biogeochemical conclusions of the model are reserved for the companion paper by De Kluijver et al. (cf. “2. Independence of the companion papers”, above).

4. Referee: “The selection of candidate parameters (p. 9462, l. 10): whether a model is sensitive to a particular parameter often depends on values of other parameters, but apparently this was not considered when selecting the candidate parameters.”

*Reply: Our sensitivity analysis and calibrations *are* an iterative procedure, converging to one set of parameters. This was mentioned on several places in the MS, (p*

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9462, starting from line 10; original version). In line 15 on the same page parameter correlations and dependence are mentioned explicitly. On page 9464, (line 6-8 and line 25-26) makes explicit mention of the choice to fix a subset of parameters that strongly correlated with other parameters. The fact that our ultimate sensitivity results are local in parameter space is explicitly mentioned in line 28 on page 9464 – line 2 page 9465. In addition, the conditional nature of our parameter estimates (and by extension the model sensitivity) on the value of fixed parameters is made explicit from line 9 (page 9466) onward. The conditional nature of our analyses on model choice and parameter selection/estimation is now more explicitly mentioned.

5. Referee: “The whole first paragraph of the conclusions does not appear substantiated by the MS. While this may all be true or not, the problem is that none of this material is covered in the preceding main text. For example, which assumptions involved in sampling, measurement and experimental design (p. 9470, l. 10) were made or explicitly in the model? What uncertainties in the experiment (l. 13) are the authors referring to?”

Reply: This paragraphs was completely reworked and is no longer part of a conclusion.

6. Referee: “How could the model analysis aid quality control (l. 15)?”

Reply: Modelling the experimental variability promotes reflecting over the experiment in a formal, more rigorous way. Provided that the conceptual model underlying the mathematical model is adequate to represent the experiment, the model calibration results in confidence intervals for the estimated flows. As a result, experimental uncertainty (e.g. zooplankton migration into the sediment traps biasing export estimates based on simple POM measurements) is analysed in a more integrated way, using mechanistic information, rather than only variability in replicates.

7. Referee: “... the statement that uncertainty analyses can help to define the condition under which such experimental findings and parameter values can be transferred to Earth System Models is problematic. Global models are not even mentioned once in

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the main text. Also, I do not believe this is possible unless several local studies from geographically distant places were combined.”

Reply: We agree with the reviewer. Earth System Models are no longer mentioned.

8. Referee: “Over-parametrisation is not the only cause for insufficiently constrained parameters. A mismatch between a process and the corresponding equation can also make parameter estimation difficult, e.g., by increasing multicollinearity. For example, as Aksnes and Egge (1991) have pointed out, maximum nutrient uptake rate and half-saturation constant are tightly correlated, whereas the affinity (ratio of maximum rate and half-saturation constant) is independent of maximum uptake rate. Thus, the choice of phytoplankton growth function will directly affect the multicollinearity index and hence the ability to constrain the model parameters.”

Reply: We agree with the reviewer on the conditional nature of our analyses and choices in model structure, process equations and fixed parameters, which are all underlying assumptions of the analyses. This is made more explicit in the revision. However, by fixing the half-saturation constants, we needed to estimate exactly one parameter per flux. As a result, correlations between parameters in our calibrations are essentially correlations between modelled transformation rates. This means that unless you have some information on the transformation, rather than only concentration data, you have no idea about the importance of alternative flows.

Moreover, our MS emphasises the difference between models with and without isotopes. The two presented model calibrations differ only in the availability of stable isotope data and not in specific model formulations and parameter fixation. Therefore, we do not believe that alternative model formulations and parameters would influence our overall conclusions.

B. Specific replies to comments from referee 2:

1. “The authors claim that it is new that isotope data improve the predictive capabilities of a marine biogeochemical model.”

