(egusphere-2022-91) entitled “Physiological flexibility of phytoplankton impacts modeled biomass and primary production across the North Pacific Ocean” by Sasai et al.

Response to Reviewer #2

General Comments

The manuscript "Physiological flexibility of phytoplankton impacts modeled biomass and primary production across the North Pacific Ocean" by Y. Sasai and colleagues compares modeled phytoplankton biomass and primary production from a flexible plankton community model accounting for photoacclimation and variable C:N:Chl, with an inflexible plankton community model assuming constant C:N:Chl ratios. These models are coupled to a 3-D eddy-resolving ocean circulation model of the North Pacific. The authors compare the performance of these models by using Chl, nutrient, and primary production observations and find that primary production and chlorophyll were better predicted/modeled by incorporating photoacclimation and variable C:N:Chl ratios.

This manuscript provides valuable results that are important for the future implementation of plankton community models. However, as the manuscript stands, I suggest major revisions to outlay a more clear motivation and revise the methods, results, and discussion sections to allow readers to more easily follow this manuscript.

We thank Reviewer #2 for valuable comments on our manuscript. The major revised points are 5 items below. The individual responses (fine characters) to the Reviewer #2’s comments (bold characters) are described after the list of major 5 items.

1. Title changed “Physiological flexible of phytoplankton impacts modeled chlorophyll and primary production across the North Pacific”. Because phytoplankton biomass changed chlorophyll.

2. Introduction
   We added the aim and objective in the last paragraph of Introduction.

3. Methods and Materials
   We revised the two subsections “2.2 Formation of Phytoplankton Growth in the Biological Model” and “2.3 Observed Data” in section 2.

   In subsection 2.2, we changed from simple phytoplankton growth rate (InFlexPFT) description to complex phytoplankton growth rate (FlexPFT) description.

   In subsection 2.3, we revised the description of observed data to compare the model results. The observed year and modeled year are not same, but they are compared to confirm the reproducibility of the model climatological averaged field (e.g., season). We revised the first paragraph of subsection 2.3.

4. Results
   We changed section title from “Results and Discussion” to “Results”.

We changed three subsection titles.

Title of subsection 3.1 is “Comparison of Surface Chl Pattern”.

Title of subsection 3.2 is “Comparison of Vertical Distributions of Chl and PP along Two transect Lines”.

Title of subsection 3.3 is “Vertical Profiles of PP at three stations and PP pattern”.

We added the quantitative description in section 3, everywhere.

5. We added the “Discussion” and revised the “Conclusion”.

Specific comments:

1. There should be a more clearly description of the structural differences between models. Although the description of the models is easy to follow, there is some confusion about what the key differences between models are. For example, throughout the manuscript, the text deviates on whether only the complex model implements photoacclimation or both models do. In Table 1, the differences in potential maximum growth rates can create confusion on whether it is the same model simply having a higher growth rate, or understanding where the main differences between models are coming from.

Thank you for your comment. As your suggestion, we revised the “Methods and Materials” section based on the suggestions above and the minor comments below. In the revised manuscript, we now specify that only the FlexPFT model includes photoacclimation. Please see the attached manuscript file.

Description of difference in maximum growth rate was added in section 2.2.
New Lines 183-186: **“**For example, the potential maximum growth rate, mu_max, is 1.5 (day^-1) for the InFlexPFT, compared to 2.2 (day^-1) for the FlexPFT. Increasing the potential maximum growth rate decreases the surface N concentration in the subpolar gyre, to the point of depleting nutrient during summer, while increasing the surface Chl concentration across the whole gyre.”

1. The results section can be hard to follow in some parts, and quantitative information backing up the results stated will allow readers to better understand the variation between models and models and observations.

Thank you for your comment. Following your suggestion, we revised the “Results” section based on this comment and other minor comments. Please see the attached file.

1. The aims and objectives of the study are lacking throughout the manuscript, especially when stating what observations are being used.

