Letter to the Editor

Dear Dr. Emmanuel Boss,

We highly appreciate the opportunity for submitting a revised version of our manuscript entitled "Seasonal Patterns in Phytoplankton Biomass across the Northern and Deep Gulf of Mexico: A Numerical Model Study", co-authored by Sang-Ki Lee, Yanyun Liu, Frank J. Hernandez Jr., Frank E. Muller-Karger, and John T. Lamkin. We are thankful for all the valuable reviewer comments and suggestions. Please find attached the new version of the responses to the reviewers, as well as a new manuscript version with the 'track change' option. In the revised manuscript version, we have addressed all the reviewers' indications, including a validation of the physical and biogeochemical model components. During the validation process, we detected an error in the prescribed boundary conditions for silicate, which produced a significant underestimation of the silicate concentration in the deep Gulf of Mexico (GoM). Consequently, we had to re-run the model for the entire study period correcting for the right silicate boundary conditions. For this new model run, we did minor changes in the model parameters, which help to reduce part of the disagreement between the simulated and satellite chlorophyll in the coastal regions. The results from the new model run do not modify the main finding described in the previous paper version, but the silicate limitation patterns. We obtained that model diatom growth in the deep GoM is silicate-limited only during winter, and not year-round as in the previous version.

We believe that the manuscript is significantly improved, and we hope it is suitable for publication in Biogeosciences.

Sincerely,

Fabian Gomez, on behalf of the co-authors.

1. Response to Dr. Fennel

1.1 Validation

1.1.1. Physical validation:

The authors provide no validation of the physical model. If there are previous publications in which this is reported, it would be fine to refer to those. Otherwise some physical model validation should be provided.

We agree that the manuscript needs some physical-component validation. In this new manuscript version we have included a validation of the physical model in the Appendix, which includes model-data comparison of SST, coastal sea level anomalies, eddy kinetic energy, surface salinity, and vertical profiles of temperature, salinity, and density.

1.1.2. Chlorophyll patterns:

On page 6 (first paragraph) the authors state that the model underestimates mean satellite chlorophyll by factors between 2.5 to 3. These are rather large deviations in the mean. They then give reasons for why the satellite can't be trusted. There are two problems with this: first, the simpler models of Fennel et al. (2011) and Laurent et al. (2012) reproduced satellite chlorophyll without such large biases; and, second, if chlorophyll cannot be trusted it shouldn't be used in validation. However, satellite derived chlorophyll is essentially the only data set that is used in this manuscript to validate the model.

We understand the concern pointed out by the reviewer regarding to the chlorophyll validation section. We have included now a comparison between model outputs and in situ observations derived from the Coastal Waters Consortium (Rabalais, 2015; Smith, 2015), as well as from APEX profiling floats (Hamilton and Leidos, 2017). The comparison between in-situ and satellite chlorophyll in the Louisiana-Texas shelf actually suggests chlorophyll overestimation by the satellite sensors in the MS delta region during fall-winter.

Regarding to the first related problem (a simpler model reproduces better the chlorophyll variability), we agree that the Fennel model matches better the chlorophyll pattern in the Louisiana-Texas shelf, as shown by Fennel et al. (2011) and Laurent et al. (2012). However, the Fennel model tends to overestimates satellite chlorophyll in the open ocean region, which can be noted in the chlorophyll patterns reported by Xue et al. (2013). We have included a direct comparison between our biogeochemical model (hereinafter GoMBio) and Fennel model, which is presented in the Appendix version.

Regarding to the second problem (if chlorophyll cannot be trusted it shouldn't be used in validation), previous studies have shown that although satellite chlorophyll can largely overestimate in situ chlorophyll in regions influenced by river runoff (until by 300%), there is a significant correlation between satellite and in situ chlorophyll (as example, see Figure1.10 in Nababan, 2005). Besides, the bias associated to optically complex waters occurs mainly in the coastal region but not in Open Ocean. These two aspects, added to the fact that satellite sensors provide large spatial and temporal coverage to properly describe seasonal and interannual variability, makes the model-satellite comparison of chlorophyll valid.

1.1.3. Biomass and nutrients:

There should be some validation of the biogeochemical model with in situ observations of phytoplankton biomass and nutrients.

Such observations are available in the NODC and GOMRI databases. Profile comparisons for the open Gulf should be included.

In the new manuscript version we have included a comparison with satellite chlorophyll, in-situ chlorophyll derived from the Coastal Waters Consortium (Rabalais, 2015; Smith, 2015) and APEX profiling floats (Hamilton and Leidos, 2017), diatom to total chlorophyll ratios reported by Zhao and Quigg (2014), primary production (Lehrter et al., 2009; Biggs, 1992, Sanchez, 1992), and nutrients (Rabalais, 2015; Smith, 2015; Parson et al, 2015; Wanninkhof et al., 2014).

1.1.4. Diatom and nanophytoplankton:

Perhaps the largest omission, given the objective of the study, is that there is no validation of the different phytoplankton groups. I recognize that it is hard to get good data sets for this purpose, but there are some algorithms that can be used to separate satellite-derived chlorophyll into different size groups (see Hirata et al. 2011, Mouw et al. 2017 and references therein).

As Dr. Fennel indicates, it is difficult to obtain data set to validate the diatom and nanophytoplankton components. We are not including a satellite-based analysis on phytoplankton group biomass pattern, as time limitations preclude performing this type of analysis (which we think can be the topic for an independent paper). However, we have used chlorophyll data of functional phytoplankton group reported by Zhao and Quigg (2014). Based on these data, we estimate the diatom to total chlorophyll ratio for two stations in the Louisiana shelf. The model-data comparison showed that our biogeochemical model does reasonable well reproducing the observed diatom ratios, including a documented diatom chlorophyll decline during summer (see paper Fig. 5).

1.2. Terminology

With regard to terminology: In section 3.4 the authors define the "biological term" as the balance between phytoplankton production and biological losses. This is the same as Net Phytoplankton Growth, a widely used term in biological oceanography. It is not only unnecessary to redefine this as a new term, but also potentially confusing. Then the authors state that the balance of the biological and physical terms determines the change in net phytoplankton growth. This is wrong. Net phytoplankton growth is equal to what they defined as the biological term. The balance between the biological and physical terms is the local rate of change of phytoplankton.

We highly appreciate the term names clarification, and understand that is preferable avoid any confusing terminology in the budget analysis. We modified the term names following Dr. Fennel indications.

1.3. Improving description of the results and the context in the existing literature:

1.3.1. In the last sentence of the abstract, they claim that their study shows the importance of representing large and small plankton in order to describe PP patterns. This is not supported by the results presented. On the one hand, there is no validation of the contributions of large and small phytoplankton to biomass and PP (see 1 above). On the other hand, there is no comparison to simulated phytoplankton abundance and PP from a model with only one phytoplankton group. Simpler models exist that, in fact, reproduce chlorophyll from satellite more accurately than this model in the Mississippi plume region (see comment 1.2).

We agree that that sentence is not supported by the result presented and was removed from the abstract.

1.3.2. In the second to fourth sentences of the discussion the authors make statements about their results that are not supported. “Inclusion of two phytoplankton components allowed for realistic representation...” is not accurate as simple models arguably reproduced this better (see comment 1.2). “The good agreement between model outputs and observations of chlorophyll...” is a questionable statement (see again comment 1.2).

We decided to tone down our statement and reformulate the entire first discussion by:

“We configured an ocean-biogeochemical model for the GoM that explicitly represents two types of phytoplankton and zooplankton, and nitrogen and silica as limiting nutrients for phytoplankton growth. Our model reproduces reasonable well the main physical and biochemical patterns, although an underestimation of the mean surface chlorophyll is evident in the northern shelf, especially on bottom depth < 20 m. A comparison with in situ chlorophyll observations suggests that part of the model-satellite chlorophyll disagreement could be linked to chlorophyll overestimation by satellite sensors during fall-winter. Realistic representation of phytoplankton variability in region with strong physical and biochemical gradients, like those in the northern GoM, is challenging. Previous modeling efforts on the Louisiana-Texas shelf based on Fennel’s model reproduced better the mean satellite chlorophyll condition than our model (e.g. Fennel et al., 2011; Laurent et al., 2012). However, Fennel’s model tends to overestimate satellite chlorophyll by a factor of >3 in the Deep Ocean region during winter, which could be linked to misrepresentation of microzooplankton grazing (see section 4 in Appendix). We acknowledge that additional components and processes could be included in our model, such as phosphorus cycling, iron limitation and nitrogen fixation, to represent more realistic biogeochemical dynamics. We also recognize that more observational studies will be required to constrain better our model parameters, as well as the biogeochemical fluxes between land and ocean. Nevertheless, we believe that the current model configuration can capture well enough the seasonal dynamics of diatoms and nanophytoplankton biomass in the GoM. It is known that variations in phytoplankton composition can have important repercussion for the ecosystem, including changes in upper trophic levels dynamics, carbon export (carbon export is enhanced in diatom-dominated food webs) and bottom hypoxia (Dagg et al., 2003; Green et al., 2008). Therefore, modeling efforts exploring variability in phytoplankton component, such as this study, are needed to advance our understanding of ecosystem variability in the GoM.”

1.3.3. With respect to phosphorus (P) the authors seem to be diminishing previous findings in an effort to justify why their model does not include P. On page 3 (line 8, sentence starting with “Although: : :”) they seem to suggest that previous studies (specifically Laurent et al. 2012) suggest P limitation to be unimportant. This is not the conclusion of Laurent et al. (2012) nor of the follow-up studies by Laurent and Fennel (2014) and Fennel and Laurent (2017), which are consistent with the observational studies by Sylvan et al. (2006, 2007). All these studies do suggest the P limitation is critically important in the region influenced by the Mississippi River plume. Saying that P limitation is “moderate” while N and Si limitation are “critical” seems disingenuous. To be clear, I do not object to the fact that P is neglected in this model. All models are simplifications. It would be fine to state that their model neglects P, although it has been shown to be important in a portion of the model region. In the Discussion (end of first paragraph) it would be appropriate to be more forthcoming about previous studies on P limitation.

We understand the point indicated by the reviewer and recognize that phosphorous limitation can be critical in the region influenced by the Mississippi River. We modified the statement in the ‘Model description’ section to:

"The model does not include phosphate as limiting nutrient for phytoplankton growth. Although previous studies have indicated the existence of phosphate limitation near the MS-A deltas during May-July (Sylvan et al. 2006, 2007; Laurent et al., 2012; Laurent and Fennel, 2014; Fennel and Laurent, 2017), we focus here on the role of N and Si, as observational studies suggest that N and Si can modulate phytoplankton production and composition across the northern GoM (Dortch and Whitledge, 1992; Nelson and Dortch, 1996; Lohrenz et al., 1997; 2008; Rabalais et al., 2002; Zhao and Quigg, 2014)."

1.3.4. The statement in the Discussion (last sentence starting on page 11) about consistency with the dilution-recoupling hypothesis of Behrenfeld seems a bit cavalier. No detailed analysis in support of this statement was presented in this manuscript. The authors may want to consider the study by Kuhn et al. (2015), which used the same data set as Behrenfeld, and later papers by Behrenfeld where he backtracked himself somewhat from his early paper (Behrenfeld et al. 2013).

We agree with the reviewer that more analyses need to be done to support the consistency between the dilution-recoupling hypothesis and our model results. Since this aspect is beyond the paper goals, we decided to remove the dilution-recoupling hypothesis part from the discussion.

Other comments (not in order of importance):

1.4. P1, Line 13: Suggest inserting "improving" after "tools for"

The change was done accordingly.

1.5. P1, Line 14: Suggest removing "However"

The change was done accordingly.

1.6. P1, Line 19, sentence starting with "The model results show..." and following sentences in the abstract. Because diatoms in the model are strongly silica-limited doesn't necessarily mean they are in reality. Making inferences about reality from the model requires that the model accurately reproduces reality, which in this case is hard to prove. The authors certainly haven't (see my comments about validation). I would suggest that here and throughout the remainder of the abstract and manuscript the authors are more precise in their language. It is fine to say "diatoms in the model are silica limited" or some variation thereof. And "Simulated nanophytoplankton are..." rather than "Nanophytoplankton are..."

Agree with the suggestion. We precise better our result's statements in the revised paper version.

1.7. P1, Line 27: Suggest replacing "vertical diffusion" with "turbulent vertical diffusion" or "vertical mixing." Diffusion typically refers to molecular diffusion which acts on too small scales to make any difference to the processes considered here.

Agree with the suggestion, change was done accordingly.

1.8. P1, Line 27, sentence starting with "This study highlights the..." This is an overstatement not supported by the results actually presented in this manuscript. See major comment 3.

This statement was removed.

1.9. P2, Line 9: ...because of deleterious impact on coastal ecosystems." The authors should provide one or more references in support of this statement, or modify it. I would like to challenge them to find a study that shows deleterious impacts on the ecosystem in the northern Gulf of Mexico (I am not aware of one). There are studies about specific aspects of the ecosystem, which would be fine to cite if sentence is slightly modified.

Following the reviewer suggestion, we modified this statement, mentioning the specific ecosystem aspects that are negatively impacted by bottom hypoxia, such as individual growth and metabolism (Rosas C, et al., 1998; Craig and Crowder, 2005) and specie distribution (Craig, 2012).

1.10. P3, Line 5, sentence beginning with "New modelling efforts..." I object to the logic of this statement. Adding complexity to biogeochemical models is not in itself a worthwhile undertaking. It has to be motivated by the scientific questions (e.g. one might be interested in species succession). Sentence should be reformulated accordingly.

The sentence was reformulated to:
"New modeling efforts are required to examine spatiotemporal patterns of main phytoplankton functional groups across the northern and deep GoM."

1.11. P3, Line 8: "...diatoms require..." Citing a modeling study (Kishi et al.) in support of a general statement about diatom traits seems inappropriate. There are more appropriate references. I suggest the authors look up publications by Elena Litchman and collaborators. She has worked extensively on documenting phytoplankton functional traits.

We agree with the suggestion. We included Litchman and Klausmeier (2008) as reference for the diatom traits [Litchman, Elena, and Christopher A. Klausmeier. "Trait-based community ecology of phytoplankton." Annual review of ecology, evolution, and systematics 39 (2008): 615-639.]