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Reply: This is certainly NOT what we wanted to convey. The introduction actually makes mention of the fact that using isotope data in concert with modelling is NOT new, and that Van Oevelen et al. (2006) already showed the added value of isotope data for constraining carbon flows in food web models. However, although it may not be new, it is certainly not common practice to measure tracer dynamics in mesocosm experiments, where it surely has benefits. Clearly this is interesting feedback to experimentalists. Here, the combination of modelling with isotopes serves an illustrative purpose, and is not intended as a novelty.

2. “There is a disconnect between title, introduction, results and conclusions.”

Reply: We acknowledge this problem and have made amends to resolve it (cf. “1. our message”, above).

3. “Are there any suggestions the authors have to improve mesocosm experiments?”

Reply: The revision has two new sections “More is better” and “Feedback to the experimentalist” which summarize the messages to modellers and experimentalists and mainly to experimentalists, respectively.

4. “Page 9456-9457: Examples why isotopes improve model ! why is this study still needed? What is new here?”

Reply: This study illustrates how models can be used to think about the results of large-scale experiments, in addition to just parameter estimation. To extent of the author’s knowledge, it is one of the few studies that communicates so elaborately on the applied calibration procedure, and exploits the information from this calibration procedure for the purpose of rigorously quantifying uncertainty in the experiment and suggesting future improvements (i.e. meta-analysis of the experiment).

5. p. 9458, line 10-13. The authors use only the ambient CO_2 , no nutrient addition (“control state”). I would be interesting to see whether similar parameters would be estimated for higher CO_2 etc.

Reply: This is reported and discussed by the companion MS (cf. 2. Independence of the companion manuscripts”, above). Two manuscripts are clearly needed to communicate all our findings...

6. “2.2 Model description: Is this the first time the model is described? What is its history? What is it based on? Give references to put the model assumptions into perspective with other models or observations. A sketch of the model state variables and fluxes would help much to illustrate the model.”

Reply: This model was designed specifically to obtain information on organic matter transfer within the food web of this experiment. The types of equations are fairly standard and used since decades. We thank the reviewer for the suggestion on the illustration and have included this in the revised MS (Fig. 1 in this reply).

7. Is a model with a fixed C:N ratio adequate to study fluxes in mesocosms with future CO_2 levels, which have been previously used to argue for carbon overconsumption. One would think that this misses important information and needs at least explanation if not comparison with the second model in the appendix, Recom with variable stoichiometry.

Reply: A N-quota model such as CN_Recom needs even more data to constrain parameters. Our analysis illustrates that even Monod + fixed Redfield ratios is over-parameterised relative to the given data set. We consider a comparison to the CN_Recom model from the appendix and a full treatment of design choices for this model within a literature context beyond the scope of this paper. However, we have elaborated on the choice of an N-quota model in the context of additional ^{15}N measurements in the revised discussion. In addition, we now illustrate the uncertainty in model output due to uncertainty in the C:N value. Although this does not fully address the fixed stoichiometry, it provides some insight in the effect of deviations from the Redfield value of 106/16 (Fig. 3 in this reply).

8. “Line 24: What type of measurement do you refer to when you state that the two

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phytoplankton groups were distinguished based on experimental observations?”

Reply: This was based on polar lipid-derived fatty-acid (PLFA) measurements, which were converted to biomasses. This conversion is now also treated in the discussion.

9. “p. 9459, line 1: “the data showed no strong changes...” over which time period considered and in which mesocosm (only present day CO₂ or also other?)?”

Reply: In all enclosures and over the course of the experiment, and therefore a fortiori in our subset of data (present CO₂ and first phase).

10. “Line 13: “the nature of the increase in phytoplankton isotope signature combined with the increase in phytoplankton carbon indicated that mortality had to be negligible in the first few days“. So phytoplankton ¹³C and phytoplankton C increased by the same rate? Specify.”

Reply: This was rephrased.

11. “Line 19: DIC is not conserved, because it is implemented as a forcing – how does it evolve over time?”

Reply: Both the DIC concentration and isotope signature are now included in the original figure 2.

