Seasonal photoacclimation in the North Pacific Transition Zone

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Key Points:

- Interpretations of North Pacific transition zone chlorophyll have not accounted for photoacclimation in the chlorophyll to carbon ratio
- Chlorophyll concentrations are negatively correlated with carbon concentrations in the transition zone (30-40°N)
- Deep winter mixing drives low light availability and high nitrogen supply, causing elevated chlorophyll:carbon ratios via photoacclimation

Abstract

The Transition Zone Chlorophyll Front (TZCF) is a dynamic region of elevated chlorophyll concentrations in the Northeast Pacific that migrates from a southern winter (February) extent of approximately 30°N to a northern summer (August) extent of approximately 40°N. The transition zone has been highlighted as important habitat for marine animals and fisheries. We re-examine the physical and biological drivers of seasonal TZCF variability using a variety of remote sensing, reanalysis, and *in-situ* datasets. Satellite-based remote sensing estimates of chlorophyll and carbon concentrations suggest the seasonal TZCF migration primarily reflects a seasonal increase in the chlorophyll to carbon ratio, rather than changes in carbon biomass. Chlorophyll to carbon ratios increase due to photoacclimation to low light availability and elevated nutrient supply in the transition zone winter. Seasonal mixed-layer-averaged light availability is positively correlated with carbon and negatively correlated with chlorophyll. Analysis of climatological nitrate profiles show that chlorophyll to carbon ratios are further enhanced by wintertime nitrate entrainment. These empirical results are consistent with physiological data and models describing elevated chlorophyll to carbon ratios in low light, nutrient-replete environments, demonstrating the need to incorporate phytoplankton ecophysiology into biogeochemical interpretations of remote-sensing observations.

Plain Language Summary

Satellite-observed marine chlorophyll concentrations are regularly interpreted as phytoplankton biomass. However, the chlorophyll content of cells can vary due to several environmental factors, thus complicating the interpretation of satellite-observed chlorophyll variability. In this study, we examine the relationship between chlorophyll concentration and carbon biomass in the Northeast Pacific – a region that has been highlighted as important habitat for marine animals. We find that satellite-observed chlorophyll variability is strongly correlated with light and nutrient availability but relatively uncorrelated with phytoplankton biomass due to changes in the chlorophyll to carbon ratio. Deep winter mixed layers are the primary physical factor driving the seasonal cycle in light and nutrient availability. These results provide a new perspective on marine ecosystem productivity in the Northeast Pacific and extend previous studies that examined North Pacific chlorophyll variability without accounting for changes in the chlorophyll to carbon ratio.

1 Introduction

The North Pacific Transition Zone Chlorophyll Front (TZCF) is a basin-scale chlorophyll feature noted in early satellite observations of ocean colour (Glover et al., 1994). The front exhibits marked seasonality, moving from a summertime northern position at approximately 40°N, to a wintertime southern position at approximately 30°N (Figure 1). The transition zone (30-40°N) has been repeatedly highlighted as a congregation area for marine animals and fisheries (Block et al., 2011; Hazen et al., 2013; Kappes et al., 2010; Polovina et al., 2017; Xu et al., 2017). Tagging data, where animals are fitted with geo-locators, have shown migratory and feeding behaviors throughout the transition zone, including commercially important tuna (Polovina et al., 2017; Xu et al., 2017), seabirds (Block et al., 2011; Kappes et al., 2010), and a variety of other marine animals (Block et al., 2011; Hazen et al., 2013).

Since early satellite observations, several studies have investigated the physical, chemical, and biological drivers of TZCF variability, with authors noting the uniqueness of the apparent wintertime productivity maximum at mid-latitudes (Ayers & Lozier, 2010; Bograd et al., 2004; Chai et al., 2003; Glover et al., 1994; Le et al., 2019; Polovina et al., 2001, 2017). Glover & Mcclain (1994) and Chai et al. (2003) suggested that deep winter mixed layers entrain nitrate and drive the apparent wintertime productivity maximum, while Ayers & Lozier (2010) and Le et al. (2019) suggested a stronger role for southward Ekman transport of nitrate.