1.12. P4, Line 30: Which basin does "basin-scale" refer to here?

It refers to the Atlantic Ocean. We precise the statement in the revised manuscript version.

1.13. P5, Line 18: ...randomly selected year" Which year?

We modified the sentence to make the spin-up procedure clearer:

"A 40-year model spin-up was completed before starting the historical simulation. To spin-up the model, we used the basin-model boundary conditions and the ERA surface fluxes of randomly selected years from 1979-2014, following Lee et al. (2011)."

1.14. P5, Line 23: Stating the model "reproduces" the observations is an overstatement. It would be more appropriate to say they agree qualitatively.

The sentence was modified to:
"Modeled surface chlorophyll agreed qualitatively well in the spatiotemporal patterns with the satellite chlorophyll (Fig. 2)."

1.15. P5, Line 31: The authors should make it much more clear upfront that these are anomalies (i.e. that the bias was removed).

We decided presenting the chlorophyll time series without removing the long-term mean, and make easier the comparison with observations (Fig. 3).

1.16. Results, general: No oxygen results are shown. Given this, there is not much point saying the model includes oxygen.

We agree with Dr. Fennel so we excluded oxygen from the model.

2. Response to Referee #2

2.1. My major concern is associated with the validation of the coupled physical biogeochemical model:

First, there is no physical validation presented in the paper, despite that the authors have emphasized the importance of physical processes on the net phytoplankton growth. Has the physical validation work been done and/or published elsewhere? If yes, it is important to summarize that here in some way. If not, I think it's worthwhile to do some extra work on physical validation to make the presented results here more convincing considering how important the physics is controlling the biogeochemical cycling in this region (e.g., the mixing and transport by riverine waters to northern GoM, Loop Current and eddy interactions to deep GoM, etc.). For example, the simulated spatial extent of the high chlorophyll river plume in northern GoM is narrower than that observed in satellite (visually viewed from Fig. 2), could it be associated with the distant transport of riverine nutrients?

We agree that a validation of the physical model component is required. In the revised manuscript version, we have included in the Appendix a validation for SST, coastal sea level anomalies, eddy kinetic energy, surface salinity, and vertical profiles of temperature, salinity, and density.

Second, the validation of biogeochemical (BGC) model doesn't seem sufficient to me. The BGC validation in the paper primarily relies on comparing model simulated and satellite observed surface chlorophyll. While the model overall reproduces the dominant seasonal and spatial patterns in satellite chlorophyll, it significantly underestimates the coastal chlorophyll both in magnitude (2.5-3 times lower in the model) and spatial extent. The authors attribute the mismatch to satellite overestimating in situ observations of chlorophyll in northern GoM. If true, it would be useful to also include comparisons between simulated and in situ observations of chlorophyll in the paper for justification. In addition, while satellite chlorophyll observations have the advantage for model validation due to its spatial and temporal coverage, they are limited to the first optical depth that could hardly represent the plankton dynamics in subsurface water (e.g., the deep chlorophyll maxima). Hence a good complement to the validation might be including comparison to chlorophyll profiles, which to my knowledge is available in GoM during the model simulation period (e.g., the bio-optical profiling float results presented in Green et al., 2014). Also, there are relatively 'abundant' observations, apart from chlorophyll, in the northern GoM, such as those provided by Mechanisms Controlling Hypoxia (MCH) program (http://hypoxia.tamu.edu/field-program), in situ observations of primary production (Lehrter et al. 2009), and water column community respiration rates (Murrell et al. 2013). These datasets might improve the BGC validation in coastal region where satellite chlorophyll is considered to have higher uncertainty.

We have included now a validation section for the biogeochemical model. We performed model-data comparison of chlorophyll, primary production, diatom to total chlorophyll ratios, and nutrients.

2.2. One novelty of this work is that the model includes two phytoplankton types and two zooplankton types that complement the previous modeling work in GoM that mostly only includes one phytoplankton and one zooplankton type. While the additional complexity added to the BGC model is more faithful in representing the lower-trophic level dynamics in real system, it also adds more complexities and challenges in calibrating and validating the model. With respect to calibration, have the parameter values shown in Table 1 (especially those with *) been informally or formally tuned or optimized? Are the conclusions presented here sensitive to the selected parameter values? I think providing more information/comments on these would be helpful to others. The additional complexity of the BGC model also adds difficulties in model validation, e.g., the model-data chlorophyll comparison alone cannot tell how reasonable the model simulates each type of phytoplankton group as it could not distinguish the contribution from small- and large-size phytoplankton groups. How has the added complexity benefit us to understand the plankton dynamics in this region? Does the presented model do a better job than the previous modeling work that only include one phytoplankton type (e.g., compared with Xue et al. 2013)? I think readers would appreciate with a bit more discussions/comments on these.

*The selected parameters are within ranges reported in previous studies, with * indicating minor variations from reported values. We agree with the reviewer that more information and comments sensitivity analysis and comparison with previous model can be helpful to other biogeochemical modelers. In the Appendix section we have included a direct comparison to Fennel's model, where we pointed out that although Fennel model is able to catch better the mean satellite chlorophyll condition in the coastal region, it overestimates satellite chlorophyll during winter in the Deep Ocean region. A coupled of sensitivity analyses were performed to show that this winter overestimation could be linked to misrepresentation of zooplankton grazing in the Deep Ocean region.*

2.3. Specific comments:

Page 4, Line 6: Would it be more appropriate to list an observational rather than a modeling work (Xue et al., 2013) as a reference?

We modified the citation to Green and Gould (2008).

Green, R. E., and R. W. Gould (2008), A predictive model for satellite-derived phytoplankton absorption over the Louisiana shelf hypoxic zone: Effects of nutrients and physical forcing. Journal of Geophysical Research: Oceans, 113(6): 1–17, https://doi.org/10.1029/2007JC004594

Page 4, Line 14: delete one 'to' either in front of the ':' or after the number.

The change was done accordingly.

Page 4, Line 22: Why listed MODIS SST here? Has it been used anywhere in the paper?

We apologize for this mistake. We have corrected it in the new manuscript version.

Page 4, Line 28: Horizontal diffusivity is non-zero here, but it seemed to be neglected when analyzing the role of advection and diffusion in section 3.4.

We did not include horizontal diffusivity term in the budget analysis because is 2 orders of magnitude smaller than the advection and vertical diffusion terms, so it contribution can be neglected. We mentioned this aspect in new Figure's legend of the Budget Analysis (current Fig. 12).

Page 4, Line 30: Does the basin-scale model also include biogeochemistry and provide BGC initial conditions? If not, how do you specify them? Could you also provide more information on how you specify open boundary conditions? Has tide been included?

The basin model specifies the boundary and initial condition for both the physical and biogeochemical model. Tides were not included in the model. We have precise better those aspects in the revised Data and Model section.

Page 5, Line 18: Where were the boundary conditions and surface fluxes extracted from? the basin-scale model?

The basin model provides the boundary conditions, and the surface fluxes are from ERA-interim (same surface forcing as in the basin model). We clarified those aspects in the revised version.

Page 6, Line 23: 'mean production values', is it spatial or/and temporal mean? Maybe also provide the standard deviation if available, since the primary production is highly variable?

To validate our simulated production rates, we show in current Figure 6 boxplots for the simulated and observed primary productivity rates in the MS delta, Texas shelf, and Deep Ocean regions.

Page 7, Line 29: change 'ranges' to 'range'?

The change was done accordingly.

Page 8, Line 26: In the text, it's switching between 'summer' (or winter) and 'months' back and forth. Could you specify the summer and winter months at the first time they appear?

We now opt for using month intervals instead of seasons.

Page 10, Line 22-24: This statement is a bit exaggerated to me since the validation is on chlorophyll, a combination of two phytoplankton groups, that how well each type of phytoplankton is simulated by the model is not directly validated.

We agree with the reviewer. We re-wrote completely the first paragraph from the Discussion section, making more accurate our statements.

Fig.2: the lower limit of the color bar is missing? From 0? What does the gray contour line represent? 200m isobath?

The lower and upper limits for the color bar are now indicated. The contour grey line represents the 200 m isobath. We mentioned this in the Figure 2 legend.

Fig.8: should be '...in panels a-b depict...'
Change was done accordingly.

3. Response to Referee #3

3.1. Validation of the physical model

The paper stated that the boundary conditions were from a HYCOM model, yet the model (ROMS)'s own performance regarding circulation and T/S fields was not evaluated, without which, I would have a big question mark about the results presented in the manuscript;

We included now a validation of the physical model in the Appendix section. That includes data-model comparisons for SST, sea level anomalies, eddy kinetic energy, surface salinity, and vertical profiles of temperature, salinity, and density.

3.2. Validation of the biogeochemical model

The author evaluated their model's performance via a comparison against satellite data and admitted that their model underestimated the Chl-a. And unfortunately, these satellite data were the only source used for model evaluation. How about the model's performance on nutrient and plankton sgroups? Without such information, it is hard to conclude that the model could at least represent the nutrient and biological cycle in the Gulf;

We have included model-data comparisons in the revised paper version. We used satellite chlorophyll data, in-situ chlorophyll from the Coastal Waters Consortium (Rabalais, 2015; Smith, 2015) and APEX profiling floats (Hamilton and Leidos, 2017), diatom to total chlorophyll ratios reported by Zhao and Quigg (2014), primary production (Lehrter et al., 2009; Biggs, 1992, Sanchez, 1992), and nutrients (Rabalais, 2015; Smith, 2015; Parson et al, 2015; Wanninkhof et al., 2014).

3.3. Given that point 1) and point 2) were addressed, I could not find the benefit of introducing the new plankton group (2 phytoplankton and 3 zooplankton vs. 1 phytoplankton and 1 zooplankton by Fennel at al. 2011), which, indeed, could be the most important contribution of this study

We understand the reviewer concern regarding to the benefit of introducing a more complex representation of lower trophic levels, as the first manuscript version did not include any contrast with outputs from simpler biogeochemical models. In the revised manuscript version, we have included a comparison between chlorophyll patterns derived from our model (GoMBio), Fennel's model, and SeaWiFS, which shows that our model simulates better the seasonal patterns of chlorophyll in the deep GoM (see Appendix, section 4). Sensitivity analysis suggests that representation of microzooplankton grazing is relevant to modulate the amplitude of the winter chlorophyll peak in that region.

Besides that comparison, we consider that biogeochemical modeling efforts addressing more complex lower-trophic level dynamics are needed in the GoM, as observational studies suggests that changes in plankton composition can significantly *impact on upper-trophic levels abundance/distribution, carbon export, remineralization process, and bottom hypoxia (e.g. Dagg et al., 2003; Green et al., 2008). We recognize that still we need more observational studies to constrain better model parameters, and that additional model component and processes may be required to improve the representation of biogeochemical dynamics. However, we believe that our study gives an initial framework, which is a step forward to advance our understanding of phytoplankton functional group dynamics in the region. This aspect of our modeling effort is pointed out in the revised Discussion section (see first paragraph in Discussion section).*

Additional author's comments

Figures 5, 8, and 12 from previous paper version were eliminated, as four new figures were added in the new validation section. Few paragraphs from the previous version that we consider less relevant for the current paper narrative were also discarded.

The extension of the three sub-regions used to describe the model phytoplankton patterns were slightly changed from previous version. The reason of this change was trying to encompass zones with in-situ observations, in order to make more robust the model-data comparison. The MS delta region was extended west from 90.8°W to 91.4°W, the east limit of the Texas shelf region was extended east from 92.25°W to 92°W, and the Deep Ocean region was extended east from 86.5°W to 85.5W.

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Seasonal Patterns in Phytoplankton Biomass across the Northern and Deep Gulf of Mexico: A Numerical Model Study

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Abstract. Biogeochemical models that simulate realistic lower trophic levels dynamics, including the representation of main phytoplankton and zooplankton functional groups, are valuable tools for improving our understanding of natural and anthropogenic disturbances in marine ecosystems. Previous three-dimensional biogeochemical modeling studies in the northern and deep Gulf of Mexico (GoM) have used only one phytoplankton and one zooplankton type. To advance our modeling capability of the GoM ecosystem and to investigate the dominant spatial and seasonal patterns phytoplankton biomass, we configured a 13-component biogeochemical model that explicitly represents nanophytoplankton, diatoms, micro-, and mesozooplankton. Our model outputs compare reasonable well with observed patterns in chlorophyll, primary production, and nutrients over the Louisiana-Texas shelf and deep GoM region. Our model suggests silica limitation of diatom growth in the Deep GoM during winter, and near the Mississippi delta during spring. Model nanophytoplankton growth is weakly nutrient limited in the Mississippi delta year-round, and strongly nutrient limited in the deep GoM during summer. ~~The~~ Our examination of primary production and net phytoplankton growth from the model indicates that the biomass losses, mainly due to zooplankton grazing, play an important role modulating the simulated seasonal biomass patterns of ~~the~~ nanophytoplankton and diatoms. Our analysis further shows that the dominant physical process influencing the local rate of change of model phytoplankton is horizontal advection in the northern shelf, and vertical mixing in the deep GoM. This study highlights ~~the importance of representing small and large size plankton dynamics to describe primary production patterns, and emphases~~ the needs for an integrated analysis of biologically and physically driven biomass fluxes to better understand phytoplankton biomass phenologies in the GoM.

1 Introduction

The Gulf of Mexico (GoM) is characterized by large spatial differences in plankton productivity and biomass, ranging from the oligotrophic Loop Current to the highly productive northern shelf. Productivity in this last region is strongly influenced by river run-off. The Mississippi-Atchafalaya (MS-A) River System is the largest river input with a mean river discharge of

21,524 $m^3 s^{-1}$ (Aulenbach et al., 2007), contributing more than 80% of the entire dissolved inorganic nitrogen (DIN) load into the northern GoM (Xue et al., 2013). The large plankton production and vertical stratification driven by the MS-A river system discharge promotes the development of a hypoxic bottom layer a few meters thick off Louisiana and Texas during summer (Obenour et al., 2013). This hypoxic layer can negatively impact metabolism and growth of fish and invertebrates (Rosas et al., 1998; Craig and Crowder, 2005), and disturb species distribution and composition (Craig, 2012). The influence of river runoff on plankton production substantially decreases offshore (Green and Gould, 2008~~Xue et al., 2013~~). In the oligotrophic deep GoM, the spatiotemporal patterns in phytoplankton biomass are mainly associated with seasonal changes in thermal stratification and mesoscale ocean dynamics (e.g. Muller-Karger et al., 2015).

