We thank the two reviewers for their constructive comments on our work which have improved the manuscript. In this version, we have

1) replaced the term “North Pacific Ocean Desert (NPOD)” with “North Pacific oligotrophic ocean gyre (NPOG)”.

2) included phytoplankton carbon data and calculated light level within the mixed layer and further discussed how El Niño–Southern Oscillation (ENSO) modifies light availability in the mixed layer, thereby leading to phytoplankton photoacclimation response and affecting the variation of the NPOG. This analysis shows that carbon is well correlated to Chlorophyll in the NPOG, demonstrating that, while photoacclimation is important, it does not invalidate our conclusions.

3) provided a more balanced comparison between the Earth System Models (ESMs) and the Elman Neural Network (ENN) model, highlighting that the latter does not account for dynamical and biological processes.

4) added discussion acknowledging the equal importance of phytoplankton loss processes (e.g., grazing) alongside growth, clarifying how such processes are represented in ESMs.

5) revised several figures for clarity by using high-contrast colours and distinct markers to differentiate lines and indicated the statistical significance of the fitted regressions within the figures.

We sincerely thank both reviewers for providing valuable biological and ecological insights that have broadened our understanding and greatly enhanced the ecological context of this study.

Please note that in the responses to the comments below, reviewer comments are in green, our responses are in black, and relevant changes made from the manuscript are in blue.

List of Responses

To reviewer #1:

1-1. I think it would be beneficial for the science community to avoid using the term ‘ocean desert’. The oligotrophic central ocean gyres are not comparable to deserts on land. The gyres are actually very biologically active and their water column net primary production is not much lower than, for example, mesotrophic systems. I recommend replacing ‘ocean desert’ with ‘oligotrophic ocean gyre’.

Reply: Thank you for the suggestion. We agree with the comment and have replaced “North Pacific ocean desert” with “North Pacific oligotrophic ocean gyre (NPOG)” throughout the manuscript.

1-2-1. One of my primary concerns with this manuscript is that the analysis is based on spatial-temporal changes in surface chlorophyll concentration, and these are interpreted as reflecting phytoplankton biomass. Chlorophyll concentration, however, reflects both phytoplankton biomass and physiology (i.e., Chl:C) and the latter element reflects both nutrient availability and mixed layer light conditions. Distinguishing these factors controlling chlorophyll concentration is important as it can fundamentally impact the interpretation of observations. For example, it should be assumed a priori that chlorophyll concentration will decrease in response to a shoaling of the mixed layer and/or increasing incident sunlight (even in the total absence of change in nutrient availability or phytoplankton biomass) simply because phytoplankton will adjust Chl:C in response to changing mixed layer light levels (i.e., photoacclimation).

Reply: We understand the reviewer's concern and have added data, analyses, and discussion to address this issue.

First, we now distinguish between surface chlorophyll concentration, phytoplankton biomass and primary productivity in the revised manuscript: In this study, we emphasise that surface chlorophyll concentration should not be interpreted as phytoplankton biomass and is even less indicative of primary productivity (lines 128-129 in clean version manuscript).

Second, to further examine biomass variations driven by nutrient changes together with Chl:C variations driven by light conditions, we incorporated (1) particulate organic carbon (POC) data from MODIS and calculate phytoplankton carbon to estimate phytoplankton biomass following the approach of Behrenfeld et al. (2005), from which we also derive chlorophyll-to-carbon ratios (Chl:C). (2) mixed layer light availability, defined as the average photosynthetically available radiation (PAR) within the mixed layer, following Behrenfeld et al. (2005). This metric represents the light environment experienced by phytoplankton in the upper ocean and is a key driver of photoacclimation. Together, these datasets allow us to distinguish changes in chlorophyll concentration driven by phytoplankton biomass from those resulting from changes in the Chl:C ratio induced by light conditions (lines 131-137). These findings demonstrate that Chlorophyll is well correlated with phytoplankton biomass, and thus supports our main conclusions regarding the influence of ENSO and climate change on the NPOG.

Then, in the Introduction we now state the assumption that, even if nutrient supply and phytoplankton biomass remain unchanged, a shallower mixed layer or higher surface irradiance is expected to decrease chlorophyll concentration, as phytoplankton lower their pigment content in response to higher average light levels within the mixed layer (Behrenfeld et al., 2005, 2016) (lines 59-61).

We also added an analysis to show that changes in the NPOG area may be driven by both nutrient availability and photoacclimation effects (see reply 1-2-2 below).

1-2-2. One can easily envision that the strong seasonal cycle in surface chlorophyll concentration reported in this manuscript is entirely due to this photoacclimation response and may have nothing to do with changes in phytoplankton biomass or nutrient vertical transport (see for example figure 2 in Behrenfeld et al. 2005 GLOBAL BIOGEOCHEMICAL CYCLES, VOL. 19, GB1006, doi:10.1029/2004GB002299). It can also be easily envisioned that the observed relationships between chlorophyll concentration and ENSO cycles likewise primarily reflects changes in mixed layer light levels.

