Dear Editor,

Please consider below our responses to second referee's comments to our manuscript, entitled "Dissolved organic matter release by phytoplankton in the context of the Dynamic Energy Budget theory", by E. Livanou, A. Lagaria, S. Psarra and K. Lika. We thank referee 2 for the time invested and for the thorough review of our manuscript. In the following, we present our detailed responses to his comments (referee's comments are presented in bold, our replies in blue and relevant changes in the text are highlighted in red to facilitate reading). All citations in our responses are listed at the end of the document. Citations in the original and modified text are included in the references list of the original ms.

**Referee #2**

**This work presents a DEB-based model purporting to describe the production of DOM by phytoplankton under N or P stress. The general topic is important, and does align with the subject areas of the journal.**

**The model is shown to broadly align with a single data set for N-limitation, and is then operated under different conditions with an aim to consider differential consequences of N vs P limitation. I have the following general observations upon this work which I am afraid makes me question the usefulness of the approach and application.**

**Firstly, the structure of the model, as shown in Fig.1, is contrary to that which aligns with the physiology of real phytoplankton. Indeed the structure, with its partitioning of inorganic N and P and within different organic structures appears most strange. I find this very worrying. The model is complex, and claims to be mechanistic (as are DEB models), but it just does not tally.**

**There are also other facets of the model description that are of concern to me: the stoichiometry of cellular components (which is not shown to collectively reproducing observed changes in cellular C:N:P); the explanation of internal ammonium (which in reality is essentially zero) and of internal nitrate (which is also usually very low, and indeed contrary to some reports can never attain a significant % of cell-N because of nitrate-solubility issues) and the interactions between ammonium and nitrate usage (which perpetuate various classic misleading literature articles); the whole rational for DIN and DIP release (perhaps a hangover from the heterotrophic origins of the DEB concept?) appears to be unsupported unless the simulations are running in a light-dark cycle (are they?); comments about cell size variation gloss over the fact that P-limited cells are very much larger than nutrient-replete cells, and N-limited cells are much smaller; and so on.**

**Response**

Regarding the model structure, presented in Fig. 1 in the ms, it follows directly from DEB theory's assumptions that biomass of an organism is partitioned into reserves and structure (Kooijman, 2010). The need to consider multiple reserves follows from DEB theory's strong homeostasis assumption (i.e. the chemical composition of a reserve or a structure does not change during the organism's life cycle), that implies that multiple reserves should be considered, one for each assimilation pathway, when they are independent as is the case for phytoplankton. The partitioning of phytoplankton biomass into different compartments is not new (e.g., Ross and Geider, 2009; Talmy et al., 2014; Ghyoot et al., 2017). Generally, all

elements (e.g. C, N, P) included in the models are partitioned within different compartments (e.g., reserves, structural and functional components of the cells).

Regarding the inorganic reserves the model aligns with existing information about the physiology of phytoplankton cells. As it is also discussed in detail in our response to referee's 1 comment about ammonium and nitrate reserve, a substantial body of literature indicates that phytoplankton cells have the ability to store nitrate and ammonium to measurable quantities (Dortch et al., 1984; Lomas and Glibert, 2000; Lourenço et al., 1998; Raimbault and Mingazzini, 1987). Based on these studies, we include in our model the reserves for nitrate and ammonium in order to simulate the well known behaviour of excess uptake and internal accumulation of inorganic nitrogen when uptake rate exceeds growth rates. This approach is not new as internal pools of inorganic nitrogen (i.e. reserves) are also explicitly modelled in other phytoplankton models (Flynn et al., 1997; Talmy et al., 2014; Ghyoot et al., 2017).

It is acknowledged in the literature that there are significant differences among species in their ability to accumulate large intracellular nitrate or ammonium pools. Our aim was to present a general model for phytoplankton. Differences among species regarding the extent to which ammonium and/or nitrate are accumulating intracellularly can be accommodated by the model by the choice of parameter values. For example, if for a certain species intracellular ammonium pools do not accumulate a very large turnover rate for ammonia reserve would give an extremely low reserve density for ammonia and thus the ammonia reserve could be omitted (Kooijman, 2010).

Regarding inorganic phosphorus reserves, it is well documented that phytoplankton cells store intracellularly excess inorganic phosphorus, as orthophosphate or polyphosphate, not needed immediately to support cell metabolism (Geider and La Roche, 2002; Lin et al., 2016). In addition, inorganic phosphorus reserves have been also described in other modelling studies (John and Flynn, 2000; Ghyoot et al., 2017).