Multiple ocean-biogeochemical modeling studies have been conducted in the northern GoM to understand the drivers of phytoplankton biomass variability, carbon export, nutrient cycling, and bottom hypoxia variability. Green et al. (2008) configured a zero-dimensional Lagrangian model of the Mississippi (MS) river plume, which included two types of phytoplankton (small and large size), two types of zooplankton (micro- and mesozooplankton), bacteria, detritus, ammonium and nitrate. This study derived distinct production patterns for small and large size phytoplankton production, concluding that primary production was mainly limited by physical dilution of nitrate, light attenuation, and the sinking of diatoms (large phytoplankton). More complex modeling efforts for the region include a series of three-dimensional (3-D), fully coupled ocean-biogeochemical models, based on Fennel's biogeochemical model (Fennel et al., 2006). The original Fennel's model formulation included ammonium, nitrate, phytoplankton, chlorophyll, zooplankton (representing mesozooplankton), and two detritus types as state variables. Fennel et al. (2011) examined the underlying factors determining seasonal patterns in phytoplankton biomass in the Louisiana-Texas shelf, and concluded that phytoplankton production was not nitrogen limited near the MS delta. They also showed that zooplankton grazing played an important role in defining phytoplankton biomass changes, and speculated that physical transport of phytoplankton could impact biomass seasonality. Xue et al. (2013) configured Fennel's model for the entire GoM, describing main spatiotemporal patterns in plankton biomass and DIN in the coastal and oceanic domains. However, since they did not investigate underlying drivers (production, biomass losses) of phytoplankton biomass as was done in Fennel et al. (2011), less is know about the factors modulating the seasonality of phytoplankton in the deep GoM.

Significant differences in plankton production and carbon export can be expected between food webs dominated by small-size (nanophytoplankton, microzooplankton) and large-size (diatoms, mesozooplankton) plankton components. Sedimentation rates are enhanced (decreased) in diatom (small phytoplankton) based food webs, and therefore changes in phytoplankton composition could influence bottom remineralization processes (Dortch and Whiteledge, 1992; Dagg et al., 2003; Green et al., 2008; Zhao and Quigg, 2014). In addition, changes in phytoplankton composition may modulate trophodynamics, which can impact the reproductive success of upper trophic levels, and therefore modulate marine population abundance (Rykaczewski and Checkley, 2008). In the GoM, 3-D regional ocean-biogeochemical models that include more than one plankton functional group have been implemented only for the western Florida shelf (Walsh et al., 2003). New modeling efforts are required to examine spatiotemporal patterns of main phytoplankton functional groups across the northern and deep GoM.~~adding complexity to the representation of lower-trophic level dynamics are required for the northern and deep GoM~~. A key modeling aspect is the characterization of diatoms and nanophytoplankton growth. It is well known that: 1) nanophytoplankton uptake nutrients more efficiently than diatoms; 2) diatoms can achieve greater growth rates than nanophytoplankton in nutrient-rich environments; and 3) diatoms require silicate as an additional nutrient for frustule formation (Litchman et al., 2006;~~Kishi et al., 2007;~~ Falkowski and Oliver, 2007). These differences should be considered when simulating phytoplankton responses to changes in nutrient availability.

The present study explores ~~examines~~ underlying factors determining spatial and seasonal patterns in phytoplankton biomass across the coastal and ocean domains in the GoM, using an ocean-biogeochemical model that explicitly simulates small- and large-size plankton groups. After validating the model results with available observations, we examine main seasonal patterns of phytoplankton biomass. Our main goals are ~~to~~: 1) to describe the spatiotemporal patterns in growth limitation for diatoms and nanophytoplankton; and 2) to evaluate the coupled role of biological (phytoplankton production and biological losses) and physical (advection and turbulent diffusion of biomass) processes as drivers of phytoplankton seasonality. This study complements Fennel et al. (2011) on phytoplankton variability in the northern GoM, by adding complexity to the modeled lower-trophic level dynamics, extending the description of phytoplankton growth-limitation patterns to the deep GoM, and quantifying the role of advection and diffusion.

2 Data and model

2.1 Data

Monthly mean composite fields of SeaWiFS (1998-2011) and MODIS (2003-2014) chlorophyll-a were retrieved from the Institute for Marine and Remote Sensing, University of South Florida (http://imars.usf.edu). These data were processed using the NASA OC4 and OC3 band ratio algorithms (O'Reilly et al., 2000). All products followed the latest implementation of the atmospheric correction based on Ding and Gordon (1995). In situ observations of chlorophyll and nutrients for the Louisiana-Texas shelf were obtained from the Coastal Waters Consortium (Rabalais, 2015; Smith, 2015; Parson et al, 2015). Chlorophyll observations in the deep GoM were derived from APEX profiling floats measurements collected during the Lagrangian Approach to Study the Gulf of Mexico Deep Circulation project (Hamilton and Leidos, 2017). Nutrient observations in the deep GoM were obtained from water samples collected in the Gulf of Mexico and East Coast Carbon Cruises (GOMECC, Wanninkhof et al., 2014). Observed primary production rates are derived from measurements collected by Lehrter et al. (2009) in the delta and Texas shelf, and Biggs (1992) and Sanchez (1992) in the deep GoM.

2.1 Model description

We use a 13-component biogeochemical model (hereinafter refer to as GoMBio) that simulates nitrogen (N) and silica (Si) cycling. The model includes nitrate (NO_3), ammonium (NH_4), nanophytoplankton (small phytoplankton, PS), diatom (large phytoplankton, PL), chlorophyll of nanophytoplankton and diatom (ChlS and ChlL), microzooplankton (small zooplankton, ZS), mesozooplankton (large zooplankton, ZL), small and large detritus (DS and DL), opal, labile dissolved organic nitrogen (DON), and silicate ($SiOH_4$). Small detritus is particulate nitrogen linked to SZ egestion and small plankton (PS + ZS) mortality, while large detritus is particulate nitrogen associated with LZ egestion and large plankton (PL + ZL) mortality. Opal is non-living particulate Si linked to diatom mortality and zooplankton egestion. The state variables NO_3, NH_4, PS, PL, ZS, ZL, DS, DL, and DON are simulated in terms of mmol N m^{-3}, silicate and opal in terms of mmol Si m^{-3}, and ChlS and ChlL in terms mg chlorophyll m^{-3}. The model does not include phosphate as limiting nutrient for phytoplankton growth. Although previous ~~modeling~~ studies ~~suggested~~ have indicated ~~moderate~~ the existence of phosphate limitation near the MS-A deltas~~, mostly limited to~~ during May-July (Sylvan et al. 2006, 2007; Laurent et al., 2012; Laurent and Fennel, 2014; Fennel and Laurent, 2017), we focus here on the role of N and Si, as observational studies ~~strongly~~ suggest that N and Si ~~are critical in modulating~~ can modulate phytoplankton production and composition across the northern GoM (Dortch and Whitledge, 1992; Nelson and Dortch, 1996; Lohrenz et al., 1997; 2008; Rabalais et al., 2002; Zhao and Quigg, 2014).

~~The model~~GoMBio describes the following processes: 1) phytoplankton growth as a function of temperature, light, NO_3 and NH_4, including NH_4 inhibition of NO_3 uptake; 2) silicate limitation of PL growth; 3) photo-acclimation, 4) phytoplankton exudation, 5) ZS grazing on PS and PL, 6) ZL grazing on PS and PL, and predation on ZS, 7) zooplankton egestion and zooplankton excretion, 8) phytoplankton and zooplankton mortality, 9) nitrification, 10) detritus, DON and opal remineralization, 11) detritus, diatoms, and opal sinking, and 12) sediment coupled nitrification/denitrification (instantaneous remineralization~~, and 13) oxygen production and consumption~~. Processes 1, 3, 9, and 12 follow Fennel *et al.* (2006; 2011) formulations, while processes 2, 4-8, and 10-11 follow Kishi *et al.* (2007) formulations. Descriptions of the model equations and parameters are included in Appendix. Model parameter values are presented in Table 1.

The model domain encompasses the entire GoM and is based on the Regional Ocean Model System (ROMS) (Shchepetkin and McWilliams, 2005). The model's horizontal resolution is about 8 km and has 37 sigma-coordinate (bathymetry-following) vertical levels. Boundary conditions are Flather (Flather, 1976) and Chapman (Chapman, 1985) for the barotropic velocity and free surface, respectively, and a combination of radiation and nudging for the baroclinic velocity and tracers (Marchesiello et al., 2001). Tidal constituents were not included in the model. The open boundary nudging timescale is 4 days for the incoming signal and 90 days for the outgoing signal. A third order upstream scheme and a fourth order Akima scheme are used for horizontal and vertical momentum advection, respectively. Multidimensional positive definitive advection transport algorithm (MPDATA) is used for horizontal and vertical tracer advection (Smolarkiewicz and Margolini, 1998). Horizontal viscosity and diffusivity are set to 1 m^2 s^{-1}, increasing gradually to 4 m^2 s^{-1} in a 100 km wide sponge layer at the open boundaries to reduce signal reflection problems. Mellor and Yamada 2.5-level closure scheme is used for vertical turbulence (Galperin et al., 1988). Initial and open boundary conditions are derived from a 25 km-resolution Modular Ocean Model basin-scale model for the Atlantic Ocean (Liu et al., 2015), which includes the Tracers of Ocean Phytoplankton with Allometric Zooplankton (TOPAZ) as biogeochemical model (Dunne et al., 2010). Since TOPAZ does not include zooplankton as state variable, we assumed zooplankton correspond to 20% of the total phytoplankton biomass, assigning 30% to mesozooplankton and 70% to microzooplankton, assuming that the microzooplankton is the dominant zooplankton component near the model open boundaries for the Gulf of Mexico. Sensitivity simulations indicated that changes to those allocations do not affect greatly the derived plankton biomass patterns.

The model is forced with monthly surface water flux, daily shortwave and longwave radiation, and 6-hourly resolution air temperature, sea level pressure, humidity, and winds from the European Center for Medium Range Weather Forecast (ECMWF) ERA-Interim reanalysis product (0.75° resolution, Dee et al., 2011). Surface net heat flux and wind stress are estimated using bulk parameterization. River runoff from 54 river sources (35 in the US) is explicitly represented. Daily water discharges from US rivers were retrieved from the US Geological Survey (USGS) river gauges (https://waterdata.usgs.gov). Climatologies from Mexican river discharges were derived from He et al. (2011), Munoz-Salinas and Castillo (2015), and Martinez-Lopez and Zavala-Hidalgo (2009). Monthly observations of dissolved inorganic nutrients (nitrate, ammonia, silicate) and organic nitrogen in the MS-A Rivers were retrieved from the USGS (http://toxics.usgs.gov; Aulenbach *et al*., 2007). Following Yu *et al*. (2015), the MS-A particulate organic nitrogen (PON) was determined as the difference between unfiltered and filtered total Kjendahl nitrogen (TKN), while the dissolved organic nitrogen (DON) was estimated as the difference between filtered TKN and ammonia. Only 10% of the estimated DON was incorporated into the model as labile DON, considering that most of the observed MS-A DON corresponds to refractory material (Green et al., 2006). Riverine PON was assigned to the small detritus pool. For river sources other than the MS-A, dissolved inorganic nutrients and organic nitrogen concentrations are prescribed as climatological averages (USGS; Dunn, 1996; He *et al*., 2011; Livingstone, 2015). Because Submarine Groundwater Discharge (SGD) is a significant source of nitrogen off the west Florida shelf (Hu et al., 2006), we included SGD-NH_4 fluxes based on rates reported by Swarzenski et al. (2007). We assumed that SGD-NH_4 fluxes occurred in regions shallower than 30 m, decreasing exponentially from 0.694 mmol m^{-2} day^{-1} at 10 m (minimum model depth) to 0.069 mmol m^{-2} day^{-1} at 30 m. Surface photosynthetically active radiation (PAR) is assumed to be 43% of the surface shortwave radiation. Light attenuation includes a salinity dependent coefficient (K_{salt}) as in Fennel et al. (2011).

A 40-year model spin-up was completed before starting the historical simulation. To spin-up the model, we used the basin-model boundary conditions and the ERA surface fluxes of randomly selected years from 1979-2014, ~~Boundary conditions and surface fluxes for the model spin-up in each model year were extracted from a randomly selected year from the period 1979-2014,~~ following Lee et al. (2011). After spin-up, the model was run continuously from January 1979 until December of 2014, with monthly averaged fields saved.

3 Results

The ocean-biogeochemical model reproduces reasonably well main patterns of temperature, salinity, sea level anomaly, and eddy kinetic, and biogeochemical variables. A model-data comparison of selected physical variables is presented in Appendix. In the following section we perform a validation for chlorophyll, diatom to total chlorophyll ratio, primary production, and nutrients.