Reply: We thank the reviewer for this comment. We agree that in the NPOG, temporal variations in chlorophyll and phytoplankton biomass result from a combination of biological and physical factors. Following the reviewer's suggestion, we have calculated mixed layer light availability (Behrenfeld et al., 2005) and incorporated a corresponding discussion in the revised manuscript. First, in response to comment 1–5, we have redefined our study region as the area spanning the range between the interannual maximum and minimum extent of the NPOG seasonal maximum area (between the yellow and blue lines in Fig. R1). Within this region, surface chlorophyll variations largely determine the interannual variations in the NPOG area seasonal maximum and NPOG area seasonal cycle (lines 214-217). We then discuss that the interannual variations of chlorophyll in this region may be influenced jointly by two main factors:

ENSO-driven changes in the vertical thermal structure can modify nutrient availability, thereby affecting phytoplankton biomass (based on phytoplankton carbon data) and chlorophyll. Within the study region (Fig. R1), ENSO-related changes in mixed layer depth (MLD) (Fig. R2a), chlorophyll, and phytoplankton carbon are significantly correlated (Fig. R2b). Spatially, the correlation between chlorophyll and phytoplankton carbon is also significant in the study region (Fig. R1). Based on these results, we now apply the vertical nutrient flux calculation to the new study region in order to examine how ENSO affects thermal structure, MLD, nutrient transport, phytoplankton biomass and chlorophyll (Fig. 4 in the manuscript).

Our results show that chlorophyll and phytoplankton carbon are closely related in this region (Fig. R1), although variations in surface chlorophyll are not solely driven by nutrient-induced changes in biomass. Our estimates of mixed layer light levels indicate that ENSO can also affect the MLD and the average light availability within the mixed layer, inducing the photoacclimation response in phytoplankton that alters Chl:C ratio and thereby surface chlorophyll concentration (Fig. R2c) (lines 227-230).

We thank the reviewer again for the suggestion and will incorporate the above discussion and figures into the revised manuscript.

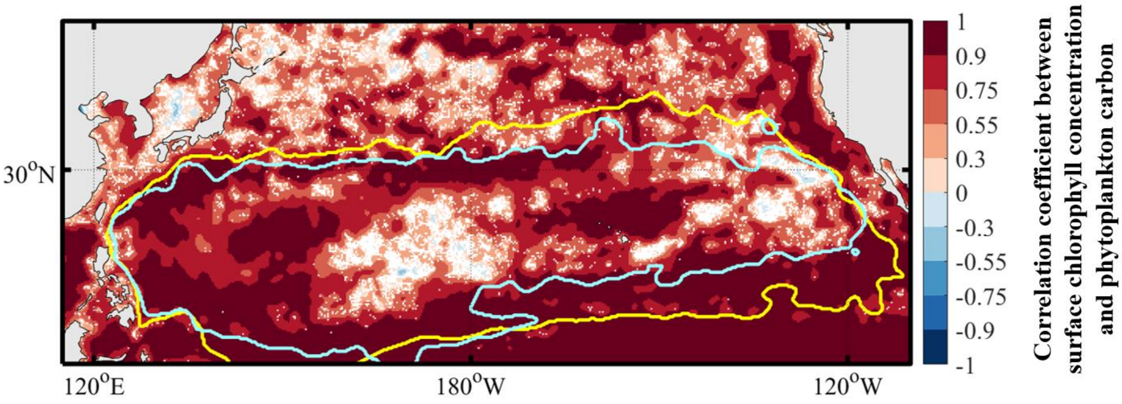

Figure R1. (Figure 2b) Boundaries of the largest (yellow) and smallest (light blue) extents of seasonal maximum NPOG area across different years. Colour shading represents the correlation coefficient between the interannual variations of summer surface chlorophyll concentration and phytoplankton carbon.