12. Line 8-9 Why did you decide to assign the two phytoplankton groups the same half saturation constant?

Reply: This is a choice of model design (see also item 7 of this section). Using different half-saturation constants would have introduced extra parameters that we could not optimize because the model was already overparameterised with respect to carbon flows connected to the phytoplankton compartments. Choosing different half-saturation constants would have influences the estimate of the maximal growth rates, but not our overall conclusions.

13. Line 18: At what depth are the sediment traps? What do you mean by “because

the zooplankton actively migrated...“? How does that relate to the preceding sentence? If zooplankton actively migrates into the traps, for me that would then be C_{zoo} and not C_{det}.

Reply: For a more elaborate description of the experiment we refer to the companion paper and references therein. This zooplankton migration was observed but the biomass of the migrated fraction was effectively sampled (not measured separately) with the sediment traps. Since it is difficult to separate this biomass from detritus, it has to be modelled as a loss to the sedimented detritus pool.

14. “p. 9461, line 3-7: Regarding the supplement, there is little description of what of this EPOCA folder is used for this MS. A readme file would be of great help.”

Reply: To avoid confusion, we will reduce this supplementary material to the relevant Fortran code only (with proper documentation).

15. “p. 9463, line 12-15: It is not clear to me, whether the model equations are different between your “first phase” and “second phase”. Do you have the same number of equations and parameters whether or not isotopes are included (I assume so, at least that was mentioned in the introduction as the advantage of using isotopes, but should be made clear)?”

Reply: Everything remained the same, except the calibration data. We also started the second calibration (non-isotope data only) with the resulting parameter estimates from the first calibration (full data-set; the expected minimum in model cost space). This ensures that the differences in over-parametrisation are only due to data availability. This is explicitly mentioned in the revision.

16. ‘Line 21-22: “a limited number”, please specify how many model runs per parameter and the ranges for the parameters including references for the “plausible range”.’

Reply: We used 100 parameter values equally spaced on an interval between a plausible minimum and maximum to get a decent resolution (visually determined). Sub-

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sequently, we took the value with minimal cost. The parameter ranges were partially based on common sense (e.g. fraction of primary production lost to DOC pool; exudation was considered to be somewhere between 0 and 1). Other ranges were chosen based on literature values (e.g. half-saturation constants provided by Franks (2009).

17. p. 9464, line 6-8: why are model sensitivities and multicollinearity indices not given in a table for the different parameters? All the paper is on the calibration procedure, so this is of interest here.

Reply: Multicollinearity indices are calculated for all parameter combinations (does not fit in a table). During the initial development of the MS we decided that a figure with the multicollinearity index as function of the number of parameters was not informative enough to show in this context, since it only serves to guide the elimination of parameters throughout the calibration process. A bar plot with the sensitivities of individual parameters after the full calibration is now provided (Fig. 2 in this reply). For an introduction to the FME package with these functionalities, we refer to the paper by Soetaert and Petzoldt (2010).

18. p. 9464 line 9-24: These automatic calibration methods are probably not known to most readers of BG, so they should be explained in some more detail here.

Reply: In the revision, we have provided references to where they are described in more detail. Adding more technical information on the routines will only distract the reader from the main messages, given the vast number of parameters in the analysis methods.

19. “p. 9465 line 22-23: Which criteria were used to choose the 7 parameters?”

Reply: 1. one parameter per carbon flow (sensitivity for choice between max growth and half-saturation)

2. parameters with highest sensitivity

3. parameter combinations with low multicollinearity index.

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4. strong parameter correlations in calibration results

These criteria were used throughout the iterative process of sensitivity analyses and model calibrations. They are mentioned in the materials and methods section. We feel that further detailing decisions and results in consecutive steps of this iterative process is not desirable, given the amount of information that is already provided in this respect. Usually, modelling papers tend to give even less information on decisions made during the calibration.

20. “Line 24-25: “even this simple model became quickly overparameterised”. What criterion is that based on?”

Reply: This was based on the very strong correlations between some parameters in the MCMC-based calibration. As noted by referee 1, parameter correlations could be the result of model-data mismatch as well, but given that the model followed the data well, we conclude that this was due to over-parametrisation. This is included in the revision.