3.1 Biogeochemical model-data comparison

Modeled surface chlorophyll agreed qualitatively well in the spatiotemporal ~~reproduced reasonably well spatiotemporal~~ patterns ~~in~~ with the satellite chlorophyll (Fig. 2). The main differences between model and satellite chlorophyll are in the coastal region. Those differences can be explained (in part) by satellite chlorophyll overestimation, due to the high concentration of dissolved colored organic matter and sediments associated with river runoff (Hu et al., 2000; Del Castillo et al., 2001; Gilbes et al., 2002; D'Sa and Miller, 2003). The greatest chlorophyll concentration values are within the MS River delta, and the lowest values within the region influenced by the Loop Current. Significant seasonal differences are evident in the oceanic region, with minimum chlorophyll during summer (June-August), when thermal vertical stratification is the strongest, and maximum chlorophyll during winter (December-February) and early spring (March), concomitant with the greatest surface cooling and wind driven mixing (Muller-Karger et al., 1991; 2015). To compare temporal patters from model outputs and satellite observations, we derived monthly time series of chlorophyll in three regions: MS delta, Texas shelf and western part of the Louisiana shelf (for simplicity hereinafter refer to as Texas shelf), and the Deep Ocean area encompassing ~~86~~85.5°-92°W and 25°-27.5°N (see regions in Figure 1). The MS-delta and the Texas shelf are two productive regions strongly influenced by the MS-A river run-off, whereas the Deep Ocean box is an oligotrophic region often influenced by the Loop Current. The simulated chlorophyll time series are strongly correlated with the satellite chlorophyll time series, reproducing main seasonal and interannual patterns (Fig. 3). However, the model tends to underestimate the long-term mean of satellite chlorophyll in the MS delta and Texas shelf (the satellite chlorophyll to model chlorophyll ratio ranges from 1.98 to 2.80; see Table 2). An underestimation of model chlorophyll is also evident when we contrast the modeled time series with in situ observations from the Coastal Waters Consortium (CWC) during spring-summer (black dots in Fig. 3a), although the CWC and simulated chlorophyll tend to agree well during fall and winter, suggesting that satellite sensors could be overestimating surface chlorophyll in these two seasons. This is not surprising for shelf waters influenced by river runoff, as previous studies in the northern GoM have reported the satellite chlorophyll overestimates in situ chlorophyll from two to four times (e.g. Nababan et al., 2011). In the oceanic region, the simulated chlorophyll overestimates the long-term mean of SeaWiFS and MODIS chlorophyll by 12% and 22%, respectively, while in situ chlorophyll estimation based on APEX profiling float (black dots in Fig. 3c) closely match the model derived patterns.

We evaluated the model's ability to reproduce interannual patterns of chlorophyll by performing Empirical Orthogonal Decomposition of chlorophyll anomaly time series (anomaly refers to monthly outputs/observations with the monthly climatological mean subtracted). The first EOF (EOF1) of model chlorophyll is consistent with the EOF1 from SeaWiFS (Fig. 4a, b) and MODIS (not shown). EOF1 is eminently a coastal pattern, with the greatest values located near the MS-A deltas. The main differences between model and satellite EOF1 are located in the northwestern Florida region, where model chlorophyll is much lower than SeaWiFS chlorophyll, probably linked to a misrepresentation of the interannual variability in riverine nutrient load. The interannual variability of the first Principal Component (PC1) time series (which represents the temporal variability of EOF1) of model chlorophyll is well correlated to the PC1 time series of SeaWiFS (r = 0.66~~0.69~~) and MODIS (~~0.60~~ 0.59).

The model's skill in reproducing the patterns in phytoplankton composition is evaluated through the diatom to total chlorophyll ratios reported by Zhao and Quigg (2014) for two coastal stations off Louisiana (Stations A and B in Fig. 5a). The model tends to overestimate the diatom ratio in Station A (29.04°N-89.56°W) and underestimate it in Station B (28.59°N-92.00°), but the differences are reasonable small considering the large variability in the observed diatom ratios (Fig. 5b). This variability can be associated with strong mesoscale variability across the MS delta (e.g. Marta-Almeida et al., 2013), which is not reflected in the monthly outputs of our 8-km resolution model. In terms of temporal variability, the model is able to reproduce the observed decline in the diatom ratio during summer.

~~We compared the model-derived estimations of vertically integrated primary production with reported observations of phytoplankton production. The 1979-2014 average rates within the Louisiana shelf, Texas shelf, and open GoM (bottom depth > 1000 m) are 0.83, 0.37 and 0.24 g C m^{-2} d^{-1}, respectively. Those estimates are in reasonable agreement with rates derived from in situ observations. Lohrenz et al. (2013) reported mean production values of 1.10 g C m^{-2} d^{-1} in the north-central shelf, 0.33 g C m^{-2} d^{-1} off Texas, and 0.28 g C m^{-2} d^{-1} in the open Gulf. The greatest disagreement with Lohrenz et al. (2013) appears in the Louisiana shelf, where the model underestimates the mean production by 25%. Primary production patterns are strongly influenced by the MS-A river plumes, which are highly variable. Production values associated with the MS-A plumes exceed 1.5 g C m^{-2} d^{-1} (Fig. 5). Strong cross-shore gradients are observed during the spring in the Texas shelf, when prevailing easterly winds determine a westward and bottom advected MS-A river plume (Fig. 5a). Cross-shore gradient weakens during summer, when westerly winds promote up-coast flow that spreads the MS-A plume offshore (Fig. 5b). Distribution patterns over the Texas shelf are very consistent with the observations by Chen et al. (2000). They estimated maximum rates of ~1.6 g C m^{-2} d^{-1} near the MS-A delta region, and values <0.4 g C m^{-2} d^{-1} in the outer and western Texas shelves (see their Fig. 13).~~ Model-derived estimations of vertically integrated primary production were compared with observed rates, assuming a carbon to nitrogen ratio of 6.625 to express model production in g of carbon m^{-2} d^{-1}. The temporal variability of the simulated production rates agrees reasonable well with the observed seasonal pattern, though a model underestimation is evident during late summer (Fig. 6a). The interquartile range of model production is 0.87-1.5, 0.32-0.47, and 0.13-0.23 g C m^{-2} d^{-1} for the MS delta, Texas shelf, and Deep Ocean region, respectively, which are within the range of production estimated by Lehrter et al. (2009) in the northern shelf, and Biggs (1992) and Sanchez (1992) in the Deep GoM (Fig. 6b).

Simulated and observed time series of nitrate and silicate in Station C6 (28.86°N-90.46°W, Louisiana shelf) are shown in Figure 7a-b (observations only available for May-October). The seasonal change in surface nitrate is well reproduced by the model, which displays values >10 mmol m^{-3} during spring and <2 mmol m^{-3} in summer. On the other hand, the simulated surface silicate concentration show a poor agreement with the observed values, which in part could be explained by the relatively weak silicate seasonality and strong mesoscale variability over the Louisiana shelf. To further examine the ability of the model to reproduce coastal patterns in nitrate and silicate concentration on the Louisiana-Texas shelf, we evaluated the relationship between surface salinity and surface nutrient during spring-summer (Fig. 7c-d). Both nitrate and silicate show conservative mixing linked to the Mississippi and Atchafalaya river discharge. The model reproduces well the observed salinity-silicate relationship, while the similarity between the modeled and observed salinity-nitrate relationship is less clear. It is likely that additional number of observations is required to objectively visualize the observed pattern. However, our simulated salinity-nitrate relationship is consistent with observations by Sylvan et al. (2006) and modeling results by Fennel et al. (2011)(see their Figure 4).

Nitrate and silicate measurement collected in the most oceanic stations of the Mississippi and Tampa lines from GOMMEC cruises 1 and 2 were used to evaluate the model's ability to simulate nitrate and silicate patterns in the Deep GoM. The modeled nutrient profiles (red lines) reproduce well the depleted nitrate and silicate levels in the upper 30 m, as well as the strong vertical gradient linked to the nutricline over 30-300 m depth (blue dots) (Fig. 8a-d). Some model overestimation of nitrate and silicate is seen at depth > 300 m, but that bias most likely has a limited impact in the nutrient concentration at the upper 100 m layer. The better model-observation agreement is observed in the station at Tampa's line.

3.2 Phytoplankton biomass patterns

~~As expected from the spatial pattern of chlorophyll and primary production, nanophytoplankton and diatom biomass show the greatest values near the MS-A delta and smallest in the deep GoM (Fig. 6a,b). Diatom concentration maxima are located west of the MS birdfoot delta, and near the mouth of the Atchafalaya River. In contrast, nanophytoplankton peaks near the Atchafalaya Bay, and dominates phytoplankton biomass over the Texas shelf. The diatom to total phytoplankton biomass ratios varied within ~0.35-0.6 on the Louisiana-Texas shelf (Fig. 6c), which is a reasonable range considering that the observed diatom ratios vary within ~0.15-0.6 (Zhao and Quigg, 2014).~~

The model-data comparison shown in the previous section, along with the physical model validation presented in the Appendix, indicates that the model is able to reproduce dominant ocean-biogeochemical processes, and consequently could be used to explore the underlying factors modulating spatio temporal changes in diatom and nanophytoplankton biomass. In this section we describe the main seasonal patterns in phytoplankton biomass in the three selected regions shown in Fig. 1. Subsequently we examine the driving factors modulating the phytoplankton biomass seasonality.

~~Seasonal patterns in plankton biomass have important regional differences.~~ The model-derived patterns in plankton biomass have important regional differences in terms of seasonality. To illustrate this, we estimated monthly climatologies of phytoplankton concentration from the surface to 30 m depth (or bottom depth if <30 m) within the MS delta, Texas shelf, and Deep Ocean regions (Fig. 9a-c; regions depicted in Fig. 1). Total phytoplankton is the greatest during March-April in the MS delta and Texas shelf, ~~March-April in the Texas shelf~~ and February-March in the oceanic region, and smallest during August in the three regions. The timing and amplitude of the seasonal maxima differ significantly between phytoplankton components. In the MS delta, diatoms peak in ~~March~~February ~~driving the phytoplankton biomass increase during late winter - early spring~~ while nanophytoplankton peak in April-May. ~~The model derived diatom seasonality agrees with observations indicating greater diatom dominance during spring (Nelson and Dortch, 1996; Zhao and Quigg, 2014).~~ In the Texas shelf, the spring phytoplankton maximum is mainly driven by nanophytoplankton. Diatoms do not have a marked spring peak like in the MS delta, displaying two maxima in January (the greatest) and June. In the oceanic region, ~~nanophytoplankton drives the phytoplankton annual cycle, representing >90% of the total biomass, whereas diatoms do not have clear seasonality, displaying slightly smallest values during winter.~~ both nanophytoplankton and diatom peak in February, with nanophytoplankton clearly dominating upon diatom (>80%).

~~In the following sections we explore the underlying factors modulating spatio temporal changes in diatom and nanophytoplankton biomass. To this effect, we examine the driving factors of the specific growth rate variability, and investigate the changes in biomass production and losses.~~

3.2.1 Limitation factors and growth

To investigate the drivers of phytoplankton growth variability, we derive climatological patterns for the nutrient limitation factors (L_P; equations A1.5 and A2.7), the light limitation factors (f_P; equations A1.6 and A2.8), the temperature-dependent growth rates (V_p; equations A1.3 and A2.3), and the specific growth rate (SGR, which is the product of L_P, f_P and V_p). ~~We focus first on the mean spatial distribution of nutrient limitation, and then we analyze the seasonal patterns in nutrient limitation, light limitation, temperature-dependent growth, and specific growth rate.~~ It is important to note that the nutrient and light limitation factors ranges from 0 to 1, with 0 indicating non-growth and 1 indicating no limitation. This implies that growth limitation is inversely related to the limitation factors. ~~Mean spatial patterns for the nutrient limitation factor from diatom (L_{PL}) and nanophytoplankton (L_{PS}) are presented in Fig. 8. Since L_{PL} is defined as the minimum value between nitrogen limitation factor (NLF) and silica limitation factor (SLF), we also present the SLF:NLF ratio to identify regions where diatoms are silica limited (SLF:NLF<1) and nitrogen limited (SLF:NLF>1) (black contours in Fig. 8a). Nutrient limitation in diatoms markedly increases away from the MS-A delta, with L_{PL} varying from ~0.9 near the Atchafalaya Bay to <0.2 in the oceanic region (Fig. 8a). The SLF:NLF ratio indicates that diatoms are mainly N-limited in the northwestern and northeastern shelves, and Si-limited in the oceanic and delta regions (Fig. 8a). Nanophytoplankton is much less nutrient limited than diatoms. L_{PS} varies from ~1 in the Louisiana shelf to 0.35 in the deep GoM (Fig. 8b), while the L_{PS}/L_{PL} ratio ranges from ~1.5 to >10 in the deep GoM (not shown). This explains the pronounced offshore decline in the diatom contribution to total phytoplankton (Fig. 6c).~~ Seasonal changes in L_{PS} and L_{PL} for the MS delta, Texas shelf, and Deep Ocean are depicted in Fig. 10a, b. In the MS delta and Texas shelf, the model nutrient-limitation factors are the greatest (i.e., the weakest limitation) during February-April ~~late winter and spring~~, and the smallest (i.e., the strongest limitation) during September-October ~~fall~~, reflecting the seasonality in river discharge along the northern shelf (the maximum river discharge in Louisiana and Texas is during April and March, respectively, and the minimum in August-September). A secondary peak in the nutrient limitation factors is observed during ~~summer~~ July in the Texas shelf, which can be related to wind-driven upwelling and a secondary peak in river discharge during summer. In the Deep Ocean region, the nutrient-limitation factors are maxima during January-March ~~winter~~ and minima during July-October ~~summer~~, a pattern associated with the seasonal cycle in thermal stratification and mixing (enhanced mixed in winter, enhanced stratification in summer). Significant differences exist between the magnitude of L_{PS} and L_{PL}. The L_{PS}/L_{PL} ratio is ~1.5 in the MS delta, ~2 in the Texas shelf, and ~3 in the deep GoM. Unlike nanophytoplankton, diatoms can be considerably nutrient limited in the MS delta region. ~~The L_{PS}/L_{PL} ratio is ~1.5 in the MS delta, ~1.9 in the Texas shelf, and ~6-15 in the deep GoM. The SLF:NLF ratio (Fig. 7c) indicates that diatoms are mostly nitrogen limited in the Texas shelf, and silica limited in the Deep Ocean. In the MS delta, diatoms are more silica limited during January-April, and more nitrogen limited during May-December. Still, the SLF:NLF ratio is close to 1 during December-June, indicating that both silica and nitrogen limitation can be important.~~ The monthly climatologies of the silica to nitrogen limitation ratio (SLF:NLF) is used to evaluate whether diatoms are nitrogen limited (SLF:NLF>1) or silica limited (SLF:NLF<1)(Fig. 10c and Fig. S10 in Appendix). Overall SLF:NLF is predominantly >1 in the three regions, implying that diatoms are mainly nitrogen limited. However, SLF:NLF shows values near or smaller than 1 during December-April in the deep Gulf, and during February-April in the MS delta, indicating that both nitrogen and silica can limit model diatom growth.