Implicit in studies of TZCF dynamics is the assumption that the observed chlorophyll variability corresponds to changes in phytoplankton biomass, while not considering potential seasonal variations in chlorophyll to carbon ratios. Like other mid- and high-latitude environments, the transition zone is characterized by large seasonal cycles in surface irradiance and mixed layer depth which drives very low wintertime light availability and elevated nutrient fluxes to the mixed layer. Physiological data and models show that nutrient-replete, low light environments will increase the ratio of chlorophyll to carbon via photoacclimation (Behrenfeld et al., 2016; Geider et al., 1996, 1998; Inomura et al., 2020; Laws & Bannister, 1980; Westberry et al., 2008), which suggests that part of the TZCF chlorophyll signal may be due to photoacclimation rather than elevated phytoplankton biomass.

Here we aim to quantify the extent to which seasonal variation in the TZCF reflect biomass and productivity vs. changes in the chlorophyll to carbon ratio. We re-examine the seasonal dynamics of the North Pacific transition zone using a variety of remote sensing, reanalysis, and *in-situ* datasets to disentangle the role of photoacclimation in the observed seasonal chlorophyll variability in the TZCF. We quantify relationships between chlorophyll concentrations, carbon concentrations, net primary productivity, light availability, and mixed layer depths over the seasonal cycle. We examine these relationships across latitudes in the North Pacific to identify the unique seasonality of the transition zone chlorophyll signal. These results will help better understand ecosystem productivity in the North Pacific and thereby improve our interpretation of the satellite chlorophyll record.

2 Methods

We assembled a variety of remote sensing, reanalysis, and *in-situ* datasets to examine the empirical drivers of seasonal TZCF variability and to evaluate the photoacclimation hypothesis. Satellite remote sensing estimates of surface chlorophyll concentrations, carbon concentrations, net primary productivity, surface photosynthetically active radiation (PAR), and the diffuse attenuation coefficient (k_d) were obtained from the Oregon State Ocean Productivity database (http://sites.science.oregonstate.edu/ocean.productivity/). These remote sensing estimates have been gap-filled for missing observations due to cloud cover according to the algorithm described at http://orca.science.oregonstate.edu/gap_fill.php. Chlorophyll concentrations are based on the Garver-Siegel-Maritorena (GSM) algorithm using MODIS observations (Maritorena et al., 2002). Carbon concentrations are based on backscatter coefficients estimated via the GSM algorithm, modeled via the functions given in Westberry et al., (2008). Net primary productivity was taken from four models that differ in their parameterization of phytoplankton growth: the vertically generalized productivity model (VGPM; Behrenfeld & Falkowski, 1997), the carbon-based productivity model (CBPM; Westberry et al., 2008), the Eppley vertically generalized productivity model (EPVGPM; http://sites.science.oregonstate.edu/ocean.productivity/eppley.model.php), and the Carbon, Absorption, and Fluorescence Euphotic-resolving model (CAFÉ; Silsbe et al., 2016). Surface PAR and k_d are estimated from MODIS observations (Son & Wang, 2015).

Reanalysis datasets of mixed layer depth were obtained from the simple ocean data assimilation product (SODA; version SODA3 12.2; available at https://www.soda.umd.edu/) and the Hybrid Coordinate Ocean Model (HyCOM; hindcast version GLBu0.08; available at http://sites.science.oregonstate.edu/ocean.productivity). SODA mixed layers were linearly interpolated from the original five-day interval to an eight-day interval to match the satellite and HyCOM datasets obtained from the Oregon State Productivity Database. We obtained mixed layer estimates from Argo based on the methods of Holte et al., (2017) (http://mixedlayer.ucsd.edu/). In the supplementary material we demonstrate a high correlation between SODA and HyCOM mixed layer estimates relative to Argo observations (**Supplementary Figure S1**), indicating robustness across mixed layer depth estimates. All satellite and reanalysis datasets were bilinearly interpolated onto a common 0.5º grid. Climatological nitrate observations were taken from the World Ocean Atlas, version WOA2018 (Garcia et al., 2019). Mixed layer-averaged irradiance was calculated according to