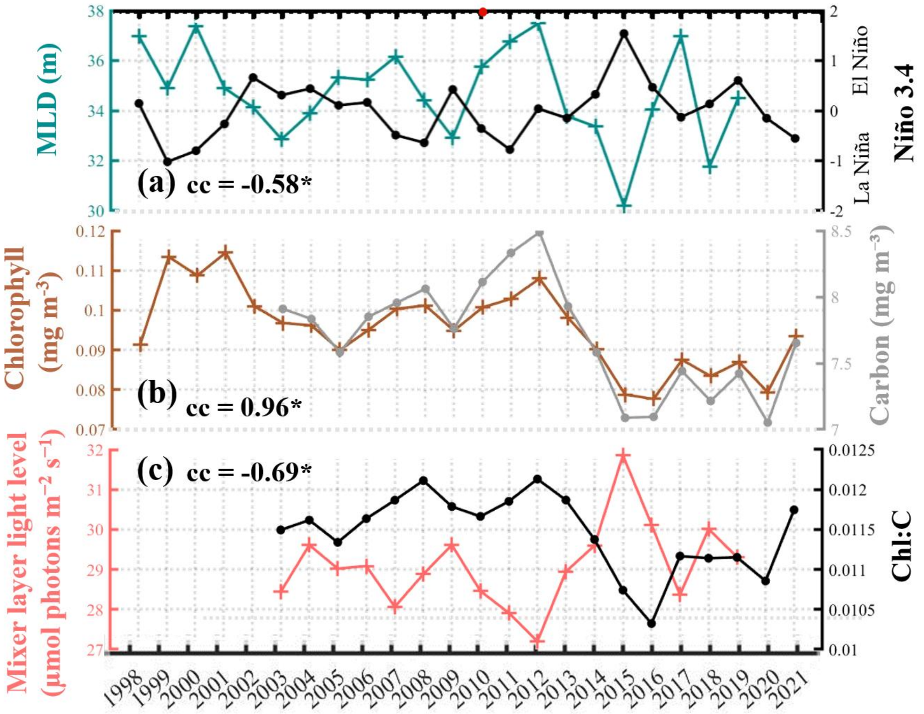

Figure R2. (Figure 4) Effects of ENSO on the interannual variations in NPOG area. Interannual variations in (a) MLD and Niño 3.4 index, (b) sea surface chlorophyll concentration and phytoplankton carbon, and (c) mixed layer light level and Chl:C. All variables are averaged over the summer half year (April–September) within the region bounded by the yellow and blue lines in Fig. R1. “cc” denotes the correlation coefficient between paired variables, and “*” indicates $p < 0.01$. The lines marked with “+” correspond to the left y-axis, while those marked with “•” correspond to the right y-axis.

1-2-3. It is worthwhile noting here that the ENN used in this model includes solar radiation as a primary input (i.e., photoacclimation, not nutrient stress) and that the other two inputs (SST and wind stress curl) are also linked to variations in mixed layer light levels.

We suggest that the interannual variability of chlorophyll is driven by both nutrient availability, through sea surface temperature (SST) and thermal stratification, and by light conditions, as discussed above. Consistently, the ENN results also identify SST and light as equally important controlling factors. The selection of these variables is also in line with the discussion in Sect. 3 and the findings of Meng et al. (2021), which emphasize the role of SST in modulating ocean vertical stratification and the influence of solar radiation on phytoplankton photoacclimation (lines 297-299).

We have also clarified in the revised text that SST and wind stress curl are linked to variations in mixed layer light levels: We note that the input variables are not entirely independent, as SST, wind stress curl, and solar radiation all interact to influence the MLD, nutrient availability, and the light level within the mixed layer, highlighting the complex coupling between physical forcing and biological responses. However, this interdependence is not a major concern here, because the ENN is designed to capture the combined, non-linear effects of correlated predictors, and our sensitivity tests (Table S3) confirm that these variables together provide the optimal explanatory power (lines 312-316).

1-2-4. Unlike the photoacclimation response, it cannot be assumed a priori that mixed layer shoaling will result in a decrease in chlorophyll concentration due to a reduction in vertical nutrient transport (see for example: Lozier et al. 2011, GEOPHYSICAL RESEARCH LETTERS, VOL. 38, L18609, doi:10.1029/2011GL049414).

We agree with the reviewer that MLD cannot directly represent vertical nutrient transport. Therefore, in our study we used the K-profile parameterization (KPP) model, which accounts for thermal and salinity stratification as well as horizontal and vertical current velocities, but is independent of MLD, to estimate vertical nutrient fluxes and explain the variations of chlorophyll concentration (Fig. 4 in the manuscript).

Lozier et al. (2011), based on a 10-year dataset, reported no correlation between stratification and chlorophyll in North Atlantic subtropical gyre. By contrast, our analysis does reveal such a relationship, which may be due to (1) the longer time period considered in our study and (2) differences in the selected study region and season. In addition, we now emphasize that changes in chlorophyll are influenced by not only nutrient mixing but also phytoplankton photoacclimation.

We also thank the reviewer for recommending Lozier et al. (2011). That study shows that wind-driven mixing should also be considered when analysing the summer weak nutrient supply induced by enhanced vertical stratification in the subtropical gyre (Lozier et al., 2011). Here, we show that the northeasterly wind anomalies north of the equator in La Niña years can also lead to stronger zonal wind stress and wind stress curl (Fig. S10d) (Chow et al., 2019; Feng et al., 2020), which can further enhance nutrient supply through wind-induced mixing and horizontal transport (Toyoda and Okamoto, 2017; Wilson et al., 2013), potentially providing a secondary contribution to the observed local chlorophyll peak (Fig. S10b) (lines 272-277).