New Lines 80-90: We the text to read, “Most of biogeochemical models have similar structure, with nitrogen as the main currency for a simplified food-web, which generally includes phytoplankton and zooplankton, and a regeneration network with detritus, dissolve organic nitrogen, and various nutrients (i.e.,Fasham et al., 1990). Whereas the more complex biogeochemical models have become more common (e.g., Follows et al., 2007, Totterdell, 2019), simple phytoplankton growth (fixed stoichiometry, without photoacclimation) models are still applied widely. In this study, we focus on the acclimative growth response of phytoplankton as incorporated in these models. To evaluate the performance and implications of this acclimative response of phytoplankton growth to varying light and nutrient conditions across the North Pacific Ocean, we compare modeled chlorophyll and primary production from an inflexible phytoplankton control model (InFlexPFT), which assumes fixed C:N:Chl ratios (fixed stoichiometry), to a recently developed phytoplankton model (FlexPFT, Smith et al., 2016), which incorporates photoacclimation and variable C:N:Chl ratios. We apply these two phytoplankton models in a 3-D eddy-resolving ocean circulation model of the North Pacific, to assess each model's performance compared to observations of chlorophyll and primary production." In the last paragraph of the Introduction.

There needs to be a better explanation of why this data was used, and why comparing the last 20 years of the model run with observations from different years instead of exact comparisons?

Since the 2000s, sea surface chlorophyll data has been accumulated for the last 20 years, and it is possible to analyze the seasonal variability. On the other hand, the vertical profiles of chlorophyll and PP from in-situ observations are mostly snapshots of limited places (time series stations, etc.) and observation lines, and there are few that are spatiotemporally aligned with nutrients and temperature, as in the WOA database. Since the 2000s, comparable data have been published in the North Pacific and used for model validation. For a more through comparison and assessment of model performance, it will be necessary to prepare more publicly available data in order to analyze variations over different timescales, from days to decades.

New Lines 200-205: We have revised the text to clearly state, "The last 20 years (2000-2019) average of model results were compared with satellite data, in-situ observations, and the climatological data (Chl, nitrate, and temperature). Although the model and observation periods differ somewhat, using the satellite and in-situ observation data observed during the simulation period (2000s), we compare whether the horizontal and vertical patterns of climatological seasonal variations can reproduce the patterns captured by the satellite and the snapshot observations. Especially, we focused on the Chl and PP patterns, which strongly reflect effects of the different assumptions about how growth rates depend on light and nutrients." at the beginning of the Observational Data section.

1. Lastly, an explanation of limitations and what still needs to be improved from these models can be useful.

In this study, we compared the two models, each with only one phytoplankton type: the FlexPFT incorporating variable C:N:Chl ratios and photoacclimation, and the InFlexPFT assuming constant composition without photoacclimation. With the FlexPFT, a single phytoplankton type adjusts its growth rate (i.e., acclimates) depending on available nutrients and light conditions. On the other hand, the InFlexPFT does not account for this physiological flexibility, and therefore either light or nutrient limitation tends to reduce growth rates more with the InFlexPFT compared to the FlexPFT. Also, we ignored other biological processes (e.g., interactions between grazers and phytoplanktons, export and recycling) of BGC model.

New Lines 480-482: We have revised the text to read, “In addition, we will proceed with research on introducing flexible physiology to the growth of multiple phytoplankton, as well as associated food quality effects on predation by zooplankton, and the uncertainty of other biological processes, such as nitrification, grazing, mortality, export and recycling.” in the last paragraph of the Conclusions section.

Technical corrections:

Abstract:

L005 - Does InFlexPFT also incorporate photoacclimation?

New Lines 6-9: The InFlexPFT control model does not incorporate photoacclimation because the Chl:C ratio (Eq. 5 in old version) is fixed by the equation of light limitation (fixed stoichiometry). We revised the text to read, “We compare modeled chlorophyll and primary production from an inflexible control model (InFlexPFT), which assumes fixed carbon (C):nitrogen (N):chlorophyll (Chl) ratios, to a recently developed flexible phytoplankton functional type model (FlexPFT), which incorporates photoacclimation and variable C:N:Chl ratios.” in the abstract.

L008 - Briefly Specify where these observations are coming from.

New Line 10: We added the “(e.g., satellite imagery and vertical profiles of in-situ observations)” after “We coupled each phytoplankton model … and evaluate their respective performance versus observations”.

L009 - What about nutrients? They are mentioned in the earlier line.

We deleted “nutrients”.

L010 - Specify where this subsurface Chl maximum is reproduced, and the Chl concentrations are overestimated.

New Line 12: We add “in the subtropical gyre” after “subsurface Chl maxima”.