Finally, the concept of the generalized reserves, E, which is assumed to be a mixture of chemical compounds that does not change in composition and thus have a fixed stoichiometry, is used to represent the more complex compounds that can be used as reserves for the phytoplankton, such as lipids, proteins, RNA etc.

In order to clarify the concept of generalised reserves we will modify the text in Sect. 2.1, p.3, lines 31-32 *"[…] to form the generalized reserves (E) which have a fixed stoichiometry."* as follows:

*"[…] to form the generalized reserves (E), which consist of a mixture of chemical compounds (RNA, proteins, lipids etc) and they have a fixed stoichiometry."*

Regarding the interactions among nitrate and ammonium, there are many reports in the literature that suggest that ammonium is taken up preferentially and that assimilation of nitrate is inhibited by a product of ammonium assimilation (e.g. Flynn et al. 1997; Glibert et al. 2015 and references therein). Based on this information, we included the information for ammonium and nitrate interaction in our model.

Regarding the release of DIN and DIP, we would like first to clarify that it stems from the multiple reserves DEB model for phytoplankton as presented in Kooijman (2010), chapter 5. The excretion of inorganic nitrogen and phosphorus from nutrient replete cells has been observed in experimental studies and we provide all the rationale and the literature supporting our choice in the Supplementary Material Sect.S2, p.2, lines 6-35:*"Apart from excretion of DOM […] back to the EP–reserve".*

Apart from that, in our model inorganic nitrogen and phosphorus can be excreted by phytoplankton as the result of maintenance processes and turnover of cellular components. This again stems from the standard DEB model. These nutrients are available for re-assimilation. We recognize that this may be unusual for phytoplankton, thus an alternative would be to redirect regenerated ammonia and phosphorus from maintenance processes back to the corresponding reserves and we intend to add this alternative in the revised manuscript. To answer the referee's question, simulations are not run over light-dark cycle but under constant light intensity.

**Referee #2**

**I therefore have a serious problem with the conceptual basis of the model. The authors have also not explained why their approach has any benefits over any other approach.**

**The model is shown to fit against only one data set, for a diatom, growing under Nlimitation. That data set comes from one of those presented in Flynn et al. 2008, who also conducted a (solely N-based) exploration of the description of DOM release. Very strangely there is no comparison with the utility of this model with that of Flynn et al for N-based scenarios; why have the authors not done this?**

**Response**

Our aim was to present a DEB based model for phytoplankton growth and exudation of DOM thus we did not focus on comparing our modelling approach with that of Flynn et al. (2008). Moreover, our approach captures the two physiological mechanisms of DOM production, without making further assumptions but rather via the existence of two alternative pathways that emerge from the theory. Based on the comments of referee 2 we will include a comparison between the presented model and that of Flynn et al. (2008), in the Discussion under Sect. 4.3, p. 15, line 23 in the revised manuscript. Please see the revised section 4.3, presented as a whole, in our response to the last comment of referee 2 (end of this document).

**Referee #2**

**Further, while this article considers P-limitation (Flynn et al did not) it does so using a framework that is unproven, and hence one that must remain speculative. Indeed, no evidence is presented for how the model handles P-limitation, or indeed how cellular C:N:P varies under N and P limitation. If the DEB model had at least been shown to handle general C-N-P interactions (there are various data sets available to which to conduct such a comparison) then this would not be of such concern.**

**Response**

Elemental composition of biomass (being the sum of reserves and structure) is monitored in terms of Carbon (C), Nitrogen (N) and Phosphorus (P). In the context of DEB theory, biomass