1-2-5. The accurate interpretation of mechanism driving observed surface chlorophyll concentrations is important throughout this manuscript. For example, a decrease in chlorophyll due to photoacclimation to higher mixed layer light levels is expected to be associated with either unchanged or increased primary production, not a decrease.

Reply: We agree with the reviewer's comment. In response, we have clarified that variations in surface chlorophyll caused by photoacclimation do not necessarily reflect changes in phytoplankton biomass or primary production. For example, an increase in light availability within the mixed layer can reduce Chl:C, leading to lower surface chlorophyll while biomass and primary production remain unchanged or even increase. Reduced surface chlorophyll also lowers the light attenuation coefficient, allowing more light to penetrate deeper layers (Manizza et al., 2005; Meng et al., 2024), potentially further supporting higher vertically integrated phytoplankton biomass and primary production. (lines 231-236).

1-2-6. Another example is that a photoacclimation-based chlorophyll response makes the evaluation of phytoplankton 'blooms' in the oligotrophic north pacific gyre very questionable. The term 'bloom' is usually associated with a significant change in phytoplankton biomass, not a seasonal change in light driven (or nutrient-driven for that matter) change in Chl:C. Thus, without carefully distinguishing light-, nutrient-, and biomass-driven changes in chlorophyll concentration, the section of the manuscript regarding bloom properties is compromised.

Reply: We agree with the concern raised. Accordingly, we have revised the manuscript by replacing the term 'bloom time' with 'chlorophyll peak time', since our definition was based on the seasonal maximum in chlorophyll concentration. In addition, we have expanded our analysis to include the relationships between chlorophyll peak time, mixed layer light availability, phytoplankton carbon and Chl concentration (see reply 1-2-7).

1-2-7. It may also be noted here that the more common NPOD_WHY feature shown in figure 4 is consistent with photoacclimation to winter minima in mixed layer light levels and that the less common NPOD_SHY also corresponds (according to the authors) to regions where summer mixed layer depths are high (i.e., lower light).

Reply: We agree with this comment. In response, we have added a discussion to clarify the mechanisms underlying these features. In most NPOG regions, chlorophyll peaks during the winter half year (October–March) (Fig. 5a), consistent with weaker stratification and deeper mixed layers that enhance nutrient supply, together with reduced light levels within the mixed layer that elevate Chl:C (lines 266-268). In the NPOG_SHY region, which is the main focus of our study, we find that during La Niña conditions, the chlorophyll peak is likely associated with the deepening of the mixed layer, which reduces light availability within the mixed layer and thereby elevates the Chl:C ratio (Fig. R3) (lines 270-272). At the same time, we also acknowledge the potential role of wind-driven mixing and nutrient supply, as noted in the manuscript (Figure S10 in the supporting information).

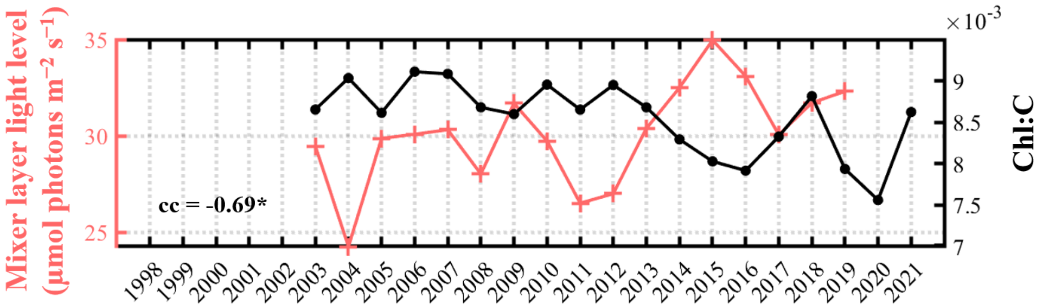

Figure R3. (Figure S9) Interannual variations in mixed layer light level and Chl:C. All variables are averaged in summer half year (April-September) over the NPOG_SHY region as shown in Figure 5a. "cc" denotes the correlation coefficient between paired variables, and "*" indicates $p < 0.01$. The line marked with "+" corresponds to the left y-axis, while the line marked with "•" corresponds to the right y-axis.

1-2-8. The importance of light- versus nutrient-driven chlorophyll changes also compromises the validity of the conceptual model presented in figure 7.

Reply: We have revised Fig. 7 (see Fig. R4 below) to better reflect the distinction between light- and nutrient-driven changes in chlorophyll. Specifically, on the left panel, which illustrates the influence of ENSO on the seasonal cycle of the NPOG area, we have included the role of light availability and its impact on chlorophyll through photoacclimation (i.e., changes in Chl:C). On the right panel, which presents model-based projections under climate change, we now highlight three key drivers, temperature, light, and wind curl, recognized by ENN model as the main factors influencing NPOG area variability.