Besides nutrients, light and temperature influence model phytoplankton growth. The strongest light limitation is in the MS delta, and the weakest is in the deep GoM (Fig. 10d-e), but the regional differences in light-limitation are much smaller than those for nutrient-limitation. Seasonally, light limitation is weakest during April in the coastal regions, and May in the Deep Ocean. Conversely, light limitation is the strongest during August and December-January in the coastal regions, and December-January in the Deep Ocean. In the coastal regions, the decline in light limitation during June-August ~~summer~~ can be linked to increased light attenuation, driven by the offshore spread of low-salinity and phytoplankton-rich waters by wind-driven upwelling. The temperature-dependent growth rate (V_p) displays the largest amplitude in the coastal regions, with a maximum in August and minimum in January-February (Fig. 10f-g). The ratio between the maximum and minimum V_p is ~2.3 in the coastal regions and ~1.4 in the Deep Ocean.

The interplay among nutrient, light and temperature conditions determines the model phytoplankton specific growth rate (SGR). The seasonal pattern in the SGR shows differences between coastal and oceanic domains (Fig. 10h-i). In the coastal regions, the inverse relationship between V_p and both light and nutrient limitation factors during March-August ~~spring-summer~~ determines the greatest SGR in June-July, while the small V_p and light limitation factors during December-February ~~winter~~ determine the minimum SGR in December-January. ~~In the Deep Ocean region, the SGR seasonality for nanophytoplankton (diatoms do not show a clear seasonal pattern) is mainly driven by nutrient and light limitation. The maximum SGR is in March, resulting from a trade-off between nutrient and light conditions during winter-spring, and the minimum SGR is in June-August, driven by the strong nutrient limitation during summer.~~ In the Deep Ocean region, the

SGR seasonality is mainly driven by nutrient and light limitation. The maximum SGR is in February (concomitant with the maximum nutrient limitation factor) while the minimum SGR is in June-August, the latter driven by the strong nutrient limitation during summer.

3.2.2 Biomass sources and losses

Now we explore how the patterns in phytoplankton production and losses influence the patterns in phytoplankton biomass. We showed that the model SGR is the maximum during June-July in the coastal regions, and February in the Deep Ocean (Fig. 10h-i). We may expect that the seasonal changes in production reflect the changes in SGR, since production is the product between SGR and phytoplankton biomass. The link between SGR and production is evident in the Deep Ocean, as SGR and production have maxima in February and minima during ~~summer~~ July-September (Fig. 11c). However, in the MS delta and Texas shelf, the simulated production peaks occur 2-3 months earlier than the SGR peaks (Fig. 11a, b). This necessarily implies that biomass losses due to biological (grazing, mortality, exudation) and physical (advection/diffusion) processes play an important role modulating production seasonality during spring-summer.

To evaluate how biologically driven processes influence the seasonal patterns in model phytoplankton biomass, we calculated the balance between production and biological losses (hereinafter the ‘biological term’; Fig. 11d-f). The biological term displays distinct patterns for each phytoplankton component and region. The maximum biological term for diatom is in January-February in the MS delta, December-January in the Texas shelf, and February in the Deep Ocean, while the maximum biological term for nanophytoplankton is in April in the MS delta, February in the Texas shelf, and January in the Deep Ocean. The biological term for diatoms and nanophytoplankton begins to decline before the production maximum. Moreover, in the Texas shelf, the biological term is negative during the production maximum. In the three regions, the biological term for total phytoplankton (diatoms plus nanophytoplankton) is positive in November-February ~~fall-winter~~, has a marked decline in spring, and is negative in May-August ~~summer~~. The seasonality of the biological term contrasts with the pattern in the SGR in the MS delta and Texas shelf, as SGR is minimum in December-January ~~winter~~ and maximum in June ~~summer~~. All these features suggest that the seasonal changes in model phytoplankton biomass are strongly modulated by biological losses. Zooplankton grazing is the dominant biological loss term (Fig. 11g-i), markedly prevailing upon mortality and exudation (not shown). Microzooplankton exert the strongest grazing pressure on nanophytoplankton biomass, and mesozooplankton on diatoms, with the grazing patterns closely following the patterns in production. The seasonal patterns for microzooplankton (mesozooplankton) grazing upon nanophytoplankton (diatoms) closely follow the patterns in nanophytoplankton (diatom) production. Peaks in micro- and mesozooplankton grazing are concomitant or lag by 1 month the peak in nanophytoplankton and diatom production.

The seasonal patterns in the biological term do not completely explain the seasonal changes in model phytoplankton biomass. To fully elucidate the ~~net~~ local phytoplankton biomass change, the role of advection and ~~diffusion~~ vertical mixing as driver of biomass fluxes need to be examined. To this effect, we estimate the variability term representing advection and turbulent diffusion of phytoplankton biomass, hereinafter the physical term, and compare it with the biological term (Fig.

12a-c). The balance between these two terms determines the local rate of change of phytoplankton biomass ~~net phytoplankton growth change~~. The physical and biological terms are generally inversely related, implying that the biologically driven changes tend to be offset by the physically driven changes. Besides, the biological term is generally larger than the physical term, and consequently the sign of the local rate of change ~~net phytoplankton growth~~ is mainly determined by the biological component. ~~The few exceptions are the negative growth during May in the MS delta, October in the Texas shelf, and April and November in the Deep Ocean region. In these cases the physical term not only influence the amplitude of the monthly biomass change but the timing of the seasonal maxima.~~ The few exceptions are the positive growth during September in the MS delta, April and September in the Texas shelf, and the negative growth in March-April in the Deep Ocean region. In the last case the physical term not only influence the amplitude of the monthly biomass change but the timing of the seasonal maxima. In the MS delta, the greatest magnitude for the physical term is during January-April, representing biomass losses mostly linked to horizontal advection (Fig. 12d). The advection can be related to the downstream export of phytoplankton rich water associated with the MS river plume. A substantial fraction of phytoplankton biomass from the MS-A delta is transported to the Texas shelf, which explains the positive physical term during March-June (Fig. 12b,e). In the Deep Ocean, the greatest magnitude for the physical term is in ~~November-March~~ December-February, representing biomass losses mainly driven by turbulent vertical diffusion (Fig. 12c,f). The close similitude between the physical and biological terms magnitude determines a much smaller local rate of change ~~net growth~~ in the Deep Ocean than in the coastal regions (about 1 order of magnitude).

4 Discussion

~~We configured a 14-component model that explicitly considers two types of phytoplankton and zooplankton, and nitrogen and silica as limiting nutrients for phytoplankton growth. Inclusion of two phytoplankton components allowed for a realistic representation of the cross-shore gradients in biomass and chlorophyll. The model chlorophyll reproduced the temporal variability without significant seasonal bias. The good agreement between the model outputs and observations of chlorophyll and primary production provides confidence in the model's ability to represent seasonal phytoplankton dynamics. Our model can be used to further advance ecological modeling capabilities, such as ecosystem responses to natural and anthropogenic disturbances in the GoM. We recognize that additional components and processes could be included in the model, such as phosphorus cycling and nitrogen fixation, to represent more realistic biogeochemical dynamics. Nevertheless, we believe that the current model configuration captures well enough the seasonal dynamics of diatoms and nanophytoplankton biomass in the GoM, which is the main goal in the present study.~~

We configured an ocean-biogeochemical model for the GoM that explicitly represents two types of phytoplankton and zooplankton, and nitrogen and silica as limiting nutrients for phytoplankton growth. Our model reproduces reasonable well the main physical and biochemical patterns, although an underestimation of the mean surface chlorophyll is evident in the northern shelf, especially on bottom depth < 20 m. A comparison with in situ chlorophyll observations suggests that part of the model-satellite chlorophyll disagreement could be linked to chlorophyll overestimation by satellite sensors during fall-winter. Realistic representations of phytoplankton variability in region with strong physical and biochemical gradients, like those in the northern GoM, are challenging. Previous modeling efforts on the Louisiana-Texas shelf based on Fennel's model reproduced better the mean satellite chlorophyll condition than our model (e.g. Fennel et al., 2011; Laurent et al., 2012). However, Fennel's model tends to overestimate satellite chlorophyll by a factor of >3 in the Deep Ocean region during winter, which could be linked to misrepresentation of microzooplankton grazing (see section 4 in Appendix). We acknowledge that additional components and processes could be included in our model, such as phosphorus cycling, iron limitation and nitrogen fixation, to represent more realistic biogeochemical dynamics. We also recognize that more observational studies will be required to constrain better our model parameters, as well as the biogeochemical fluxes between land and ocean. Nevertheless, we believe that the current model configuration can capture well enough the seasonal dynamics of diatoms and nanophytoplankton biomass in the GoM. It is known that variations in phytoplankton composition can have important repercussion for the ecosystem, including changes in upper trophic levels dynamics, carbon export (carbon export is enhanced in diatom-dominated food webs) and bottom hypoxia (Dagg et al., 2003; Green et al., 2008). Therefore, modeling efforts exploring variability in phytoplankton component, such as this study, are needed to advance our understanding of ecosystem variability in the GoM.

We examined the main model phytoplankton biomass patterns and explored the underlying factors explaining biomass variability following a similar approach to that used by Fennel et al. (2011). We used a constant depth layer (0-30 m), whereas Fennel et al. (2011) calculated seasonal patterns in a seasonally variable mixed layer depth (~10 m in summer to ~40 m in winter). We chose a constant depth layer because it makes the biomass budget analysis more straightforward. It is also worthwhile to mention that an important fraction of primary production can be distributed below the mixed layer in spring-summer (Yu et al., 2015). ~~The seasonal cycle for phytoplankton biomass in the 0-30 m layer differs in some degree from the seasonal cycle at surface (or in the mixed layer), with the latter showing a less pronounced biomass decline during late spring in the coastal regions (Fig. 12).~~ Our growth limitation analysis compared distinct regions in terms of phytoplankton production and river runoff influence, including the oligotrophic deep GoM, a region that has received less attention in previous modeling studies. ~~Diatoms are strongly silica limited in the deep GoM, nitrogen limited in most of the northern shelf, and both silica and nutrient-limited near the MS-A deltas. In the MS-A deltas, silicate limitation prevails during January-April, and nitrogen limitation during July-November, which agrees well with observations of severe silica depletion during spring, and nitrogen limitation during summer (Dortch and Whitledge, 1992; Nelson and Dortch,1996).~~ We obtained that nutrient limitation displayed the largest spatial differences compared to other limiting factors (light and temperature). Although the model indicated that the main limiting nutrient for model diatom is nitrogen, silicate also can limit model diatom production in the deep GoM during winter, and during spring in the MS delta. The latter agrees with observations of severe silica depletion during spring in the Louisiana shelf (Dortch and Whitledge, 1992; Nelson and Dortch, 1996). Although observational studies suggested the occurrence of silica limitation in the MS delta decades ago with a potential link to anthropogenic-driven declines in the MS river Si:N ratio (Turner and Rabalais, 1991), this is the first modeling study to evaluate the role of silica as driver of diatom growth in the region. The implication for silica and nitrogen limitation in the Louisiana-Texas shelf is that changes in the MS-A river nutrient load can modulate changes in diatom production, influencing phytoplankton composition. ~~Changes in phytoplankton composition can have important repercussion for the ecosystem, including changes in upper trophic levels dynamics and carbon export (carbon export is enhanced in diatom-dominated food webs). The latter may influence bottom hypoxia variability, as suggest by Dagg et al. (2003) and Green et al. (2008), and is an aspect that needs to be addressed in a future modeling study.~~

The simulated SGR patterns showed important difference between coastal and oceanic domains. Nutrients, light, and temperature are important in modulating the seasonal SGR changes on the northern shelf, while nutrients and light are the dominant factors driving the SGR seasonality in the deep GoM. The monthly averages for the SGR in small and large phytoplankton range within 0.28-0.85 and 0.18-0.57 day^{-1} in the coastal regions, with the maximum (minimum) values in ~~summer~~ June-July (~~winter~~December-January). These SGR values are within the observational range reported by Fahnestiel et al. (1995), and similar to model estimations by Fennel et al. (2011). In the oceanic region, the SGR range for nanophytoplankton is 0.17-0.40 day^{-1}, with the maximum (minimum) values in ~~late winter and early spring~~ February-March (~~summer~~June-September)~~.~~ Consistent with Fennel et al. (2011), we found that zooplankton grazing plays a leading role modulating phytoplankton biomass seasonality. This is especially evident in the coastal regions, where the balance between production and biological losses gives negative values (biomass decrease) in summer, and positive values (biomass increase) in winter, i.e. opposite to the pattern in the SGR. ~~The role of zooplankton grazing as driver of phytoplankton seasonality has received increased attention in recent years. Behrenfeld (2010) proposed that increasing mixed layer depth (and consequently zooplankton and phytoplankton dilution) leads to decreased grazing pressure during winter, resulting in a net population increase. Behrenfeld (2010) developed the Dilution-Recoupling hypothesis to explain the spring algal blooms in the North Atlantic, emphasizing the role of the biomass loss terms as drivers of net phytoplankton growth. This view challenged the prevailing Critical Depth hypothesis, which emphasizes the role of stratification, nutrients, and light as drivers of SGR and net phytoplankton growth (Gran and Braarud, 1935; Sverdrup, 1953). Our seasonal patterns in production, grazing and phytoplankton net growth are consistent with Behrenfeld's hypothesis, supporting the idea that phytoplankton seasonality is to an important degree top-down controlled.~~

Our study examined the coupled role of biologically (production and biological losses) and physically (advection and ~~diffusion~~ vertical mixing) driven biomass fluxes. Previous studies suggested the importance of advection and diffusion as driver of biomass changes in the GoM (e.g. Dagg et al., 2003; Green et al., 2008; Fennel et al., 2011). However, a quantification of these dynamics in biogeochemical model has not been done in the region. We found that the seasonal patterns in model phytoplankton biomass are largely determined by small imbalances between biologically and physically driven fluxes, the latter mainly associated with horizontal advection in the Louisiana-Texas shelf, and turbulent vertical diffusion in the deep GoM. Consequently, we cannot obtain a proper understanding of biomass seasonality when the physically driven biomass fluxes are excluded from the analysis. Disentangling the processes influencing phytoplankton seasonality is a complex task, as the mechanisms acting as physical loss terms can also influence the balance between production and biological losses. That is the case for turbulent vertical diffusion, which modulates the vertical distribution of nutrients (impacting on phytoplankton production) and zooplankton (impacting on zooplankton grazing)(Behrenfeld, 2010).