$$\bar{I} = \frac{1}{z_{ml}} \int_{z_{ml}}^{0} I(z)dz = \frac{1}{k_d z_{ml}} I_0 e^{-k_d z_{ml}} (1 - e^{-k_d z_{ml}}),$$

where $I(z)$ is the scaler irradiance at depth z, k_d is the attenuation coefficient, z_{ml} is the depth of the mixed layer, and I_0 is the PAR incident at the sea surface. Entrainment nitrate fluxes into the mixed layer during mixed layer deepening were calculated according to

$$F_N = \frac{dz_{ml}}{dt} (N_0 - N_{ml}),$$

where $\frac{dz_{ml}}{dt}$ is the entrainment velocity, N_0 is the nitrate concentration one meter below the mixed layer according a linear interpolation of World Ocean Atlas nitrate profiles, and N_{ml} is the mixed layer-averaged nitrate concentration.

For the purpose of time series analyses we binned observations according to six latitude bands across the Northeast Pacific, defined by longitudinal bounds of -180ºW to -115ºW. Latitudinal bands were defined by the intervals 0-10ºN, 10-20ºN, 20-30ºN, 30-40ºN, 40-50ºN, 50-60ºN. The western bound of -180ºW was adopted to avoid influence of the western boundary current which imparts stochastic variability on the physical and chemical properties compared to the more stable latitudinal structure observed in the central and eastern reaches of the North Pacific basin.

3 Results

3.1 Covariation between chlorophyll and carbon

The seasonal TZCF migration is readily observed by comparing chlorophyll maps for the months of August and February (**Figure 1a,d**). August corresponds to the month of the maximum northward extent at approximately 40ºN, while February corresponds to the month of maximum southward extent at approximately 30ºN. Transition zone chlorophyll concentrations are elevated three- to five-fold during the February chlorophyll maximum, relative to August. While February is the month of maximum transition zone chlorophyll, concentrations are elevated over the months of January-February-March which we hereafter refer to as transition zone winter.

We find that February transition zone chlorophyll does not spatially correlate to carbon concentrations across the basin (**Figure 1**). The transition zone shows no appreciable increase in February carbon concentrations relative to August. February carbon concentrations are also depressed to the north and south of the transition zone, in contrast to chlorophyll which remains elevated to the north. The seasonal decoupling between chlorophyll and carbon becomes clear in the climatological distribution of the chlorophyll to carbon ratio (**Figure 1c,f**), where ratios are elevated roughly five-fold in winter from the transition zone northward. Primary productivity models also disagree on the magnitude and spatial pattern of wintertime transition zone productivity with no consistent spatial correlation with chlorophyll (**Supplementary Figure S2**).

The temporal dynamics of chlorophyll and carbon concentration time series demonstrate that the patterns of covariation between the two variables depend on latitude (**Figure 2**). Over the seasonal cycle, chlorophyll concentrations in the transition zone are negatively correlated with carbon concentrations (r=-0.321, **Figure 2c**), thus quantifying the seasonal decoupling between chlorophyll and phytoplankton biomass. Negative correlations between chlorophyll and carbon extend from 10-40°N, with the strongest negative correlation at 20-30°N (r=-0.836; **Figure 2d**). Across latitudes, the seasonal correlation between chlorophyll and productivity is also negative in the transition zone when averaging over four primary productivity models (r=-0.11), with positive correlations between chlorophyll and productivity at more northern and southern latitudes (**Supplementary Figure S3)**. Across years, negative correlations between chlorophyll and carbon appear driven by a consistent offset in the timing of their respective seasonal maxima (**Figure 3**). All latitudes show an average lag between chlorophyll and carbon maxima, with chlorophyll consistently peaking prior to carbon. The average lag across latitudes is 87 days with a standard deviation of 106 days. The most consistent lag was found in the transition zone, with a mean offset of 96 days and a relatively small standard deviation of 35 days across years (**Figure 3**). Taken together, the negative correlations between transition zone chlorophyll and carbon concentrations show that wintertime chlorophyll increases are due to increases in the chlorophyll to carbon ratio rather than increases in phytoplankton biomass.