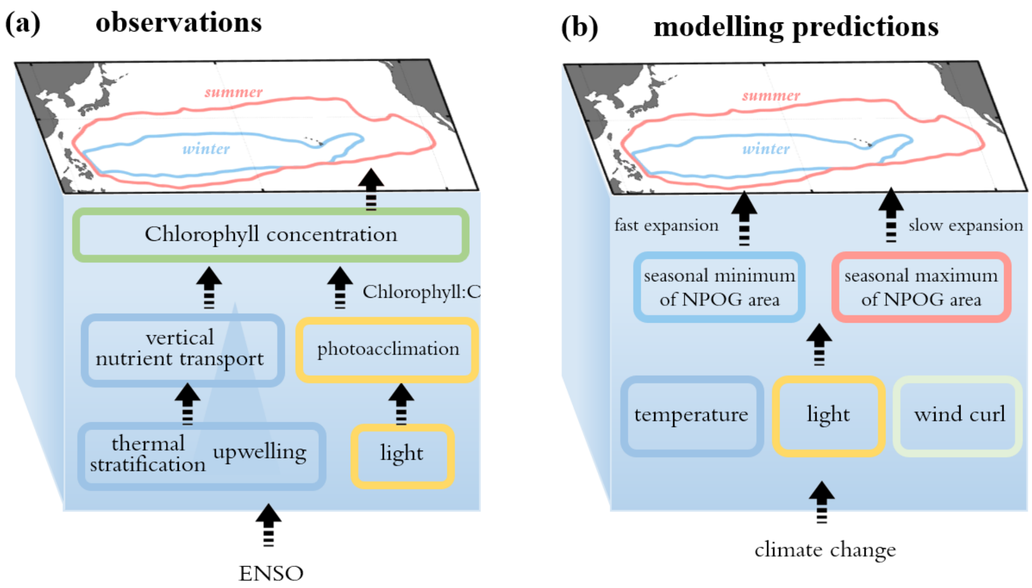

Figure R4. (Figure 8) Schematics of the response of NPOG area seasonal cycle to climate processes in observations (a) and modelling predictions (b). Red curves in the geographical figures represent the seasonal maximum of NPOG area in summer, and blue curves represent the seasonal minimum of NPOG area in winter.

1-3. It is noteworthy that a decrease in surface chlorophyll concentration will correspond to a decrease in mixed layer light attenuation coefficients, causing submixed layer light levels to increase and thus submixed layer primary production to increase, again questioning the quantitative significance of surface chlorophyll concentration changes to overall productivity.

We agree with this comment from reviewer. As we noted in our reply to comment 1-2-5, we clarified that an increase in light availability within the mixed layer can reduce Chl:C, leading to lower surface chlorophyll while biomass and primary production remain unchanged or even increase. Reduced surface chlorophyll also lowers the light attenuation coefficient, allowing more light to penetrate deeper layers (Manizza et al., 2005; Meng et al., 2024), potentially further supporting higher vertically integrated phytoplankton biomass and primary production (lines 232-236).

1-4. Figure 3 provides an interesting analysis of temporal trends in chlorophyll concentration, but it seems it would be useful to also show an overall time series of these trends. Figure 3b does this to a degree in a monthly-resolved manner, but there is no indication in this panel which of the monthly trends are statistically significant.

Reply: We thank the reviewer for this suggestion. In response, we plotted the overall time series of the NPOG area to provide a complete view of its seasonal and interannual variability. We then selected several representative months for multi-year linear fitting, which shows that the long-term area expansion trend is stronger in summer than in winter (Fig. R5). In addition, in Fig. R6 (revised from Fig. 3), the monthly trends with significant interannual trends at the 0.01 level (t-test) are highlighted by yellow lines to clearly indicate statistical significance.

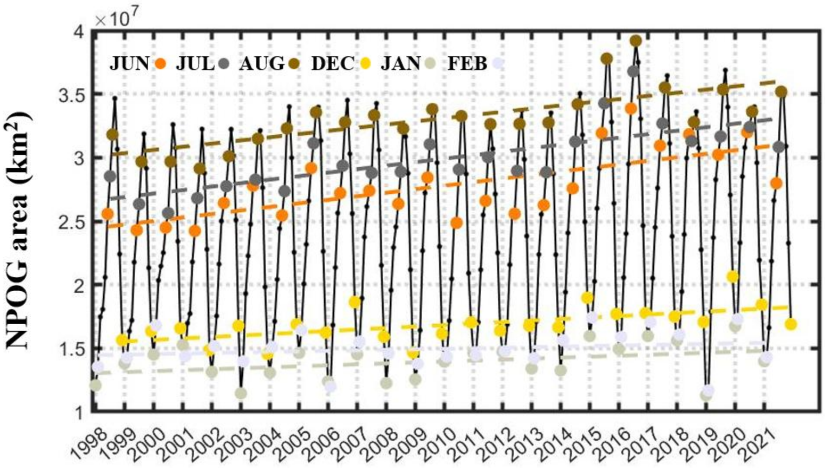

Figure R5. (Figure S6) Temporal variations in the NPOG area in 1998-2021. Linear regressions for the months of June, July, August, December, January and February of each year are shown by coloured dashed lines.