L014 - You should also state the role of FlexPFT incorporating photoacclimation.

New Lines 16-18: We revised last sentence of the abstract to read: “Compared to the InFlexPFT, the key differences that allow the FlexPFT to better reproduce the observed patterns are its assumption of variable, rather than fixed, C:N:Chl ratios and inter-dependent, rather than strictly multiplicative, effects of light- “(photoacclimation)” and nutrient- “(uptake)” limitation.”.

Introduction:

L029-L030 - Provide further details on how they are debated.

New Lines 32-35: "For example, some models include numerous phytoplankton and zooplankton types (Ward et al., 2013), others resolve complexity selectively for specific trophic levels (Follows et al., 2007, Gothlich and Oschlies, 2012), and others incorporate physiological trade-offs into ecological parameterizations (Smith et al., 2016, Pahlow et al., 2020)."

L072 - cite some of the few tests that have been conducted.

New Line 75: We added these references (e.g., Masuda et al., 2021, Matsumoto et al., 2021).

L075 - FlexPFT is also an NPZD model no?, I would recommend rephrasing this sentence to more clearly depict the differences between the control and flexible C:N:Chl model.

New Lines 84-90: The FlexPFT is a part of phytoplankton equation (Eq. A2) in the NPZD model.
We have revised as follows:
"In this study, we focus on the acclimative growth response of phytoplankton as incorporated in these models. To evaluate the performance and implications of this acclimative response of phytoplankton growth to varying light and nutrient conditions across the North Pacific Ocean, we compare modeled chlorophyll and primary production from an inflexible phytoplankton control model (InFlexPFT), which assumes fixed C:N:Chl ratios (fixed stoichiometry), to a recently developed phytoplankton model (FlexPFT, Smith et al., 2016), which incorporates photoacclimation and variable C:N:Chl ratios. We apply these two phytoplankton models in a 3-D eddy-resolving ocean circulation model of the North Pacific, to assess each model's performance compared to observations of chlorophyll and primary production."

Methods and Materials:

L085 - Very descriptive, but this sentence is a bit hard to follow, I would recommend restructuring to make it more clear.

New Lines 94-104: We have revised the text to read:
"We used a coupled physical-biological model of the North Pacific, consisting of the physical ocean model, which is an eddy-resolving (1/10) OFES2 (the Ocean general circulation model For the Earth Simulator) including sea-ice (Masumoto et al., 2004, Komori et al., 2005, Sasaki et al., 2020) coupled with a simple nitrogen-based Nitrate-Phytoplankton-Zooplankton-Detritus (NPZD) pelagic model (Sasai et al., 2006, 2010, and 2016). The OFES2 domain extends from 20S in the South Pacific to 68N in the North Pacific and from 100E to 70W. The OFES2 has 1/10 horizontal resolution with 105 vertical levels, from 5 m thickness at the surface to 300 m thickness at the maximum depth of 7500 m. The physical fields were spun up for 50 years under climatological

forcing data (wind stresses, heat flux, and freshwater flux) from the Japanese 55-year Reanalysis (JRA55-do) (Tsujino et al., 2018) and from the initial condition of the observed climatological fields of temperature and salinity (World Ocean Atlas 2009, WOA09) (Antonov et al., 2010, Locarnini et al., 2010) without no motion for 50 years. After 50 years of spin-up integration, the OFES2 was forced by 3-hourly JRA55-do from 1958 to 1979. The last day of 1979 is used for the initial physical fields for performing coupled physical-biological model simulation.”.

L101 - state the value of this initial nitrogen N field if possible, otherwise be more specific on what you mean here.

New Lines 112-115: We revised from “the WOA09” to “the observed annual climatological values of WOA09 The initial N concentration range from 5 to 20 (mmol N m^-3) in the subpolar surface and 0.1 to 5 (mmol N m^-3) in the subtropical surface.”

L102-L03 - is there a reason why these values were used? Add citation, reasoning, or state that it is part of model calibration?

New Lines 117-118: We added some citations. We added “These P, Z, and D initial values are taken from Sasai et al. (2006, 2010, 2016).”.

L104 - This sentence feels a bit out of place. I would add this to your previous description in L093.