is the sum of reserves and structure. As it is stated in Sect.2.3 of the ms (p.9, lines 28-30), the molecular elemental ratios of biomass are calculated as follows: $n_N = n_{N,E}M_E + M_{E_{NH}} + M_{E_{NO}} + n_{N,V}M_V$ is the total N-mol content, $n_P = n_{P,E}M_E + M_{E_P} + n_{P,V}M_V$ is the total P-mol content and $n_C = n_{C,E}M_E + M_{E_{CH}} + n_{C,V}M_V$ is the total C-mol content of the cells. Thus, $C:N = n_C/n_N$, $C:P = n_C/n_P$, and $N:P = n_N/n_P$. As referee 2 points out, we did not conduct a comparison with data sets for C-N-P limited growth. For our study we were interested in the DOM production by phytoplankton and in order to constrain the model parameters we would need data derived from an axenic phytoplankton culture demonstrating mass balance for all elements considered in the model. However, to our knowledge, this type of data that simultaneously describe carbon, nitrogen and phosphorus dynamics in both the organic and inorganic particulate and dissolved pools are not available for any species. Thus, to cover this gap, in addition to the data set of Flynn et al. (2008), as stated in the methods section (lines 26-27, p.9) the molecular elemental ratios of biomass (i.e. C:P, C:N, N:P) were also used in order to constrain the parameter values so that the resulting ratios (Fig. 8a-c in the ms) would fall close to observable ranges reported in Perry (1976), Goldman et al. (1979) and Flynn et al. (2008). We intend to explicitly state that in the revised manuscript by modifying lines 26-27, p.9 as follows:

*"Furthermore, the molecular elemental ratios of biomass (i.e. C:P, C:N, N:P) were also used in order to constrain the parameter values so that the resulting ratios would fall close to observable ranges reported in Perry (1976), Goldman et al. (1979) and Flynn et al. (2008)."*

In addition, the multiple reserves DEB model for phytoplankton have been used yet again to describe the internal nutrient dynamics of *Prochlorococcus* growing in cultures under balanced, N and P limited growth (Grossowicz et al., 2017). These authors also demonstrated how the DEB model for phytoplankton can handle general C-N-P interactions. Therefore, we do not think that the framework of DEB for phytoplankton models is unproven. In order to dissipate the referee's doubts on the ability of DEB multiple reserves model to handle C-N-P interactions in phytoplankton, we will explicitly cite the relevant papers in the Methods section (Sect. 2.1, p.3, line 17) by modifying the text as follows:

*"The phytoplankton model is based on the DEB multiple reserves model (Kooijman, 2010), that has already been successfully applied to model light, N and P limited growth of phytoplankton (Lorena et al., 2010; Grossowicz et al., 2017)."*

**Referee #2**

**The model is sold for potential deployment in ecosystem simulators but it appears incomplete for such usage, lacking acclimative Chl:C (which is important in DOM modelling as a failure to rapidly modulate C-fixation promotes DOM release) and indeed it has not been shown how the model reacts to light-limitation (which is of importance during bloom development and thence to DOM release).**

**Response**

We suggested that the model could potentially be used in ecosystem simulations in order to resolve the stoichiometry and degradability of DOM produced by phytoplankton, as the model structure allows for a quantification of the production of the distinct size fractions of phytoplankton exudates which can be used for the characterization of their availability for bacteria. Indeed, as referee 2 points out, in our model we did not account for acclimative Chl:C; this could be done for example through light dependence of the parameter $\rho_L$ (eq.6) (Papadakis et al., 2012). Although we agree with referee 2 that this is important for a

potential deployment of our model in ecosystem models, this will require further analysis and data and it is beyond the scope of this ms.

**Referee #2**

**In section 4.2 there is a commentary about P vs N –limitation; I suggest this requires some common basis for reference (perhaps u/Umax?). As it stands the statements appear ambiguous and potentially incorrect.**

**Response**

We based our discussion about P- vs N-limitation on specific growth rates, i.e., growth rate per structural biomass, which is a relative measure. An analytic formula for the ratio of spec. growth rate and the max spec. growth rate (when none of nutrients are limiting) cannot be obtained. Moreover, Fig. 4a in the ms shows that during the first phase of growth, which corresponds to the nutrient-replete phase, indicated also by the minimum C:N and C:P ratios of biomass (Fig. 8a,b in the ms), the specific growth rates are identical. Thus, dividing the specific growth rates by the max. value, observed in the nutrient-replete phase, would result in curves which have the same shape. Therefore, we believe that this measure is not ambiguous and our conclusions are not unjustified.

**Referee #2**

**In section 4.3 is a discussion about forms of DOM. I find the description of DOC, DON, DOP used in this article somewhat confusing; DON and DOP are also components (subsets) of DOC. The discussion lacks a consideration of CNP of DOM forms, and also (again) a comparison with the outputs of the Flynn et al. effort. Just now it is not clear to me what advantages this DEB-based approach may have over any other model. There are also some strange (to me) comments concerning glucose and polysaccharides in this section.**

**Response**

In our model we do not specify the chemical composition of DOM in terms of the various DOM forms (such as amino acids, proteins, nucleic acids etc) but we keep track of the stoichiometry of DOM produced, in terms of C:N:P. DOC consists of carbohydrates, while it can also contain the DOC fraction of organic forms of nitrogen and phosphorus (e.g. proteins, amino acids, P esters etc). The organic forms of nitrogen and phosphorus are referred to as DON and DOP, respectively, which is the standard notation used in many papers and textbooks.