21. p. 9466, line 5-6: “Only a relative weak correlation...:” The correlation is 0.49, right? That is probably acceptable, but I would reformulate the sentence to say that this is the highest correlation between all parameter pairs considered and possibly explain why you think it’s acceptable or what the trade-off would be if you would not accept it.

Reply: We thank the referee for pointing this out. This is now worked out in the revision.

22. From your analysis, can you give recommendations, which parameters are most important to constrain better from measurements, which ones can confidentially be a priori fixed because they are relatively well known etc.?

Reply: This will be included in the revision.

23. Line 21-22: It would help the reader to mention again which isotopes were measured in which compartments.

Reply: This was added.

24. p. 9468, line 3-5: If both calibration methods provide good fits, then why does it matter for your purpose whether or not isotope data are included?

Reply: Because the initial purpose of the model was to determine carbon flows, rather than to mimic data. Overparametrisation enhances good model fit, because enough degrees of freedom remain to “bend” the model according to the data (i.e. an unreasonable effectiveness of mathematics; Anderson, 2010). As stated in the introduction, the most important uncertainty in the model output is situated in the part for which no data is available.

Good model fits should not be the end of the analysis (see for instance Franks, 2009). Another question could be: “Given the data and the over-parametrisation of the model, why make the model more complex, while we cannot know more from the data?” Clearly, such questions have to be put in the context of the goals of the study. We believe this is an important additional message to both modellers and experimentalists and is included in the revision.

25. “Line 13-15: Why is $\delta^{13}\text{C}_{\text{zoo}}$ not used for the calibration? This is in contrast to Table 1 and p. 9461, section 2.3, which imply that all d13C and biomasses/concentration data were used for calibration.”

Reply: $\delta^{13}\text{C}_{\text{zoo}}$ was used in the calibration with the full data set, not with the reduced data set. This was rephrased, because it was unclear.

26. Line 22-23: What is the difference in the carbon export rate based on your analysis? How much does it “improve” by adding isotopes to the calibration data set? How big is the uncertainty, how does this compare to literature and previous studies?

Reply: This difference is summarized in figures 5h (calibration with full dataset) and 5p (calibration without isotopes). 5p shows an overestimate of carbon export (detritus sinking) relative to 5h and a wider variability in the estimates (mean \pm sd).

27. p. 9468, line 28: it is not clear how the sensitivities are calculated here.

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Reply: As explained in the materials and methods (time-dependent sensitivity). This is now repeated for clarity.

C. Specific replies to comments from referee 3:

1. several issues were introduced in different sections and then not adequately followed up...

Examples:

I. unconstrained fluxes through the zooplankton and detritus compartment: On p. 9468 we are referred to Fig. 5m,p and Table 4, yet I see nothing about zooplankton in either place.

Reply: Fig. 5m,p show very wide estimation intervals (mean+-sd and range) for the model output of the $\delta^{13}\text{C}$ values of zooplankton and the detritus sinking, relative to their counterparts based on calibration with the full data set (isotope + non-isotope data). This means they are virtually unconstrained without isotope information for calibration. We have explained this better in the revised version.

II. On p. 9458 (l. 22) the authors state that "Fixed C:N ratios (Redfield) are implemented" without further comment. It is well-known that under many conditions, C:N ratios vary over time. This is a usual assumption, but one would think that a mesocosm experiment might be a place where changing C:N could be explored, or at the very least previous studies might be cited to justify this assumption for mesocosm studies.

Reply: Please see item 7 in section B (referee 2).

III. ... under what conditions is the modelled system most sensitive to certain parameters and their values. However, the only result along this line is Figure 6.

Reply: We thank the reviewer for pointing this out. This is added to the revised version.

2. ... Conclusions are a general discussion of the philosophy of ecosystem modelling with essentially no reference to any specific results of this MS, suggesting again that it is basically a methodology description to support the de Kluiver MS. ... If the two

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manuscripts are to remain separate, then I would recommend that this MS remain only as a Discussions contribution.