This sentence leads to the previous section (explanation of the steady state of physical fields), so we revised it as follows:

New Lines: We revised from “The last day of 1979 is used for the initial physical fields for this simulation.” to “The last day of 1979 is used for the initial physical fields for performing coupled physical-biological model simulation.” in [L93].

New Lines 118-119: We revised from “Two NPZD models are incorporated after the last day of 1979 of the OFES2.” to “Two NPZD models are incorporated after the last day of 1979 of the physical fields in the OFES2” in [L104].

L115 - If Q is a function of I, N, and T, I would add that in Eq1. Q(I,N,T).

We added Q(I,N,T) and fv(I,N,T) are a function of I, N,T in equations in Section 2.2.

L116-L117 - Add citation directing to Eq.4. Fv is repeated in L125.

We added citation directing for each equation.

L124 - Explain how you determine potential maximum affinity for N. Also cite table 1.

These parameter values were determined by tuning the model to reproduce the seasonal

and spatial variability of N and Chl in the near-surface of the North Pacific.
New Lines 178-180: These parameter values were determined by tuning the model to reproduce the seasonal and spatial variability of N and Chl in the near-surface of the North Pacific. We revised “Parameter values, mu_max, V_0, A_0, and alpha (Table 1) used in Eqs. 1 to 7 for the phytoplankton growth rate were tuned, separately for each coupled model, to reproduce the seasonal variability of N, and Chl in the near-surface of North Pacific.”. after explanation of equations.

L131- cite table 1 after the theta explanation.

New Line 133: We have revised to cited table 1 after biological parameters used (potential maximum growth rate, potential maximum uptake rate for N, potential maximum affinity for N, and initial slope of growth versus light intensity).

L132 – Is there a reasoning behind the activation energy Ea used? If so, cite it. Is it derived from observations?

In this study, we set to constant Ea value for growth rate, corresponding to an doubling of rate for a 10 degree C increase in temperature (i.e., Q_10 = 2.0, which is a typical empirically-based value for the temperature sensitivity of phytoplankton growth rates (Eppley, 1972, Bissinger et al., 2008). Because it doesn’t depend on phytoplankton metabolic rates under different nitrate limitation (Maranon et al., 2018, https://doi.org/10.1038/s41396-018-0105-1).

New Lines 145-148: “E_a is the activation energy (4.8 x 10^4 J mol^-1), which is set to a constant value, corresponding to a doubling of growth rate for a 10 degree C increase in temperature (i.e., Q_10 = 2.0), which is a typical empirically-based value for the temperature sensitivity of phytoplankton growth rates (Eppley, 1972, Bissinger et al., 2008).”.

L135 – I understand why $¥mu_{InFlex}$ and $¥mu_{Flex}$ are used, but they are quite lengthy, if possible I would abbreviate them to have shorter names.

We shortened the letters. Mu_InFlex to “mu_IFL” and mu_Flex to “mu_FL” in Section 2.2 and Appendix.

L138 - since you already explained the potential maximum uptake rate and the potential maximum affinity for N above, I don't think you need to explain them again here, but do add the last part of this sentence and citations (L139) in L124.

We have deleted the explanation of the potential maximum uptake rate and the potential maximum affinity for N in this sentence.

L154 - This part is difficult to follow. Expand further on this paragraph. All these parameters are introduced, but no equation explains where they come from.

New Lines 193-198: We have revised the text to the following:

“For the InFlexPFT, Chl concentration (mg m^-3) is P (mmol N m^-3) x the constant Chl:N ratio (1.59 g Chl (mol N)^-1), and PP (mgC m^-3 day^-1) is mu_IFL P (mmol N m^-3 day^-1, Eq. 1) x the fixed C:N ratio (Redfield ratio = 106:16 mol C (mol N)^-1). In the FlexPFT, the Chl concentration (mg m^-3, = P x theta /Q) is the phytoplankton concentration, P (mmol N m^-3), x the variable Chl:N ratio (g Chl (mol N)^-1, theta /Q), and Primary Production, PP (mgC m^-3 day^-1), is mu_FL P (mmol N m^-3 day^-1, Eq. 4) x the variable C:N ratio (mol C (mol N)^-1), 1/Q) (Eq. 5 and Smith et al., 2016).”

L158-L163 More explanation/rationale is needed here on model evaluation and why these observational datasets were selected.