Our approach allows tracking the elemental composition of DOM produced which will be a result of the nutrient availability. Our model shows that, growth under nutrient replete conditions results in DOM production with balanced DOC:DON:DOP ratios as its production is associated mainly with passive leakage. On the other hand, unbalanced growth under nutrient limiting conditions will result in higher rejection fluxes of the non-limiting substrates by the SU and elevated DOC:DON or DOC:DOP ratios (depending on the limiting nutrient).

In order to make model assumptions clearer regarding the relative presence of glucose and heteropolysaccharides of various monemer composition in the excreted DOC, based on both referee's comments, we intend to modify Sect.3.2.3 (p. 13, lines 1-10) *"In order to further investigate […] exuded by the cell due to unbalanced growth (Fogg, 1983; Urbani et al., 2005; Flynn et al., 2008; Borchard and Engel, 2015)"* in the revised ms as follows:

*"Borchard and Engel (2015) showed that in steady-state, P-limited cultures of Emiliania huxleyi glucose was the dominant monomer in both the small size fraction (1–10 kDa) of*

*dissolved polysacchrides and in the particulate fraction (cell content) and less significant in the larger size fractions (>10 kDa), which contained a variety of monomers. They suggested that, due to their size and resemblance to the cellular material, low molecular weight carbohydrates should be released by passive diffusion. On the other hand, high molecular weight carbohydrates, due to their size and distinct composition from the cellular material, should be produced via active exudation (Borchard and Engel, 2015). Furthermore, in cultures of marine diatoms, glucose has been identified as the most abundant monomer during the exponential, nutrient-replete phase of growth in the extracellular carbohydrates. A pronounced decrease of glucose and an increase of heteropolysacharides, containing various monomers, has been observed in the stationary, nutrient-limited phase (Underwood et al., 2004; Urbani et al., 2005). Based on these evidence we define as $DOC_L$ the DOC produced as a result of the fluxes associated with growth ($j_{DOC,G}$ , Fig. 6, dashed line) and death ($j_{DOC,D}$, Fig. 6, dash-dot line) processes and we relate these two fluxes to the mechanism of passive diffusion mechanism. Thus, $DOC_L$ should be small in size and contain mono- and polysacharides, rich in glucose, and also DOC associated with nitrogen or phosphorus containing compounds that can be released from exponentially growing cells or from cell lysis. On the other hand, we define as $DOC_H$ the DOC produced as a result of the $j_{DOC,R}$ flux (Fig. 6, solid line) that corresponds to the rejection flux of unprocessed substrates by the SU. Consequently, this flux is related to the mechanism of active exudation. $DOC_H$ should contain high molecular weight (>10kDa) heteropolysaccharides, poor in glucose, and also DOC associated with nitrogen or phosphorus containing compounds that could be exuded by the cell due to unbalanced growth."*

In addition, in order to make clarify our findings, compare our modelling approach with the Flynn et al. (2008) work and demonstrate the utility of our approach, after comments of both referees, in the revised ms, we intend to replace lines 20-34, p.15 and lines 1-9, p.16 in the Discussion (Sect. 4.3) "In this study, using the DEB model […]consisting of a variety of monomers, have been found to escape bacterial degradation (Obernosterer and Herndl, 1995; Hama and Yanagi, 2001; Puddu et al., 2003)" with:

*"In this study, using the DEB model for phytoplankton (Kooijman, 2010), we were able to discriminate between the two major conceptual mechanisms of DOM release, i.e., passive diffusion and active exudation, in contrast to existing phytoplankton models that involve DOM exudation (Van Den Meersche et al., 2004; Schartau et al., 2007; Flynn et al., 2008; Kreus et al., 2014) but do not discriminate between the mechanisms of DOM release. For example, the most complex model presented in Flynn et al. (2008) employed an empirical description that related the relative rate of leakage of DOC and DON to the N:C status of the cells. On the contrary, in our modeling approach, the theory of SU quantifies the active exudation of the non-limiting compounds. Since the nutrients are taken up independently, one or more catabolic fluxes can limit the synthesis of the generalized reserves E´. In that case, the non limiting "molecules" will occupy the binding sites of the $SU_2$ but they will not be processed further due to the absence of the limiting flux and, thus, they will be rejected by the $SU_2$. Subsequently, a fraction of this rejection flux will be excreted. In that way, the effect of nutrient limitation on exudation rate is accounted for. Furthermore, Flynn et al. (2008) assumed a higher rate of leakage until the external concentration attained a critical value in order to account for the rapid accumulation of DOM during the initial stages of the culture. On the other hand, in our model, based on DEB theory's assumptions for product formation, we describe a second process of DOM excretion which is stoichiometrically coupled to the growth rate and results in high rates of DOM production during the initial nutrient-replete phase of the culture. This can be seen as an overhead for growth as this material is passively leaked outside the cell. Thus, the advantage of our approach lies in its ability to capture the*

*two physiological mechanisms of DOM production. It does so without making further assumptions but rather via the existence of two alternative pathways that emerge from the theory.*

*Based on experimental evidence we assumed that the different processes contributing to DOC release produce two distinct types of DOC (i.e., $DOC_L$, $DOC_H$). $DOC_L$, which is related to growth and death processes and thus to the passive diffusion mechanism, is expected to contain low molecular weight carbohydrates that have a similar composition as the cellular material with high content of glucose (Borchard and Engel, 2015), while $DOC_H$ which is related to the rejection flux of unprocessed substrates by the SU and the active exudation mechanism, has a more distinct composition from the cellular material and is rich in high molecular weight heteropolysaccharides, consisting of a variety of monomers (Biersmith and Benner, 1998; Borchard and Engel, 2015). As such, the model suggests that the relative importance of the two mechanisms and, thus, the relative presence of high and low molecular weight carbohydrates with different molecular composition signatures, is dependent on the nutrient status of the cells. Our approach is different of that of Flynn et al (2008) since they did not distinguish between the two mechanisms of DOM production. Thus, in their model they take into account only leakage, which is related to the nutrient status of the cells and produce low molecular weight DOC such as mono and disaccharides and DOC associated with amino acids. High molecular weight DOC is associated with proteins and nucleic acids and it is produced only via cell lysis, that is enhanced under suboptimal growth conditions, while cell lysis will also result in the leakage of low molecular weight DOM stored intracellularly (Flynn et al., 2008).*

*The molecular composition of DOC released may have implications for its subsequent utilization by bacteria. Many studies have shown that exudates, rich in glucose, are taken up rapidly by bacteria while heteropolysaccharides, consisting of a variety of monomers, have been found to escape bacterial degradation (Obernosterer and Herndl, 1995; Hama and Yanagi, 2001; Puddu et al., 2003). Thus, the novelty of our model is that it allows the quantification of the production fluxes associated with the two classes of DOC ($DOC_L$, $DOC_H$) that will contain carbohydrates with different molecular composition signatures and thus, different degree of degradability by bacteria. Furthermore, our model setup allows for the tracking of the elemental composition of photosynthetically produced DOM, which is also important information for the degradability of DOM.''*

**There are various detailed comments that I could give to help the authors, but just now I think that I need to see:**
**i) a more acceptable conceptual basis (I do not believe that Fig.1 does this),**
**ii) a demonstration that the whole model can describe dynamic C:N:P experimental data series,**
**iii) a more rigorous set of comparisons with Flynn et al (whose data they use, but then for some reason never further discuss in comparative terms even in the context of Nlimited growth) and indeed with the functionality of other models (ERSEM springs to mind).**

We hope that our responses cover referee's points i)-iii) and that they will dissipate his doubts on the usefulness and application of our modelling approach.

## References


Dortch, Q., Clayton, J. R., Thoresen, S. S. and Ahmed, S. I.: Species differences in accumulation of nitrogen pools in phytoplankton, Mar. Biol., 81(3), 237–250, doi:10.1007/BF00393218, 1984.

Flynn, K. J., Fasham, M. J. R. and Hipkin, C. R.: Modelling the interactions between ammonium and nitrate uptake in marine phytoplankton, Philos. Trans. R. Soc. B Biol. Sci., 352(1361), 1625–1645, doi:10.1098/rstb.1997.0145, 1997.