Reply: cf. “1. Clarifying message” and “2. Independence of the companion manuscripts”, above

3. p. 9455, l. 12 – ‘the parameter values are modified until the model output matches the data’. This is not an accurate statement, since the process minimizes a ‘cost function’ which is a normalized measure of deviation from the data. In some cases, the parameters cannot be adjusted to get a ‘close’ fit to the data.

Reply: This was changed to: “... the parameter values are modified so as to minimize the model-data mismatch”.

4. p. 9456, l. 3 – change ‘amount’ to ‘number’

Reply: This was changed.

5. p. 9456, l. 10-15 – it is not clearly stated here what assumption about fractionation is being made.

Reply: If fractionation is negligible, fractionation factors are assumed to be zero. If they are known from literature to vary little, one can assign an average value based on this literature. Fixing them (to value zero in our study) and excluding them from calibration implies an assumption in your model. This is now clearly, stated in the revision.

6. p. 9456, l. 17 – change to ‘Several deliberate tracer studies have shown :::’

Reply: This was changed.

7. p. 9457, l.3 – ‘indistinguishable’

Reply: corrected

8. p. 9457, l.18 – this sentence restates what was said at the beginning of the previous paragraph (l.4)

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Reply: This was changed

9. p.9457, l.22 – change to ‘... were maintained at different pCO₂ levels, representing potential future ...’

Reply: This was changed.

10. p.9458, l.2 – please explain what you mean by ‘at AN enrichment level of 100’ ppt

Reply: The DIC source had an isotope signature of 100 ppt above natural abundance levels.

11. p.9458, l.11 – change ‘obtainted’ to ‘obtained’

Reply: Changed.

12. p.9459, l. l. 17-18 – ‘This implies that the phytoplankton mortality rate was strongly time dependent’, but this issue is not really mentioned again. In Figs. 3 and 4, mortality is highly correlated with maximum growth rate for both groups (Fig. 4) and for group I only (Fig. 3). What does that mean – that maximum growth rate is also highly variable? The only other mention that I could find (p.9466, l.5) was that there was that a relatively weak correlation remained for group I between maximum growth rate and mortality.

Reply: The mortality rate was indeed strongly time-dependent in the experiment, most likely due to a viral infection around day 6. This was forced upon the model by switching mortality off in the first part of this experimental phase. Since this time-dependence is forced upon the model, it does not show up in the presented analyses. Correlations between the parameters in figures 3 and 4 are correlations between different parameter estimates (suggestions of the MCMC calibration that give reasonable fits according to criteria dictated by the MCMC calibration procedure). There is no time-dependence involved in these estimated parameter distributions.

13. p.9460, l.7-9 – what is the justification for giving the different phyto groups different maximum growth rates but the same half saturation coefficient for DIN uptake? Usually

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the small phyto would have a smaller half saturation coefficient, so they out-compete for nutrients at low nutrient concentrations.

Reply: cf. item 13 in section B (reply to referee 2).

14. p.9460, l.10 – change 'split up over an input' to 'partitioned into an input :::'

Reply: This was changed.

15. p.9460, l. 16 – change 'subdivided over' to 'partitioned into'

Reply: This was changed.

16. p.9462, l. 11 – change 'we can :::data' to 'is it possible to change the parameter to improve the model fit to the data'

Reply: This was changed.

17. p.9464, l. 1-2 – 'such that each parameter represented exactly one transformation in the model'. What do you mean by this? A mathematical transformation? Or do you mean a change in state or flux of an element between compartments, say DIN to cellular N in phytoplankton after photosynthesis? I am puzzled.

Reply: We meant flow. This was clarified.

18. p.9466, l.1 – I am not clear what you mean by 'parameter randomisations'

Reply: In an MCMC calibrations random parameter sets are generated based on prior knowledge. These are accepted or rejected depending on the deviation of the model relative to the data. The set of all accepted randomised parameter sets, resulting from the MCMC calibration represents a joint probability distribution of these parameters. This distribution is shown in scatter plots in figures 3 and 4.