We added the following explanation (same response to the major comment 3-2.).
New Lines 200-205: We have revised the text to clearly state, “The last 20 years (2000-2019) average of model results were compared with satellite data, in-situ observations, and the climatological data (Chl, nitrate, and temperature). Although the model and observation periods differ somewhat, using the satellite and in-situ observation data observed during the simulation period (2000s), we compare whether the horizontal and vertical patterns of climatological seasonal variations can reproduce the patterns captured by the satellite and the snapshot observations. Especially, we focused on the Chl and PP patterns, which strongly reflect effects of the different assumptions about how growth rates depend on light and nutrients.” at the beginning of the Observational Data section.

L162-170 - It would be nice to map the observations and add them as a supplementary figure. It will be easier to understand what observations you are using.

The compared observation lines and stations are summarized in Figure 1. Two transect lines (JMA and JODC observation lines) are shown in Figures 1c, 1g, and 1k in summer map. Three time series stations (Station K2, Station S1, and Station ALOHA) are shown in Figures 1d, 1h, and 1l in winter map.

Results and Discussion:

L174 - cite the satellite imagery and in-situ observations.

New Lines 220: We revised from “the satellite imagery and in-situ observations.” to “MODIS-Aqua imagery and vertical profiles of in-situ observations (JMA and JODC ship observation lines).”.

L174-177 - Should this physical evaluation go on the results. Was this part of this project or evaluated elsewhere? If so, state that.

New Lines 225-226: We added “In addition, the seasonal variability of T and N fields in the near-surface over the North Pacific are also well reproduced (not shown).” between “The eddy-resolving ocean … mesoscale eddies, and upwelling events.” and “These physical processes …”.

New Lines: In the surface Chl pattern, the contrast of Chl between two gyres, and high Chl in the coastal upwelling are clearly shown using the OFES2. We added "using an eddy-resolving (1/10) OFES2" between "Overall," and "the two models" and after "… MODIS-Aqua imagery." to "In particular, the contrast between two gyres and the coastal upwelling region more clearly than lower-resolution (e.g., 1 degree, about 100 km) models (e.g., Moore et al., 2001, Vichi et al., 2007, Follows et al., 2007, Gothlich and Oschlies, 2012) by using the OFES2.".

L182 - Throughout the manuscript, the focus is on comparing biomass and primary production between these two models, but now through the results the focus changes to comparing the chlorophyll pattern which is a proxy to biomass, but not biomass.

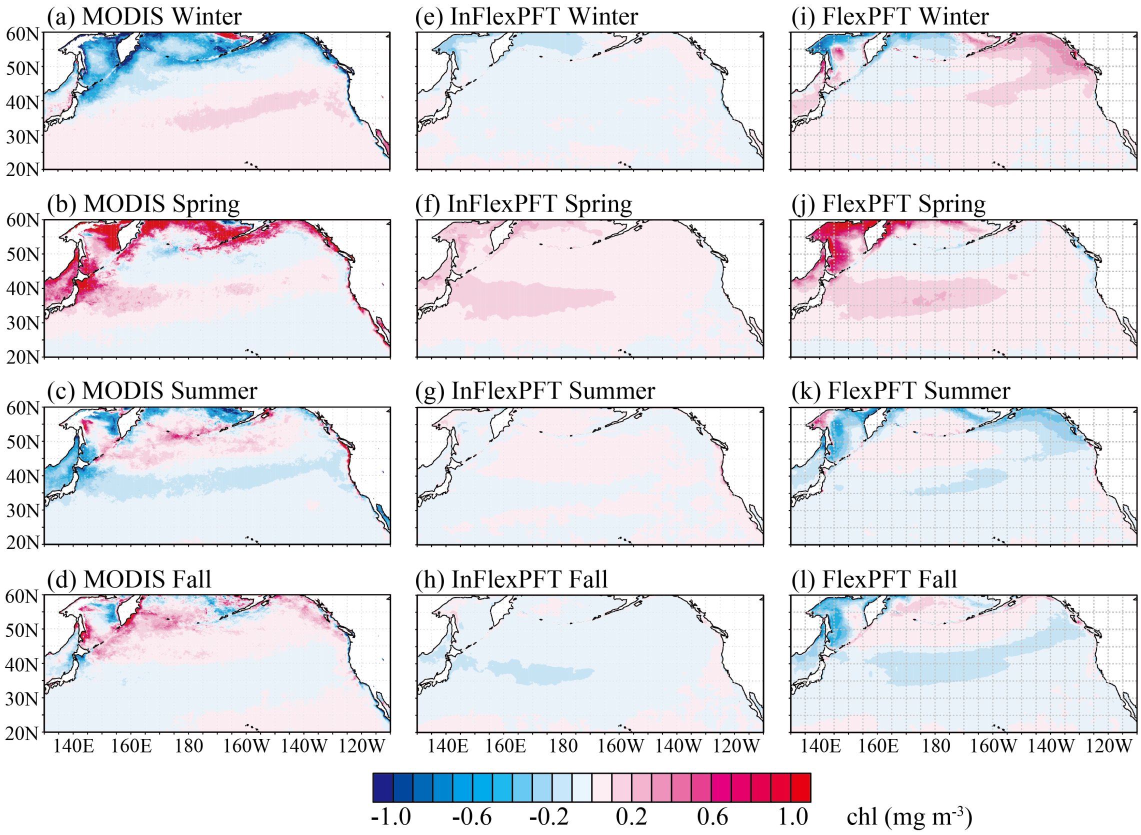
We changed from "biomass" to "chlorophyll". We changed the manuscript title to "Physiological flexibility of phytoplankton impacts modeled chlorophyll and primary production across the North Pacific Ocean"