Flynn, K. J., Clark, D. R. and Xue, Y.: Modeling the release of dissolved organic matter by phytoplankton, J. Phycol., 44(5), 1171–1187, doi:10.1111/j.1529-8817.2008.00562.x, 2008.
Geider, R. and La Roche, J.: Redfield revisited: variability of C:N:P in marine microalgae and its biochemical basis Redfield revisited: variability of C:N:P in marine microalgae and its biochemical basis, Eur. J. Phycol., 37(September 2012), 37–41, doi:10.1017/S0967026201003456, 2002.
Ghyoot, C., Flynn, K. J., Mitra, A., Lancelot, C. and Gypens, N.: Modeling Plankton Mixotrophy: A Mechanistic Model Consistent with the Shuter-Type Biochemical Approach, Front. Ecol. Evol., 5(July), 1–16, doi:10.3389/fevo.2017.00078, 2017.
Glibert, P. M., Wilkerson, F. P., Dugdale, R. C., Raven, J. A., Dupont, C. L., Leavitt, P. R., Parker, A. E., Burkholder, J. M. and Kana, T. M.: Pluses and minuses of ammonium and nitrate uptake and assimilation by phytoplankton and implications for productivity and community composition, with emphasis on nitrogen-enriched conditions, Limnol. Oceanogr., 165–197, doi:10.1002/lno.10203, 2015.
Goldman, J. C., Mccarthyt, J. J. and Peavy, D. G.: Growth rate influence on the chemical composition of phytoplankton in oceanic waters, Nature, 279(2), 1, doi:10.1038/279210a0, 1979.
Grossowicz, M., Marques, G. M. and van Voorn, G. A. K.: A dynamic energy budget (DEB) model to describe population dynamics of the marine cyanobacterium Prochlorococcus marinus, Ecol. Modell., 359, 320–332, doi:10.1016/j.ecolmodel.2017.06.011, 2017.
John, E. H. and Flynn, K. J.: Modelling phosphate transport and assimilation in microalgae; how much complexity is warranted?, Ecol. Modell., 125(2–3), 145–157, doi:10.1016/S0304-3800(99)00178-7, 2000.
Kooijman, S. A. L. M.: Dynamic Energy Budget theory for metabolic organisation, 3rd ed., Cambridge University Press., 2010.
Lin, S., Litaker, R. W. and Sunda, W. G.: Phosphorus physiological ecology and molecular mechanisms in marine phytoplankton, J. Phycol., 1, 10–36, doi:10.1017/CBO9781107415324.004, 2016.
Lomas, M. W. and Glibert, P. M.: Comparisons of nitrate uptake, storage, and reduction in marine diatoms and flagellates, J. Phycol., 36, 903–913, 2000.
Lourenço, S. O., Barbarino, E., Lanfer Marquez, U. M. and Aidar, E.: Distribution of intracellular nitrogen in marine microalgae: Basis for calculation of specific nitrogen-to-protein conversion factors, J. Phycol., 34, 798–811, doi:10.1080/0967026032000157156, 1998.
Papadakis, I. A., Kotzabasis, K. and Lika, K.: Modeling the dynamic modulation of light energy in photosynthetic algae, J. Theor. Biol., 300, 254–264, doi:10.1016/j.jtbi.2012.01.040, 2012.
Perry, M. J.: Phosphate utilization by an oceanic diatom in phosphorus-limited chemo-stat culture and in the oligotrophic waters of the central North Pacific, Limnol. Oceanogr., 21(January), 88–107, doi:10.4319/lo.1976.21.1.0088, 1976.
Raimbault, P. and Mingazzini, M.: Diurnal variations of intracellular nitrate storage by marine diatoms: effects of nutritional state, J. Exp. Mar. Bio. Ecol., 112(3), 217–232, doi:10.1016/0022-0981(87)90070-0, 1987.
Ross, O. N. and Geider, R. J.: New cell-based model of photosynthesis and photo-acclimation: accumulation and mobilisation of energy reserves in phytoplankton, Mar. Ecol. Prog. Ser., 383, 53–71, doi:10.3354/meps07961, 2009.
Talmy, D., Blackford, J., Hardman-Mountford, N. J., Polimene, L., Follows, M. J. and Geider, R. J.: Flexible C:N ratio enhances metabolism of large phytoplankton when resource supply is intermittent, Biogeosciences, 11(4), 5179–5214, doi:10.5194/bgd-11-5179-2014, 2014.