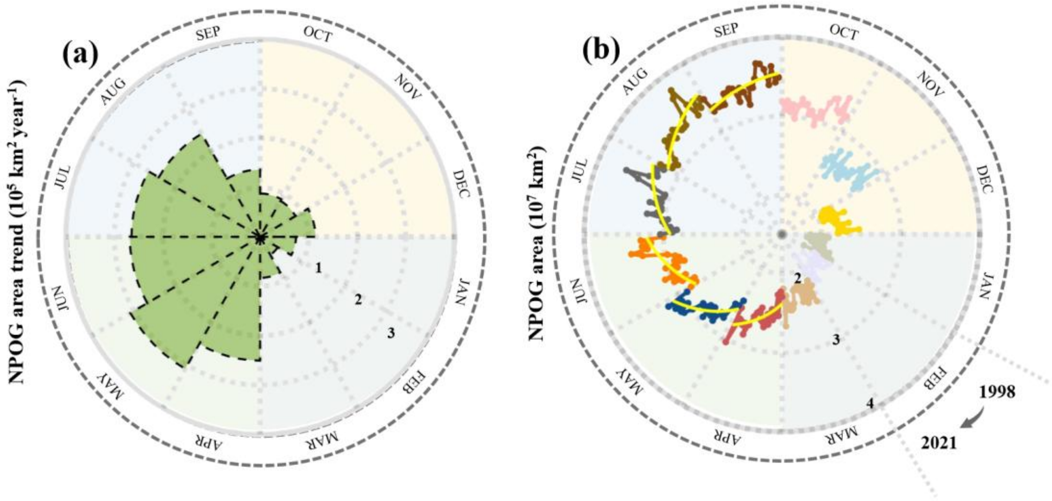

Figure R6. (Figure 3) Interannual variations of NPOG area in different months. (a) Trends of NPOG area expansion in 1998–2021 for specific months, derived from the linear-fitted regressions of NPOG area time series as shown in (b). (b) Time series of NPOG area from

1998 to 2021 for specific months. The yellow lines in (b) represent trends from linear regressions that are significant at the 0.01 level.

1-5. In figure 2 and as discussed in the text, changes in summer NPOD area between El Nino and La Nina conditions are not widespread but rather primarily isolated to the two regions indicated in figure 2. It is therefore not clear to me why the influence of ENSO was evaluated based on physical properties averaged over the entire NPOD (line 200). Why wasn't this analysis focused on physical changes only in the areas where ENSO effects are seen? If the assessed changes in physical properties are representative of the entire NPOD, why are there no changes in chlorophyll concentration observed over the entire region?

We agree with the reviewer that averaging physical properties over the entire NPOG region does not capture the spatially confined ENSO signals shown. Our study, however, specifically focuses on the interannual variability of the seasonal maximum NPOG area. To investigate this, we define our study region as the area spanning the range between the interannual maximum and minimum extent of the NPOG seasonal maximum area (between the yellow and blue lines in Fig. R1). Within this region, surface chlorophyll variations largely determine the interannual variations in the NPOG area seasonal maximum and NPOG area seasonal cycle (lines 214-217).

Within this region, we find that ENSO signals are closely linked to the interannual variability of chlorophyll, mainly through the modulation of nutrient availability and light conditions.

1-6. It seems to me that the manuscript is a bit critical of the Earth System Model results without being equally critical of the ENN results. For example, how reliable are the ENN predictions about future change when the ENN is built from hindcast data that doesn't take into account future changes in major ocean physical features (e.g., a potential northward movement in the location of the Kuroshio current) that provide critical constraints on the potential areal extent of the oligotrophic north pacific gyre? I think a more balanced evaluation of strengths and weakness of different approaches is warranted.

Reply: We thank the reviewer for this comment. We agree that a more balanced discussion of the strengths and weaknesses of the two approaches is needed. We have revised the manuscript to highlight that while ESMs provide process-based simulations, they are subject to systematic biases and model uncertainty. In contrast, while the ENN approach efficiently captures statistical relationships from historical data, it functions as a 'black box' with limited physical interpretability, and its predictions are constrained by the training dataset, without explicitly considering potential future changes in major oceanic features (e.g., shifts in the Kuroshio Current). Accordingly, the ENN-based simulations should be interpreted as reflecting correlations between environmental drivers and NPOG area, rather than a mechanistic representation of chlorophyll and NPOG variations (lines 333-345). These complementary strengths and limitations of ESMs and ENN are now highlighted in the revised text.