L185 - The title should state this is a comparison since the paragraph concentrates on the model to satellite imagery comparison.

New Lines 239: We changed the title to "Comparison of Surface Chl Patterns".

L187- Are there any biased statistics to see how well the seasonal variations compare and what the deviations are?

The seasonal variations and their biases are presented below the figure. The distribution is difference in chlorophyll concentration between season and climatological mean. The FlexPFT displays a similar pattern with the MODIS. Compared with the FlexPFT, the InFlexPFT shows a weak seasonal variation. In this study, we check the difference in the seasonal variations of the surface chlorophyll reproduced by the two models for comparison of MODIS, and not show the biases. In the future, we will discuss which process (physics, chemistry, and biology) contribute to the deviations and their biases reproduced in the model.



L190 - More quantitative information on this model to satellite imagery comparison would be useful to understand the degree of variation.

We added the comparison of quantitative information between MODIS and two models in this section.

L200 - Same comment as L185 (state that it is a comparison in the title).

New Line 261: "3.2 Comparison of Vertical Distributions of Chl and PP along the Two Transects Lines"

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L200 - This section is difficult to follow. I would suggest restructuring and incorporating tables or diagrams summarizing the major findings, and categorizing the different areas you are comparing.

We revised the results section. See attached file.

L217 - These last two sentences are a bit hard to follow, I suggest utilizing more quantitative comparisons between model and observations, to understand the degree of variation.

We added the comparison of quantitative information between in-situ observations and two models in "Results" section.

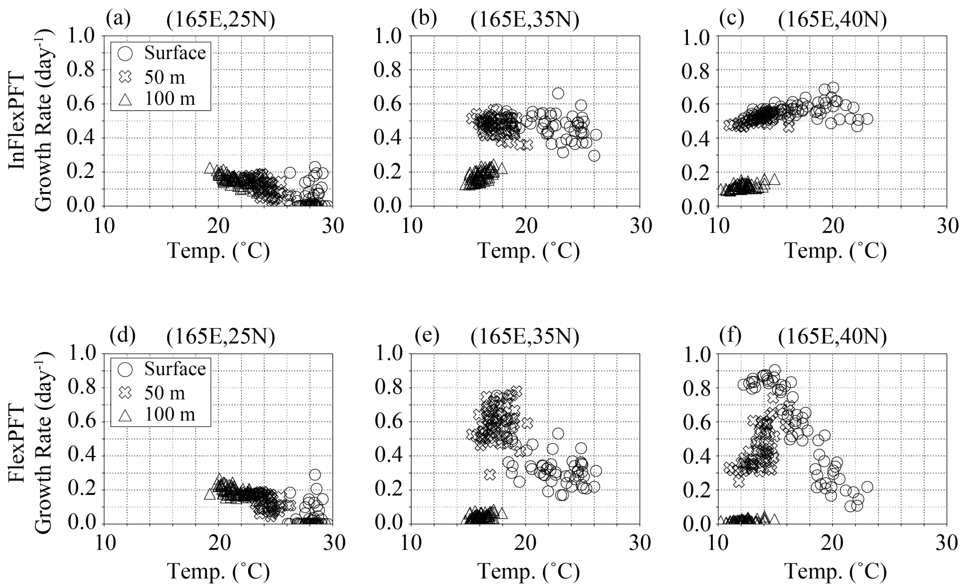
L269-271 - Is there reasoning why you think both models predict higher growth rates here?