19. p.9466, l. 5 – change 'week' to 'weak'

Reply: This was changed.

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20. p.9467, l.1 – change 'out of ' to 'from'

Reply: This was changed.

21. p.9468, bottom – delete 'coloured'; 'solid' is sufficient and the blue is so dark as to be nearly black in my document.

Reply: This was changed.

22. p.9470, l.14 – change to 'data are', the singular form is 'datum'

Reply: This was changed.

References:

Anderson, TR: Progress in marine ecosystem modelling and the “unreasonable effectiveness of mathematics”, J. Mar. Syst. 81, 4 – 11, 2010.

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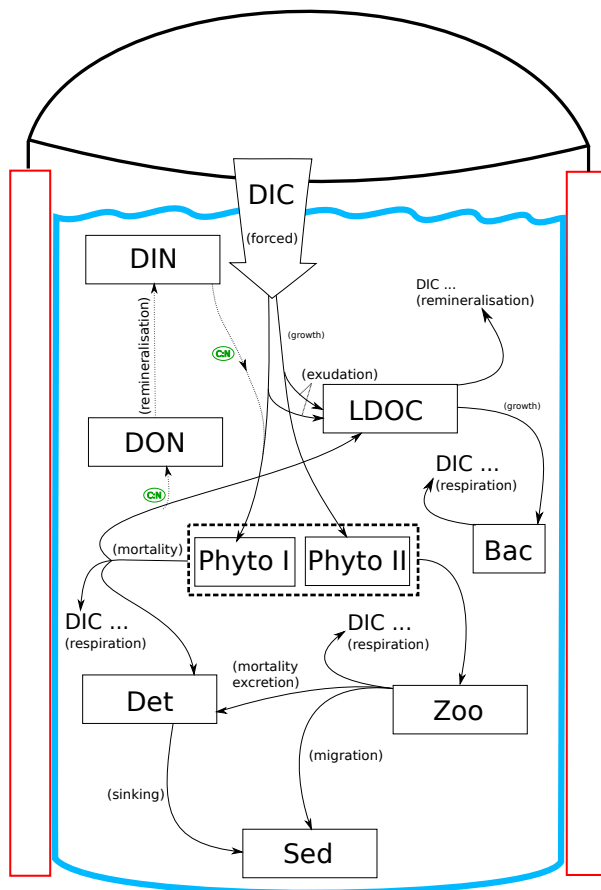


Fig. 1. Conceptual model. Apart from the bacterial (Bac) and zooplankton (Zoo) compartment, all compartments are modeled by two state variables: $\delta^{13}\text{C}$, and $\delta^{12}\text{C}$.

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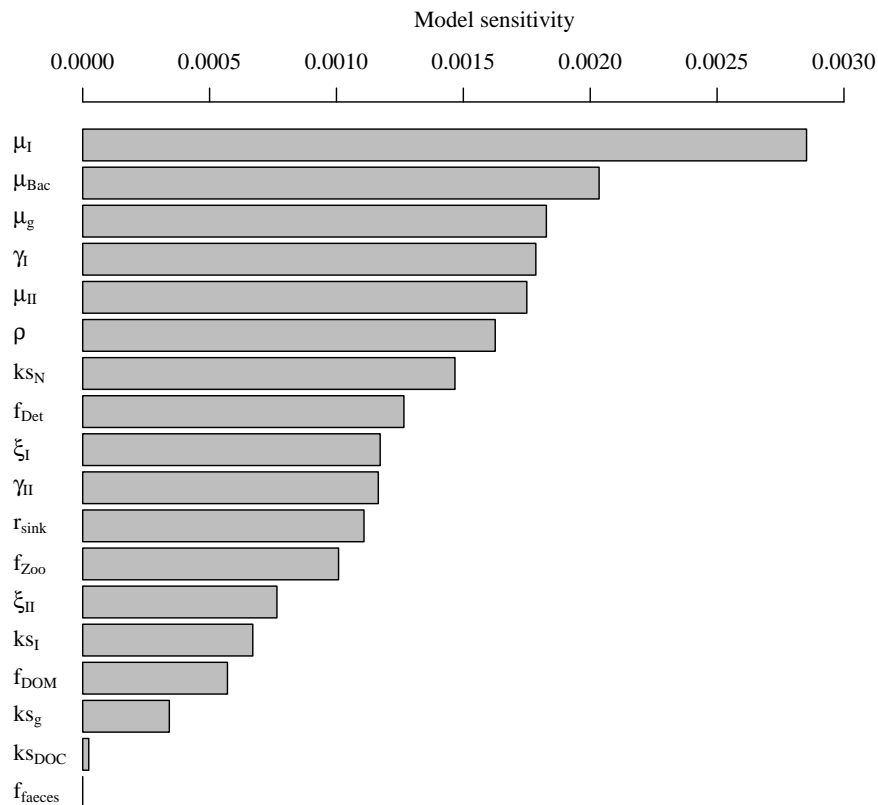
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Fig. 2. Model sensitivity to parameters involved in the calculation of inter-compartment flows (L2-norm of the sensitivity matrix).