3.2 Relationships with mixed layer depth and light availability

The seasonal covariation of chlorophyll and carbon across latitude can be interpreted in terms of latitude-specific responses to seasonal mixed layer depth variability (**Figure 4**). Across latitudes, we find a consistently negative relationship between mixed layer depth and carbon, with the strength of the relationship decreasing southward (**Figure 4a-f**). In contrast, we find both positive and negative correlations between mixed layer depth and chlorophyll across latitudes, with the largest positive slope in the transition zone (**Figure 4i**). The consistent positive slope of the transition zone chlorophyll relationship combines with a large range of seasonal mixed layer depths (20-145m) to a yield a transition zone chlorophyll cycle that is reliably predicted from a linear relationship with mixed layer depth.

The correlation of mixed layer and light availability is shown in **Figure 5**. Large seasonal cycles in surface irradiance and mixed layer depth are apparent at mid- and high-latitudes (**Figure 5a-**

b). The mean surface irradiance (around which the seasonal cycle oscillates) decreases northward, with the summer maximum surface irradiance at 50-60°N roughly equal to wintertime light availability in the tropics. Combining surface irradiance, mixed layer depth, and satellite estimates of the light attenuation coefficient k_d, we find that the largest seasonal cycle in mixed layer-averaged irradiance occurs in the transition zone, with a climatological seasonal amplitude of approximately 170μE/m^2/s and a wintertime light availability less than 10μE/m^2/s (**Figure 5c**). The minimal light availability in transition zone winter is near the minimum viable irradiance estimated for net photosynthetic growth (Platt & Jassby, 1976), highlighting the severe light limitation experienced by the wintertime transition zone phytoplankton community.

The distinct responses of transition zone carbon and chlorophyll to mixed layer depth and light availability are shown spatially by mapping the seasonal correlation coefficients across the basin (**Figure 6**). The correlation of mixed layer depth vs. carbon concentration is negative across most of the basin, with a band of weaker correlations in the transition zone (**Figure 6a**). Conversely, correlations of mixed layer depth vs. chlorophyll are weak across much of the basin, except for the band of strong negative correlations across the transition zone (**Figure 6b**). These patterns further demonstrate that deepening winter mixed layers drive increases in chlorophyll concentrations in the transition zone that are uncorrelated with variations in carbon. In terms of mixed layer-averaged irradiance, we see weak positive correlations with carbon north of 20°N (r ~ 0.20) and weak negative correlations southward (r ~ -0.10; **Figure 6c**). Again, in contrast to carbon and consistent with photoacclimation, chlorophyll strongly correlates with mixed layer-averaged irradiance throughout the transition zone, with correlations between -0.5 and -0.7 (**Figure 6d**). Zonally-averaged correlations reiterate this picture, showing diverging responses of carbon and chlorophyll with respect to mixed layer depth and mixed layer-averaged irradiance in the transition zone (**Figure 7**). We note that the correlation analysis was repeated using the alternative mixed layer reanalysis from SODA (**Supplementary Figures S4 and S5**). We found no appreciable difference in the magnitudes or spatial structure of the calculated correlations, indicating robustness in these relationships across mixed layer depth estimates.