New Lines 335: At 25N, in the surface, N concentration is close to zero. We added “, high I and T enhance the growth rate” after “… despite low N concentration”.

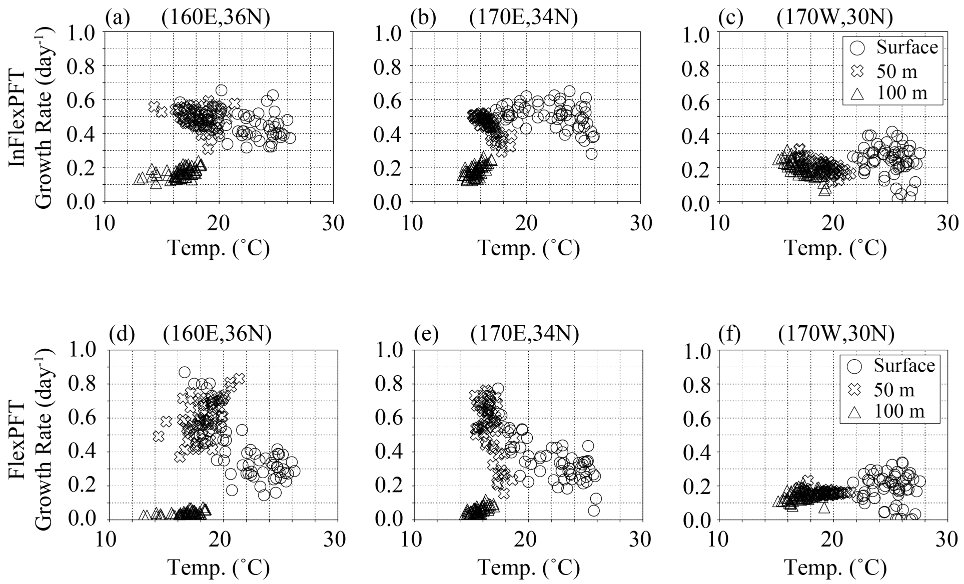
L277-L278 - By what degree more so for FlexPFT?

It is possible to separate and present the limitation factors. However, here we examine the differences by simultaneously plotting the three factors (I is different symbol, N is horizontal axis, and T is color) that control the growth rate. In addition, we explain the effect of the C:N ratio in the FlexPFT.

T-limitation is also important around 20 degree C, which is reference temperature in T-limitation equation, (in the subtropical region) for growth rate. Especially, in the subsurface layer (50m in below figure), Figures 6e and 7e show the higher growth rate compared with the that of surface layer (same N concentration and strong light intensity). Figure (e) (165E, 35N), where is the boundary between two gyres, shows the high growth rate around 20 degree C in the subsurface layer (50m). At other locations, the effect of T-limitation for growth rate is smaller than the N- and light-limitations.



In the east-west line, the similar pattern shows below. As the locations in Figures (d) and (e) are close to (165E, 35N), and the FlexPFT growth rate is the highest around 20 degree C.



L327 - Do you mean that the spring bloom occurs across latitudes and longitudes?

New Lines 408-410: We added "At the gyre boundary, in addition to the surface, primary production is greater compared to other regions. Because the nutricline depth (close to the base of the euphotic layer) and the light intensity are optimal for the spring production." after "… the spring bloom occurs both horizontally and vertically.".

L332- L335 - Explain why FlexPFT predicts this.

New Lines 418-420: We added "Compared with the seasonal variations of PP in the InFlexPFT, the FlexPFT's growth rate and the variable C:N ratio have a great influence on the spatiotemporal variations of PP (Figs. 4, 5, and 8)." after "… coastal upwelling region off California.".

L345 - Chl:C instead of Chl;C

Yes, it's a mistake. Corrected from "Chl;C" to "Chl:C".