Minor comments:

1-7. the light colored symbols and lines in figure 1 are nearly impossible to see. I suggest bolder colors. Same issue in figure 2 regarding the La Nina lines.

Reply: Thanks for the suggestion. We have modified the figures with bolder colours to improve visibility and included the revised versions in the updated manuscript submission.

1-8. the black contours in figure 4 are not defined in the caption.

Reply: Thank you for pointing this out. The black contours represent the multi-year mean NPOG boundary. We have added this information to the figure caption in the revised manuscript (see Fig. 5 in the manuscript).

To reviewer #2:

This paper provide a bottom-up (nutrient/stratification) analysis to the dynamics of phytoplankton in the North Pacific subtropical gyre. The premise of this paper is that this region is a desert that is modulated by nutrient dynamics. This premise is wrong for many reason which I will detail below:

2-1. As Ed Laws has shown in his ARMS review, phytoplankton cells in this and similar (surface) area divide once a day. If this is the case, why call it a desert?

Reply: We thank the reviewer for this comment. Following the suggestion, we have replaced the term "North Pacific Ocean Desert (NPOD)" with "North Pacific oligotrophic ocean gyre (NPOG)" throughout the manuscript, also suggested by reviewer #1. In addition, we have added the discussion to clarify that, although phytoplankton biomass is relatively low in these regions, their vast extent and the rapid division rates of phytoplankton cells (Laws, 2013) confer considerable ecological significance (lines 34-36 in clean version manuscript).

2-2. The designation of desert is based on surface. [chl a]. [Chl a] is a problematic biomass indicator due to photoacclimation. what about phytoplanton carbon or nitrogen, and in particular, depth integrated? Shouldn't the depth integrated value be what we look at when considering the contribution to the ecosystem rather than surface concentrations?

Reply: We agree with the reviewer and now we emphasise that surface chlorophyll concentration should not be interpreted as phytoplankton biomass and is even less indicative of primary productivity (lines 128-129). To further analyse the phytoplankton biomass variations driven by nutrient changes and Chl:C variations driven by light conditions, we incorporated MODIS-derived particulate organic carbon (POC) data to calculate the phytoplankton carbon based on the method described in Behrenfeld et al. (2005).

Our results show that during the MODIS observational period, ENSO is linked to the interannual variation in the summer NPOG area jointly through: (1) changing thermal stratification and thus vertical nutrient supply: In El Niño years, higher SSTs and the associated increase in the vertical temperature gradient between 5 and 55 m lead to strengthened thermal stratification (Fig. 4a,b in the manuscript). The enhanced stratification in the upper ocean shoals the MLD and inhibits upward nutrient transport (Figs. R2a and 4c), leading to concurrent reductions in phytoplankton biomass and chlorophyll concentration (Fig. R2b), and the expansion of the NPOG area during El Niño years (lines 222-225); and (2) modifying light availability within the mixed layer: Our estimates of mixed layer light levels indicate that ENSO can also affect the MLD and the average light availability within the mixed layer, inducing the photoacclimation response in phytoplankton that alters the Chl:C ratio and thereby surface chlorophyll concentration (Fig. R2c) (lines 228-230).

We also agree that depth-integrated phytoplankton biomass and productivity are more relevant measures of ecological contribution. However, such observational data are not available on a global scale and over long time periods. To address this, we have added discussion on how surface chlorophyll can potentially influence depth-integrated productivity: Reduced surface chlorophyll also lowers the light attenuation coefficient, allowing more light to penetrate deeper layers (Manizza et al., 2005; Meng et al., 2024), potentially further supporting higher vertically integrated phytoplankton biomass and primary production (lines 234-236).

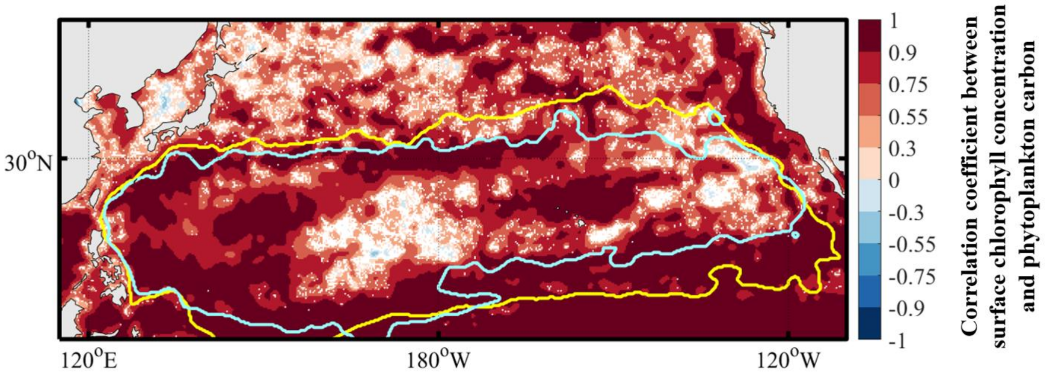

Figure R1. (Figure 2b) Boundaries of the largest (yellow) and smallest (light blue) extents of seasonal maximum NPOG area across different years. Colour shading represents the correlation coefficient between the interannual variations of summer surface chlorophyll concentration and phytoplankton carbon.