Re-expressing relationships between light, carbon, and chlorophyll in terms of the chlorophyll to carbon ratio (Chl:C) reveals a strong nonlinear association between Chl:C and mixed layer-averaged irradiance, driven by nonlinear increases in Chl:C at the lowest light availability (**Figure 8**). The relationship between Chl:C and mixed layer-averaged irradiance appears well-described by a negative exponential of the form $Chl{:}C = a\left(1 - e^{-b\bar{I}}\right) + c$, where $\bar{I}$ is the mixed layer-averaged irradiance, a is the maximum Chl:C at $I = 0$, b is the rate that Chl:C decreases with increasing light availability, and c is the Chl:C attained in light-replete environments. The nonlinear response of Chl:C occurs in the light-limited regime, as encountered during transition zone winter. The shape of the relationship is consistent with models of phytoplankton photophysiology, describing the Chl:C as a negative exponential relationship with light availability (Jackson et al., 2017; Sathyendranath et al., 2020)

3.2 Mixed layer driven nutrient availability

Deepening mixed layers can also act to entrain nutrients as deepening mixed layers penetrate layers of elevated nutrient concentrations. The resulting nutrient supply can then further enhance chlorophyll to carbon ratios due to the nitrogen requirement of chlorophyll synthesis, as faster growth rates require more chlorophyll for a given light level (Geider et al., 1998; Inomura et al., 2020). The entrainment nitrate flux is composed of the entrainment velocity from deepening mixed layers $\frac{dz_{ml}}{dt}$ and the nitrate gradient at the base of the mixed layer. We find significant seasonality in entrainment velocity from 20°N and northward, with a maximum velocity that increases with latitude (**Figure 9a-b**). Similar latitudinal patterns are found in the mean nitrate gradient at the base of the mixed layer, with the mean gradient increasing northward beyond the equatorial latitudes (**Figure 9c**). The seasonal cycle in the nitrate gradient shows a more distinct latitudinal pattern. Nitrate uptake in the spring and summer drives the gradient from 20-40°N near zero in the summer months. This pattern contrasts with latitudes to the north and south of 20-40°N where spring and summer nitrate depletion is less severe. The entrainment velocity and nitrate gradient combine to yield a seasonal cycle in entrainment nitrate flux with an amplitude that increases with latitude (**Figure 9d**). Wintertime nitrate flux exceeds 30 mmol/m^2/month north of 40°N and exceeds 10 mmol/m^2/month in the transition zone, while remaining several fold lower southward of the transition zone. These results demonstrate that the transition zone latitudes of 30-40°N is the most southern latitude to receive a significant wintertime nitrate entrainment flux, consistent with arguments of Glover et al., (1994).

4 Discussion

4.1 Photoacclimation as a primary driver of wintertime transition zone chlorophyll

The observed negative covariation of chlorophyll and carbon in the transition zone, and its relationships with light and nutrient availability, suggest photoacclimation as a primary driver of chlorophyll variability in the TZCF. The wintertime increase in transition zone chlorophyll appears to be due to an increase in the chlorophyll to carbon ratio in response to light-limited, nutrient-replete growth conditions. This conclusion is found from empirical analyses of multiple satellite, *in-situ*, and reanalysis datasets and is consistent with models of phytoplankton physiology (Behrenfeld et al., 2016; Geider et al., 1996, 1998; Inomura et al., 2020; Laws & Bannister, 1980; Talmy et al., 2013).

These findings extend previous studies investigating transition zone seasonality (Ayers & Lozier, 2010; Bograd et al., 2004; Chai et al., 2003; Glover & Mcclain, 1994; Le et al., 2019). These studies interpreted the southern extent of the wintertime chlorophyll front as a biomass signal and sought the necessary environmental drivers to explain elevated wintertime productivity. Our results, while supporting the existence of a significant vertical wintertime nitrate flux (Chai et al., 2003; Glover et al., 1994), suggest that wintertime nutrient supply has a limited impact on biomass and productivity. Instead, wintertime nitrate supply enriches the growth environment and provides phytoplankton with necessary nutrient resources to acclimatize to light-limited conditions. Under these conditions, cells mobilize nutrients toward the light harvesting apparatus, including nitrogen-rich chlorophyll pigments and associated proteins (Geider et al., 1996; Inomura et al., 2020; Laws & Bannister, 1980).