L346 - I think this paragraph should go earlier.

We changed the order of this section and the previous section.
Old Figure numbers 8 and 9 changed to new figure numbers 9 and 8.

Conclusions:

L376 - I think you should say you compared Chlorophyll instead of biomass.

We revised from "phytoplankton biomass" to "Chl".

Figures:

Figure 1.

- **Minor point, but why not average from 2003-to 2019 to make the time comparison the same?**

It is 3 years shorter because we used data that deviated for a long and comparable period (MODIS imagery). It is possible to compare the same period including other sensors (SeaWiFS etc.), but only the climatological seasonal variations of surface chlorophyll are compared in this study. We confirmed, but the difference of 3 years was not so large (not shown). In the future, we plan to undertake a comparison of fluctuation components on several scales (few days to interannual).

Figure 2.

- **State what the white areas represent in panel a.**

We added the end of caption description. “White area in Fig. 2a is missing data.”.

- **Why not use just the 2006 model year for comparison instead of 2000-2019?**

In the data from JMA, the observed location, depth, and time are different and cover a shorter period. Observations capture summer season snapshots, so chlorophyll changes significantly between north and south locations over the three months. In this study, we have compared how much the model climatological fields (smoothed fields) can explain the snapshot observation, and will investigate the impact of smaller scale process on the chlorophyll distribution, such as the snapshot, in future.

The below figure shows the daily mean chlorophyll and nitrate distributions for comparison of in-situ observation (only chlorophyll). This chlorophyll pattern in the FlexPFT model reflects the effect of small variability of vertical nitrate pattern (1 mmol N m^{-3}).

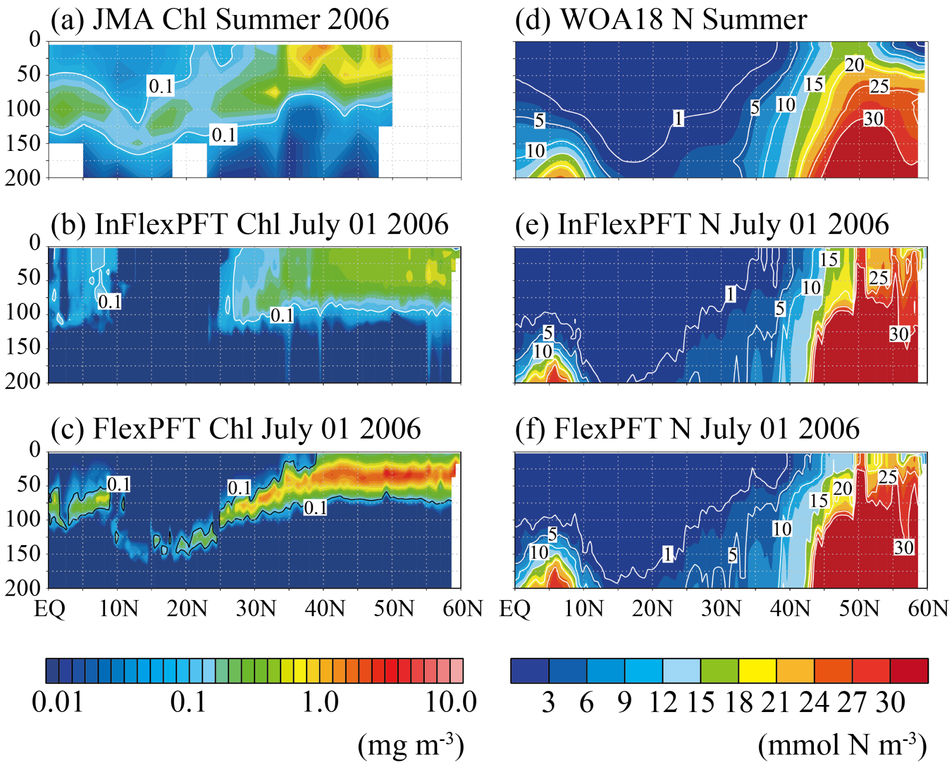


Figure 3.

- **I would add the text again from Figure 2. Instead of saying "same as for Fig. 2.).**

We described the same way as in Fig.2 caption.

Figure 5.

- **Same comment as figure 3. I would restate the information of the figure here.**

We described the same way as in Fig.4 caption.