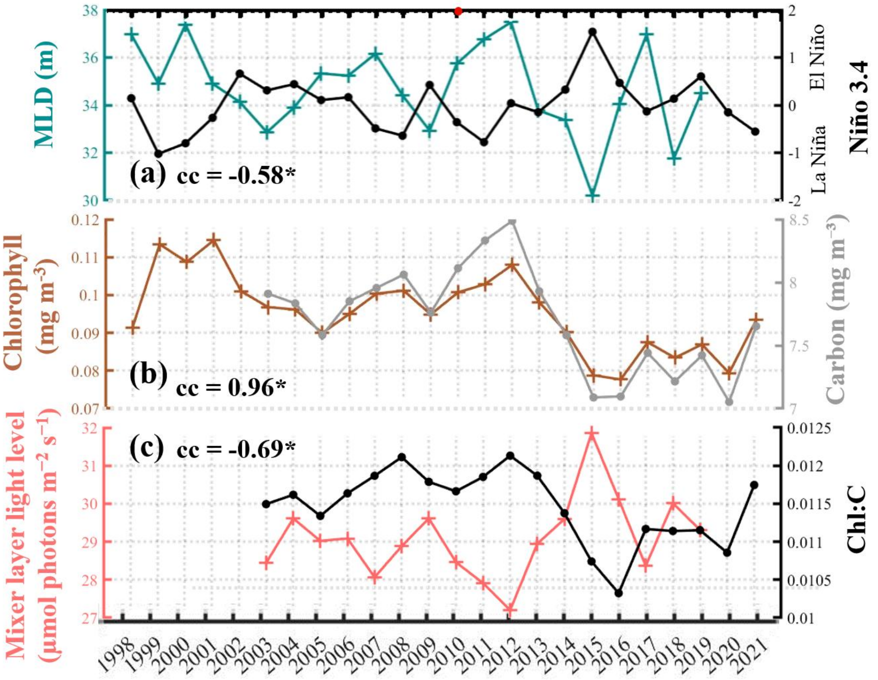

Figure R2. (Figure 4) Effects of ENSO on the interannual variations in NPOG area. Interannual variations in (a) MLD and Niño 3.4 index, (b) sea surface chlorophyll concentration and phytoplankton carbon, and (c) mixed layer light level and Chl:C. All variables are averaged over the summer half year (April–September) within the region bounded by the yellow and blue lines in Fig. R1. “cc” denotes the correlation coefficient between paired variables, and “*” indicates $p < 0.01$. The lines marked with “+” correspond to the left y-axis, while those marked with “•” correspond to the right y-axis.

2-3. Phytoplankton accumulation, e.g. the change of concentration with time, is one to two order of magnitude smaller than their growth-rate, indicating that loss processes (e.g. grazing and viruses) are just as important as growth inducing processes in the dynamics of phytoplankton. While I do understand that it is hard to study these processes, ignoring them will not help in understanding their accumulation dynamics. In the least one has to acknowledge the equal importance of these processes and the assumption models do when parametrizing them (e.g. tuning to get correctly the average chlorophyll, etc').

Reply: We thank the reviewer for raising this important issue. We fully agree that phytoplankton accumulation is the net outcome of both growth and loss processes, and that the latter (e.g., grazing) play an equally important role in regulating dynamics. First, we clarified that our study does not account for phytoplankton dynamic processes, e.g., growth and loss, whose rates are typically one or two orders of magnitude greater than the changes in phytoplankton biomass (lines 376-378). Although these processes are indeed difficult to quantify, we acknowledge their importance and add the discussion below in the revised manuscript.

In biogeochemistry models within ESMs, phytoplankton growth and loss processes are usually represented through simplified empirical or semi-mechanistic parameterizations. For example, grazing is often represented as a fixed fraction of phytoplankton biomass or growth, while other losses (e.g., mortality, viral lysis) are combined into mortality terms. Such simplifications are necessary for computational efficiency, but they rely on assumptions and tuning (e.g., adjusting grazing coefficients) to reproduce observed mean chlorophyll levels (Freilich et al., 2021). Therefore, future work should aim to explicitly integrate grazing and loss processes to improve mechanistic understanding of phytoplankton accumulation dynamics (lines 334-340).

Reference:

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