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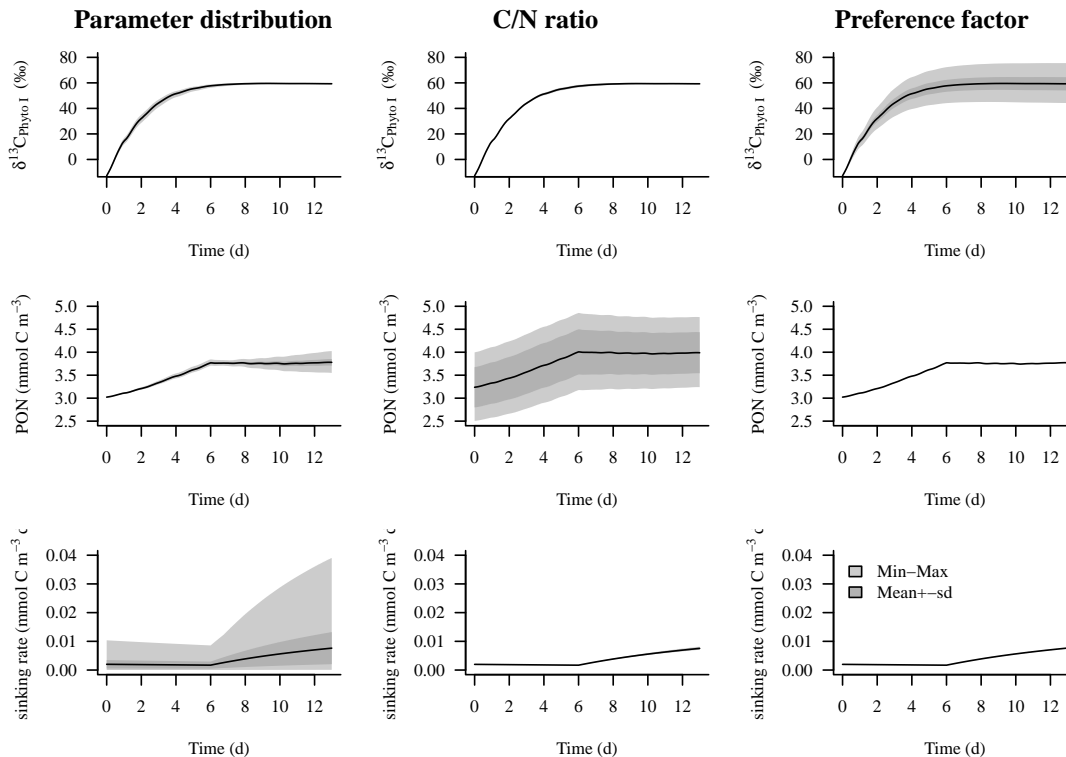


Fig. 3. Model output after calibration (left), and with additional random distributions for the fixed C:N ratio (middle) and preference factor (fractionation; right).

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