Finally, future projections of environmental scenarios suggest substantial increases in both river runoff and thermal stratification in the northern GoM due to anthropogenic climate change (Tao et al., 2014; Liu et al., 2015). Therefore, how such environmental disturbances acting at multiple timescales can alter the subtle imbalances between primary production and biological losses (or between biological and physical driven biomass fluxes) is a topic that deserves further attention.

5 Summary and Conclusions

A coupled ocean-biogeochemical model was configured for the GoM to examine underlying mechanisms determining spatial and seasonal variability in diatoms and nanophytoplankton biomass. We investigated the factors modulating the specific growth rate (SGR), and explored the seasonal changes in biologically and physically driven biomass fluxes. We found that model diatoms growth was ~40% and ~~>95%~~ >80% nutrient-limited in the Louisiana shelf and deep GoM, respectively, whereas model nanophytoplankton growth was ~10% and 40-85%~~40-80%~~ limited. ~~These differences strongly influenced the diatom contribution to total phytoplankton, which ranged from 50% near the MS delta to <10% in the deep GoM. Nutrient limitation for diatoms was mainly due to Si in the deep GoM, Si and N in the MS delta, and N elsewhere.~~ Our model indicates that diatom growth is mainly limited by nitrogen. However, silica limitation can occur in the deep GoM during winter, and in the MS delta during spring. The interplay among nutrient, light, and temperature determined the SGR seasonal timing (max/min) in the Louisiana-Texas shelf, while nutrient and light determined the simulated SGR seasonal timing in the deep GoM. Primary production in the model was driven by changes in SGR, but also influenced by biomass losses linked to zooplankton grazing. Moreover, the balance between primary production and biological losses revealed top-down control of phytoplankton growth. The physically driven biomass fluxes, mainly associated with horizontal advection in the Louisiana-Texas shelf and turbulent vertical diffusion in the deep GoM, played a key role modulating amplitude and phase in the seasonal phytoplankton biomass cycle. These results stress the importance of an integrated analysis of biologically and physically driven biomass fluxes to better characterize phytoplankton biomass phenologies.

Authors contributions

S-KL and FAG designed the study. FAG configured the model and performed the model simulations. FAG wrote the paper with contributions from all the authors.

Conflicts of interests

The authors declare that they have no conflict of interest.

Acknowledgments

We would like to thank Chris Kelble for his thoughtful comments and suggestion. This work was supported by the Northern Gulf Institute (NGI) and by the base funding of NOAA AOML

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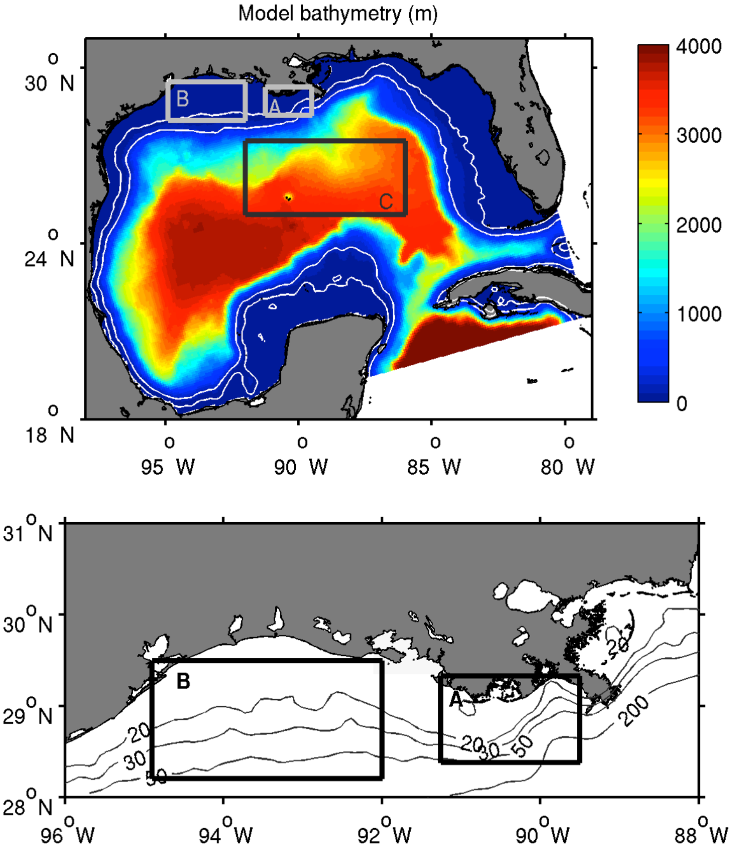


5 **Figure 1: Model domain and bathymetry. Polygons A, B, and C depict the MS delta, Texas shelf, and Deep Ocean region, respectively, selected to describe plankton patterns. Gray contours show the 20, 30, 50, and 200 m isobaths.**

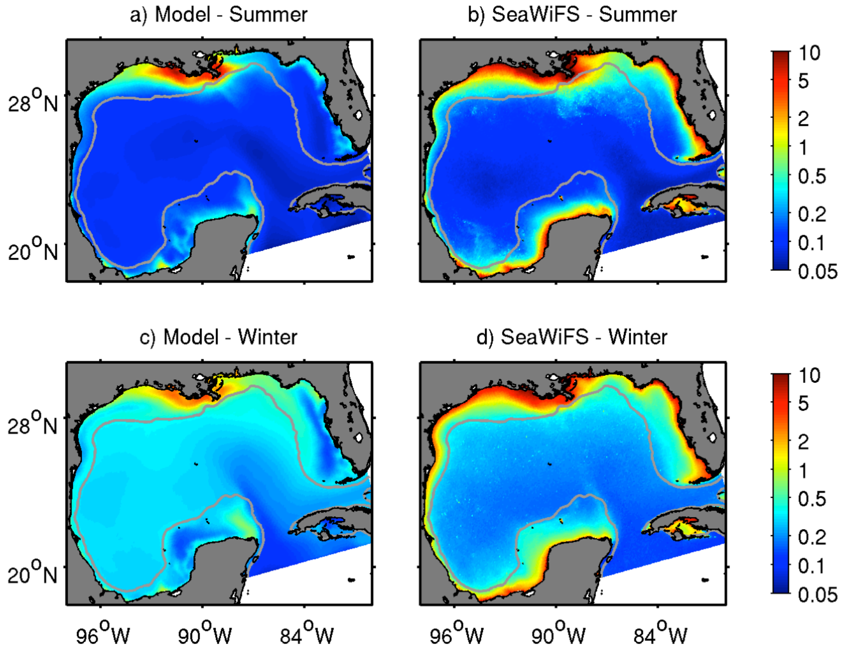
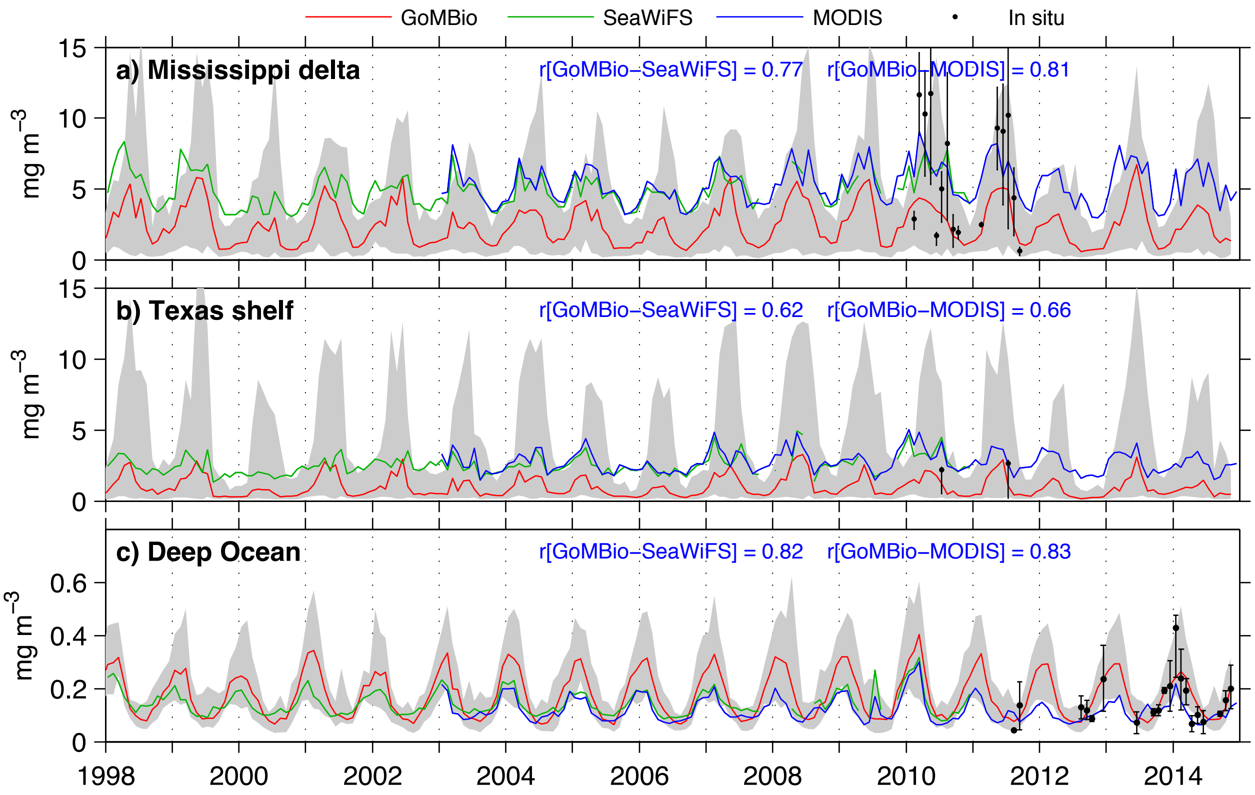


Figure 2: Spatial patterns of model and satellite chlorophyll. Comparison between surface chlorophyll concentration (mg m^{-3}) derived from model outputs (a, c) and SeaWiFS (b, d) during summer and winter. Gray line depicts the 200 m isobath.



5 Figure 3: Monthly chlorophyll time series derived from model (GoMBio, red line), SeaWiFS (green line), and MODIS (blue line). Grey area depicts the model chlorophyll range. Correlation coefficient between model and satellite time series is indicated at each panel. Black dots with vertical bars depict the monthly mean and inter-quartile range of in situ chlorophyll from the Coastal Waters Consortium dataset (panels a and b) and APEX profiling floats (Lagrangian Approach to Study the Gulf of Mexico Deep Circulation project, panels c). Ticks on the ordinate mark January 1st of each year.

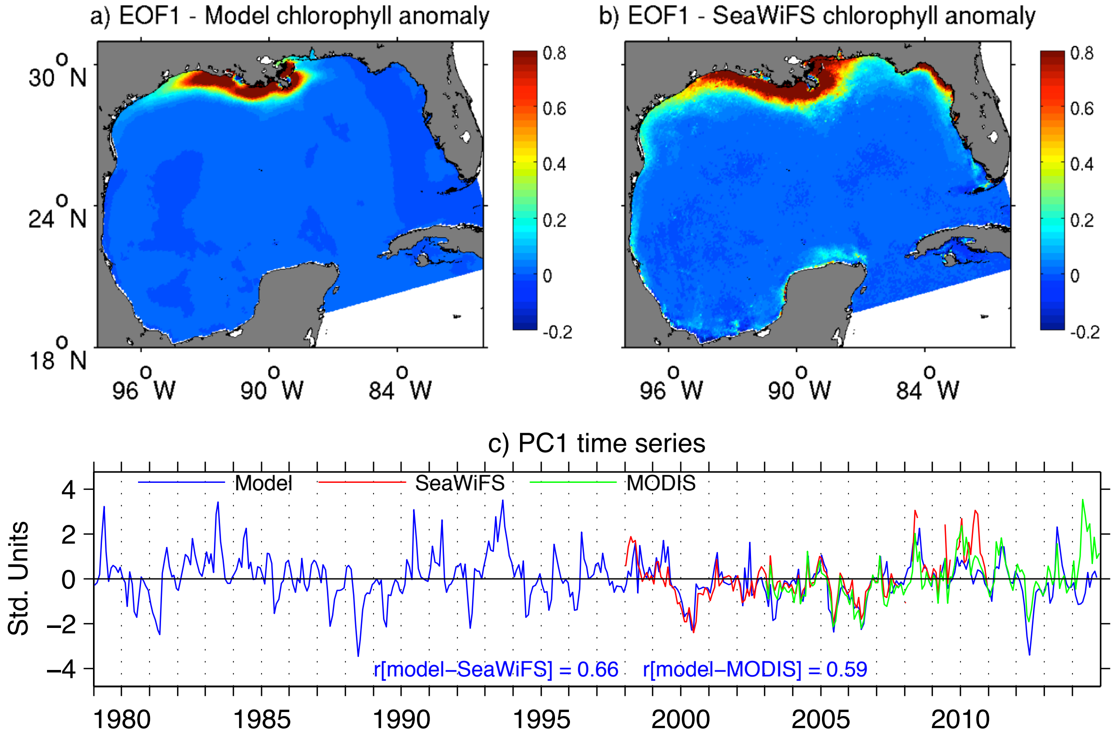


Figure 4: EOF analysis of chlorophyll anomalies. a, b) First EOF mode of surface model chlorophyll (a) and SeaWiFS chlorophyll (b). c) Principal component associated with the first EOF mode of model, SeaWiFS, and MODIS chlorophyll. Correlation coefficient between model and satellite PC1 series is indicated in panel c.

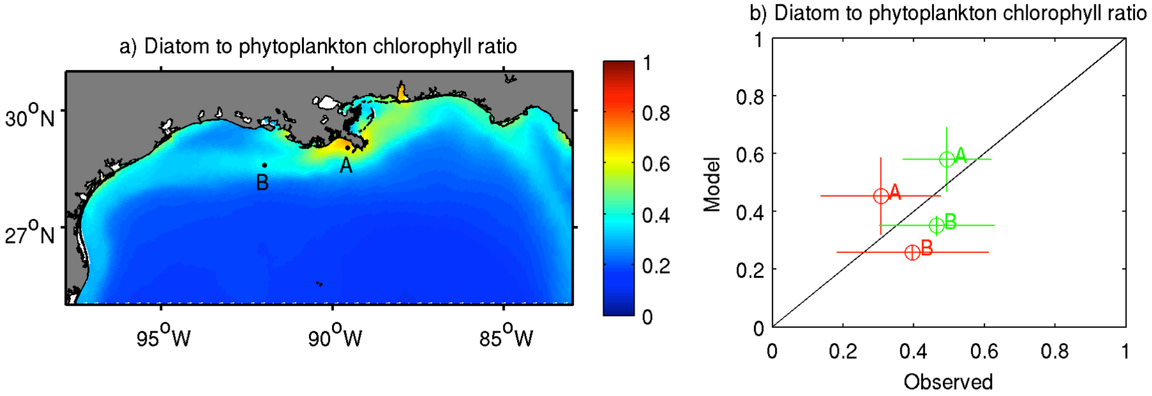


Figure 5: Chlorophyll ratios. a) Climatological mean of the diatom to total phytoplankton ratio of chlorophyll; (b) Comparison between observations and model-derived diatom to total phytoplankton ratio of chlorophyll in the Louisiana shelf (coastal stations A and B depicted in panel a) during April (green) and August (red) of 2010-2012. Vertical and horizontal bars depict ±1 standard deviation. Mean and standard deviation of observed chlorophyll ratio are derived from values reported by Zhao and Quigg (2014).

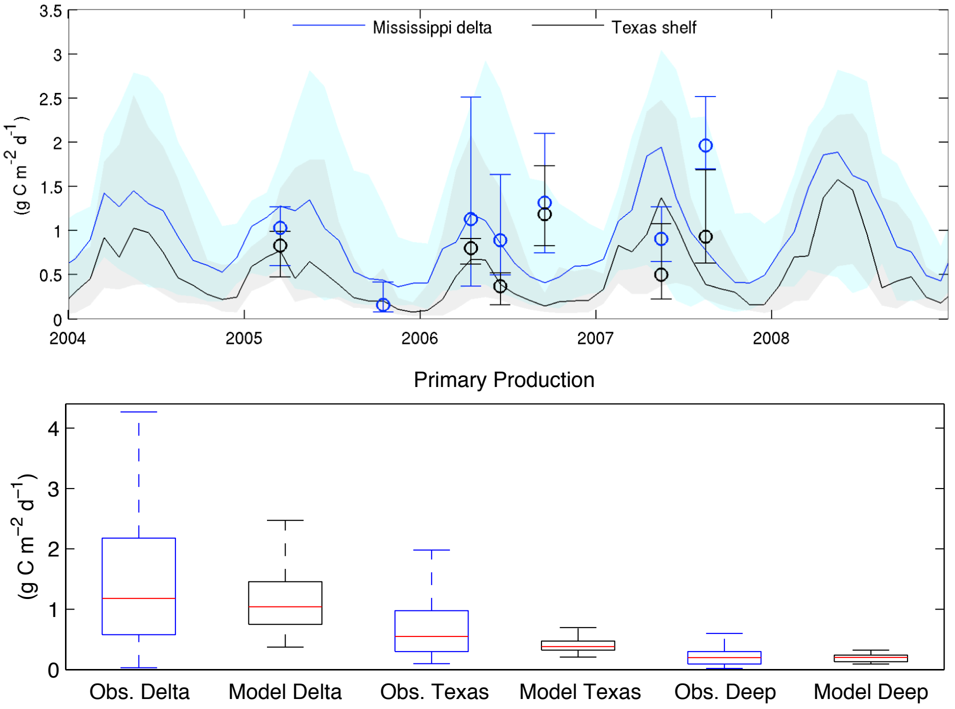


Figure 6: a) Modeled and observed time series of primary production for the Mississippi delta and Texas shelf; grey and light blue shades depict the model production ranges for the Mississippi delta and Texas shelf, respectively; b) boxplots of primary production in the Mississippi delta, Texas shelf, and Deep Gulf region derived from observations and model (GoMBio) outputs during spring-summer. Red lines, bottom and top edges of the boxes, and whiskers represent the median, interquartile interval, and non-outlier range, respectively.

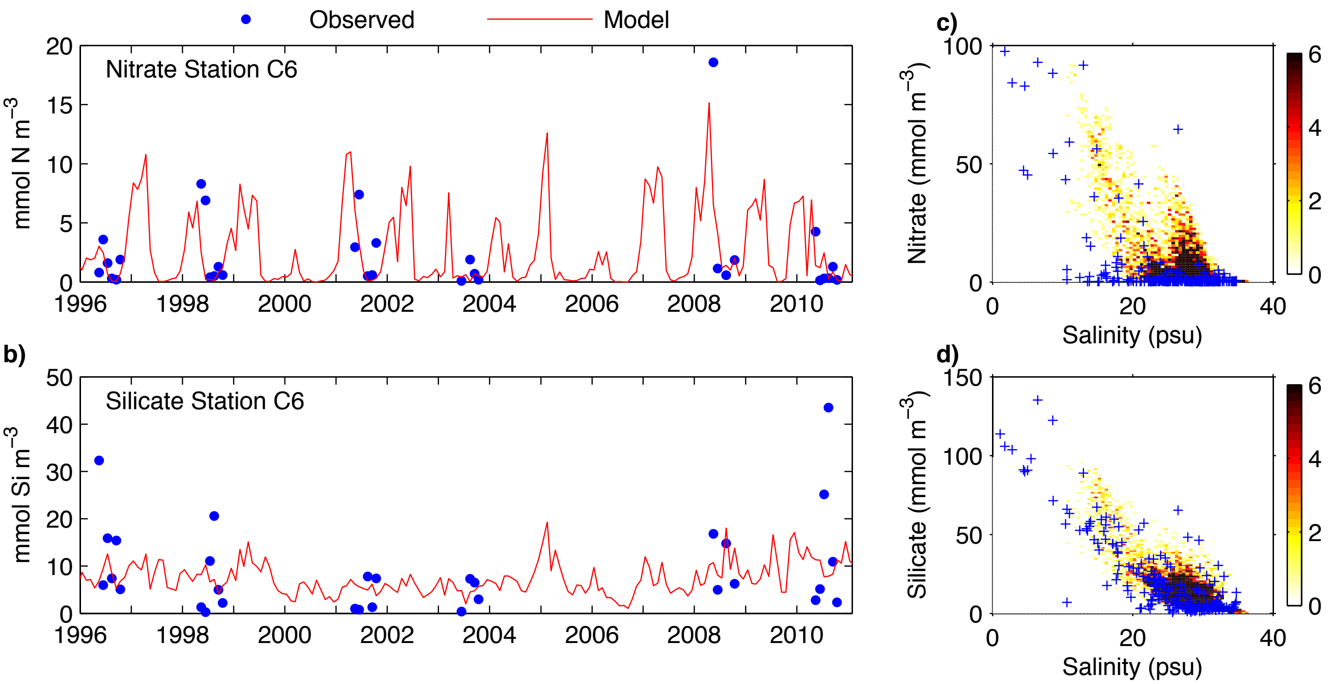


Figure 7: a-b) Model-data comparison of nitrate and silicate time series at Station C6 (28.86°N, 90.46°W); c-d) relationship between surface salinity and both nitrate and silicate concentration over the Louisiana-Texas shelf. Modeled values are shown as 2-dimensional histogram (color scale) and observations as blue marks.

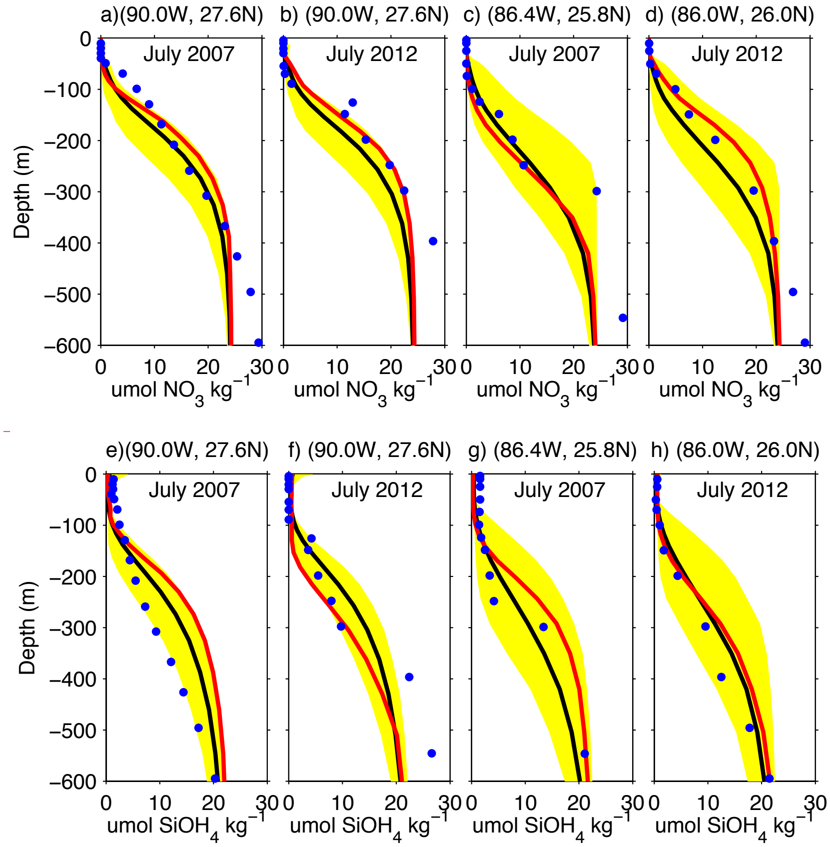


Figure 8: Comparison between profiles of nitrate and silicate derived from model outputs (red lines) and GOMECC data (blue dots). The model's climatological mean and range for July are also shown as black line and yellow area, respectively. Panels a, b, e and f (c, d, g and h) show the profiles associated with the most oceanic station from the Mississippi (Tampa) line for GOMECC cruises 1 (July 2007) and 2 (July 2012).

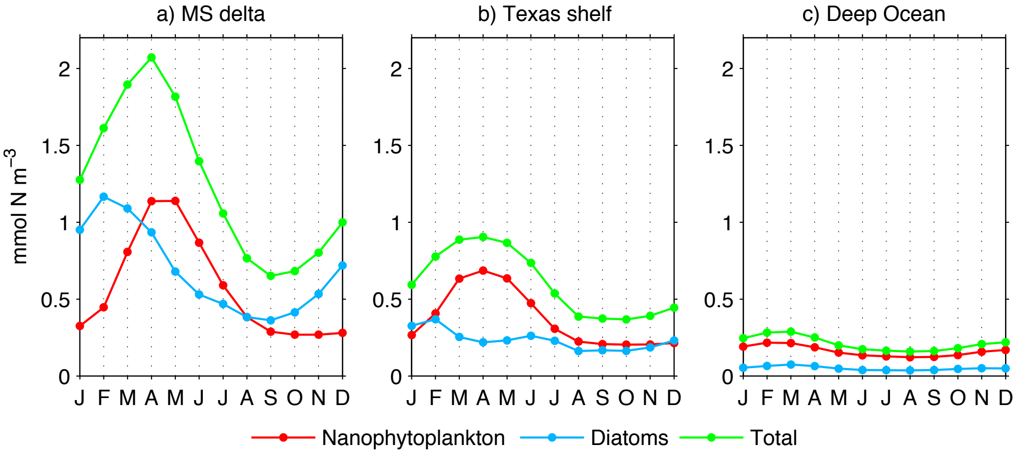


Figure 9: Climatological seasonal cycle of phytoplankton biomass in the 30 m upper layer from the Mississippi delta, Texas shelf, and Deep Ocean (regions depicted in Fig 1, gray polygons).

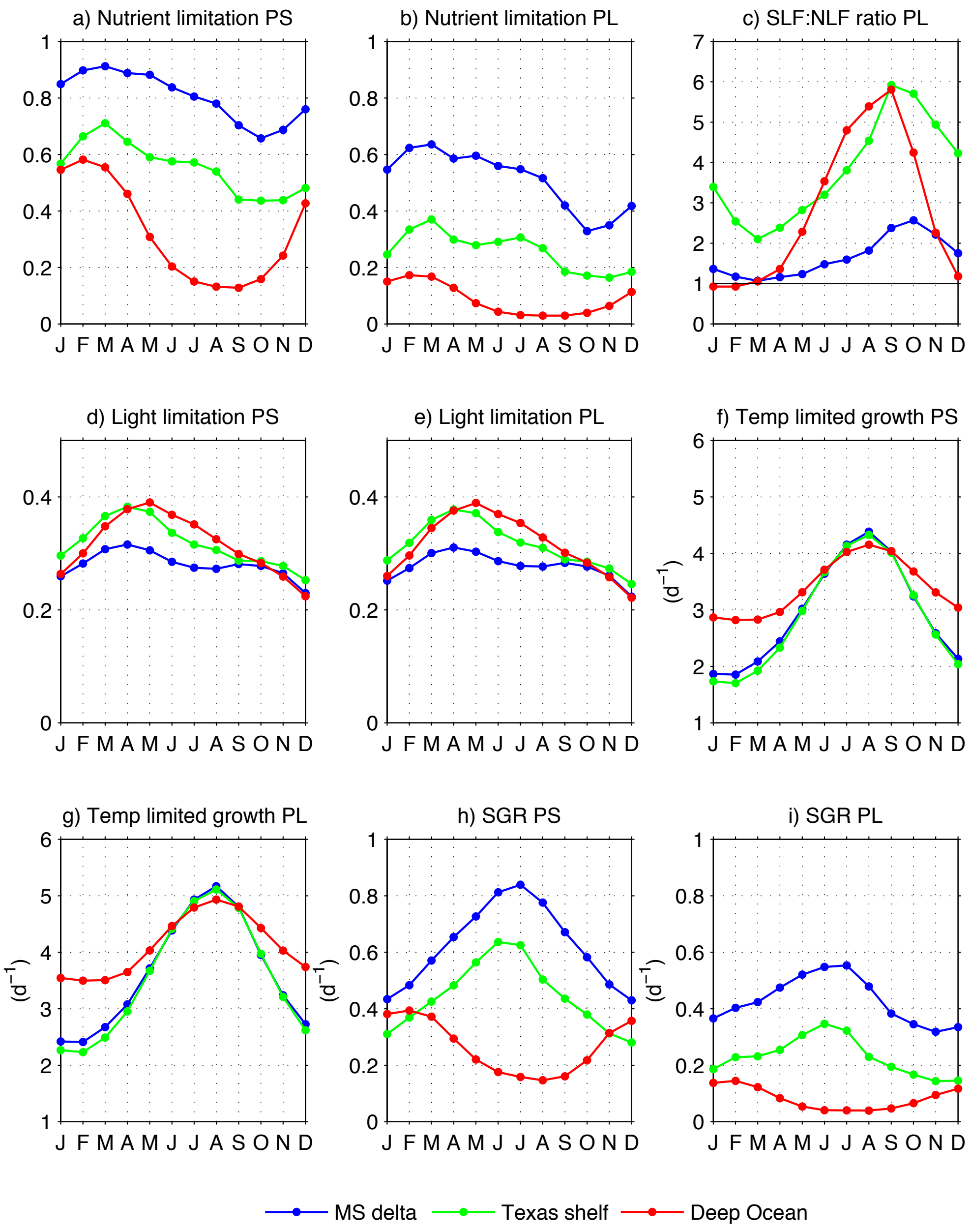


Figure 10: Growth limitation and specific growth rates for nanophytoplankton (PS) and diatoms (PL): a-b) nutrient limitation factors; c) silica to nitrogen limitation ratio (SLF:NLF; for diatoms only); d-e) light limitation factors; f-g) temperature-dependent growth; h-i) specific growth rates. Factors were averaged in the upper 30 m layer from the Mississippi delta, Texas shelf and Deep Ocean regions (depicted in Fig 1, gray polygons).

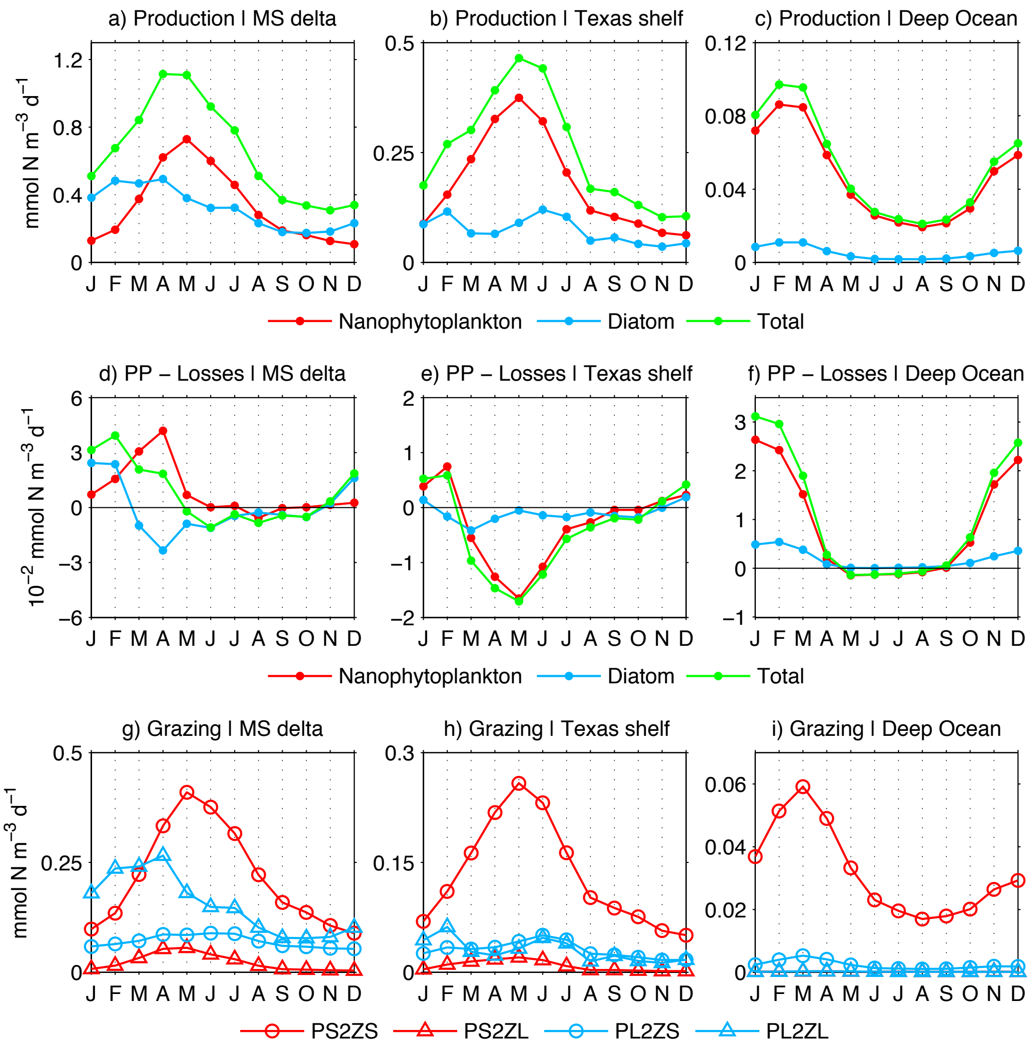


Figure 11: Phytoplankton production, production minus losses (biological term), and grazing estimated for the upper 30 m layer of the Mississippi delta (left), Texas shelf (middle) and Deep Ocean (right) (regions depicted in Fig 1, gray polygons). Grazing terms are microzooplankton upon nanophytoplankton (PS2ZS) and diatoms (PL2ZS), and mesozooplankton upon nanophytoplankton (PS2ZL) and diatoms (PL2ZL).

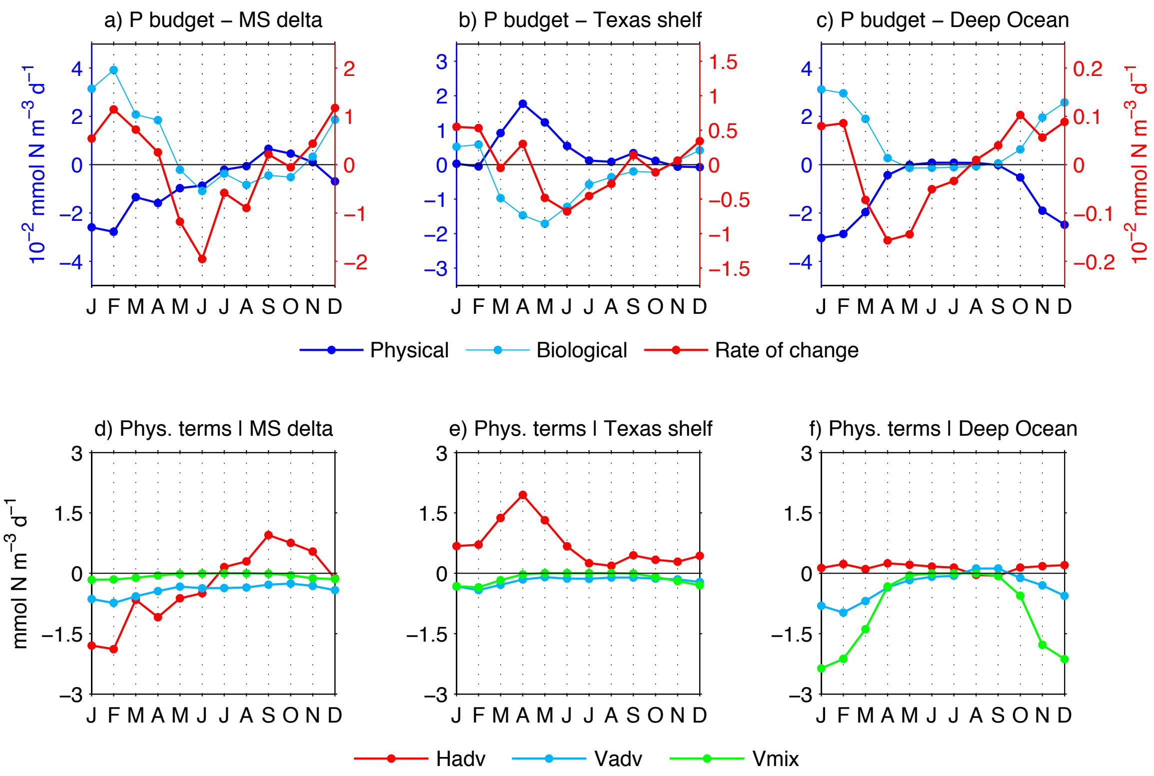


Figure 12: a-c) Phytoplankton biomass budget: the physical term represents advection plus diffusion, the biological term is production minus biological losses, and ~~net growth (change rate)~~rate of change is the balance between the physical and biological terms. Right y-axis (red) is for net growth, and left y-axis (blue) is for the physical and biological terms. d-f) Physical terms components: Hadv, Vadv, and Vmix correspond to horizontal advection, vertical advection, and vertical mixing, respectively. Patterns are averages within the upper 30 m ocean layer from the Mississippi delta, Texas shelf and Deep Ocean (regions depicted in Fig. 1). Horizontal mixing can be neglected in the budget analysis, as it is 2 orders of magnitude smaller than other physical terms components.

Table 1. Model parameter values

Parameter	Name			Source
	Phytoplankton parameters	SP	LP	
V_{max}	Maximum photosynthetic rate at 0°C (d^{-1})	0.52	0.78	a, b, *
k_{Gpp}	Temperature coefficient for photosynthesis $(°C)^{-1}$	0.0693	0.0615	a
α_P	Initial slope of the P-I curve (m^2 W^{-1}) d^{-1}	0.028	0.035	b
KNO_3	Half saturation constant for nitrate (mmol N m^{-3})	1.0	3.0	a
KNH_4	Half saturation constant for ammonium (mmol N m^{-3})	0.1	0.5	a
KSi	Half saturation constant for silicate (mmol Si m^{-3})	-	3.0	a
θ_{max}	Maximum chlorophyll to carbon ratio	0.0428	0.0535	b, c, *
φ_P	Phytoplankton ratio extracellular excretion	0.08	0.08	a
PMor	Mortality at 0°C (m^3 $mmolN^{-1}$ d^{-1})	0.016	0.016	*
k_{PMor}	Temperature coefficient for mortality $(°C)^{-1}$	0.0588	0.0693	a
Att_P	Light attenuation due to chlorophyll $(m^2\ mg)^{-1}$	0.0248	0.0248	b
w_P	Sinking rate (m day^{-1})	-	0.1	b
	Zooplankton parameters	SZ	LZ	
GR_{mPS}	Maximum grazing rate at 0°C on PS (d^{-1})	0.27	0.04	d, *
GR_{mPL}	Maximum grazing rate at 0°C on PL (d^{-1})	0.07	0.24	d, *
GR_{mZS}	Maximum grazing rate at 0°C on ZS (d^{-1})	-	0.14	d, *
k_{Gra}	Temperature coefficient for grazing $(°C)^{-1}$	0.0531	0.0531	d
K_{SPZ}	Half saturation on SP $(mmol\ N\ m^{-3})^2$	0.17	0.90	d, *
K_{LPZ}	Half saturation on LP $(mmol\ N\ m^{-3})^2$	0.10	0.90	d, *
K_{SZZ}	Half saturation on SZ $(mmol\ N\ m^{-3})^2$		0.90	d, *
ZMor	Mortality at 0°C (m^3 $mmolN^{-1}$ d^{-1})	0.023	0.030	*
k_{ZMor}	Temperature coefficient for mortality $(°C)^{-1}$	0.0693	0.0693	a
α_Z	Assimilation efficiency	0.70	0.70	a
β_Z	Growth efficiency	0.30	0.30	a
	Detritus parameters	SD	LD	
τ_{NH4}	Decomposition to NH_4 rate at 25°C (d^{-1})	0.045	0.020	b
τ_{DON}	Decomposition to DON rate at 25°C (d^{-1})	0.045	0.020	b
w_D	Sinking rate (m day^{-1})	1	10	a, b, *
k_D	Temperature coefficient for remineralization $(°C)^{-1}$	0.0693	0.0693	a

[a] Kishi et al. (2007); [b] Fennel et al. (2006; 2011); [c] Dune et al. (2010); [d] Gomez et al. (2017); [e] Yu et al. (2014), [f] Jiang et al. (2014); * Present study.

Table 1 (Continuation)

Parameter	Name	Value	Ref.
Nit	Nitrification rate at 25°C (d^{-1})	0.05	b
k_{Nit}	Temperature coefficient for nitrification $(°C)^{-1}$	0.0693	a
I_{th}	Radiation threshold for nitrification inhibition ($W\ m^{-2}$)	0.0095	b
D_p	Half-saturation radiation for nitrification inhibition ($W\ m^{-2}$)	0.1	b
γ_{NH4}	DON decomposition to NH4 rate at 25°C (d^{-1})	0.04	e, *
τ_{Si}	Opal dissolution to $SiOH_4$ rate at 25°C (d^{-1})	0.02	f
k_{DON}	Temperature coefficient for DON remineralization $(°C)^{-1}$	0.0693	a
k_{Si}	Temperature coefficient for opal dissolution $(°C)^{-1}$	0.0693	a
w_{Opal}	Opal sinking rate ($m\ d^{-1}$)	10.0	*
Att_{sw}	Light attenuation due to seawater (m^{-1})	0.037	b
C:N	Carbon to nitrogen ratio (mol C $(mol\ N)^{-1}$)	6.625	a, b

Table 2. Long-term mean and standard deviation of model and satellite chlorophyll.

	MS delta	**Texas shelf**	**Deep Ocean**
	Mean (Std. Dev.)	Mean (Std. Dev.)	Mean (Std. Dev.)
Model:			
1979-2014	2.61 (1.49)	1.09 (0.83)	0.17 (0.08)
1998-2010	2.48 (1.39)	1.03 (0.73)	0.18 (0.09)
2003-2014	2.46 (1.38)	0.98 (0.70)	0.18 (0.09)
SeaWiFS:			
1998-2014	4.91 (1.21)	2.52 (0.68)	0.15 (0.05)
MODIS:			
2003-2014	5.30 (1.37)	2.75 (0.77)	0.14 (0.05)
	Ratios	Ratios	Ratios
SeaWiFS/Model	1.98	2.44	0.88
MODIS/Model	2.15	2.80	0.78