This new perspective on seasonal productivity in the transition zone may motivate additional analyses of higher trophic animal usage patterns in the region. Niche models have been developed for these species using satellite chlorophyll to represent bottom up drivers (Abrahms et al., 2018; Block et al., 2011; Hazen et al., 2013). However, our results suggest that chlorophyll serves as a poor proxy for transition zone biomass. Because chlorophyll correlates strongly with sea surface temperature (Bograd et al., 2004), periods of decorrelation between chlorophyll and phytoplankton biomass, as characterized here, may provide the opportunity to isolate the roles of temperature and biomass on animal habitat utilization.

4.2 General implications for satellite observing of marine ecosystems

This study reiterates the need to account for photoacclimation when interpreting the satellite chlorophyll record, echoing calls from previous authors (Behrenfeld et al., 2016; Fox et al., 2020; Graff et al., 2016; Omta et al., 2009). Although the dynamics and interannual trends in chlorophyll have been insightful (Ayers & Lozier, 2010; Boyce et al., 2010, 2017; Glover et al., 1994; Hammond et al., 2020), many studies continue to use chlorophyll as a proxy for biomass and productivity. Complex relationships between chlorophyll, biomass, and productivity, including the latitudinal dependence demonstrated here, complicate this interpretation.

Beyond the North Pacific, our results suggest the potential for a more general latitudinal dependence of seasonal photoacclimation across ocean basins. Winter conditions at the 30-40°N mid-latitude band exhibits relatively deep winter mixing that entrains nitrate and drives a relatively large seasonal cycle in mixed layer-averaged light availability and nitrogen supply. The global planetary configuration of seasonal heat and solar fluxes suggest that mid-latitudes will experience similar seasonal cycles in surface irradiance and mixed layer depth in other ocean basins. This would predict seasonal photoacclimation at mid-latitudes globally. This prediction can be empirically tested in future work using the same datasets examined here.

The relationship between mixed layer-averaged irradiance and Chl:C also has important implications for observing climate impacts on marine ecosystems (Behrenfeld et al., 2016), including multiple studies that have examined multidecadal trends in chlorophyll (Boyce et al., 2010; Hammond et al., 2020; Henson et al., 2010). Warming of the upper column has increased stratification and reduced mixed layer depths in the North Pacific (Freeland, 2013) and across the global ocean (Li et al., 2018), with trends expected to increase into the future (Fu et al., 2016). These changes are often associated with reduced nutrient supply and productivity (Behrenfeld et al., 2006; Fu et al., 2016), which are invoked to explain chlorophyll declines. However, our results suggest that chlorophyll declines may also occur with reduced mixed layers due to photoacclimation (higher light availability with mixed layer shoaling) and may be uncorrelated or negatively correlated with changes in phytoplankton biomass and productivity.

Going forward, we highlight the need to further integrate eco-physiological modeling with satellite observing of marine ecosystems to better understand the physiological growth conditions of phytoplankton at large spatial scales. Continued progress has been made with empirical algorithms (Behrenfeld et al., 2016; Fox et al., 2020; Westberry et al., 2008); however, integration of mechanistic growth models has also been suggested in other contexts (Tanioka et al., 2020). These mechanistic approaches may provide additional constraints on phytoplankton physiology by explicitly resolving phytoplankton resource allocation strategies as a function of environmental conditions (Inomura et al., 2020).

5 Conclusions

In conclusion, our results suggest chlorophyll variability in the transition zone is primarily driven by photoacclimation to nutrient replete, light-limited growth conditions found in the transition zone winter. In general, photoacclimation processes complicate the interpretation of the satellite chlorophyll record, where relationships between chlorophyll, carbon, and productivity depend on latitude via relationships to seasonal light and nutrient availability. Further synthesis of eco-physiological models with satellite remote sensing will improve our understanding of the phytoplankton growth environment and reduce uncertainties in detecting climate change impacts on ocean ecosystems from space.

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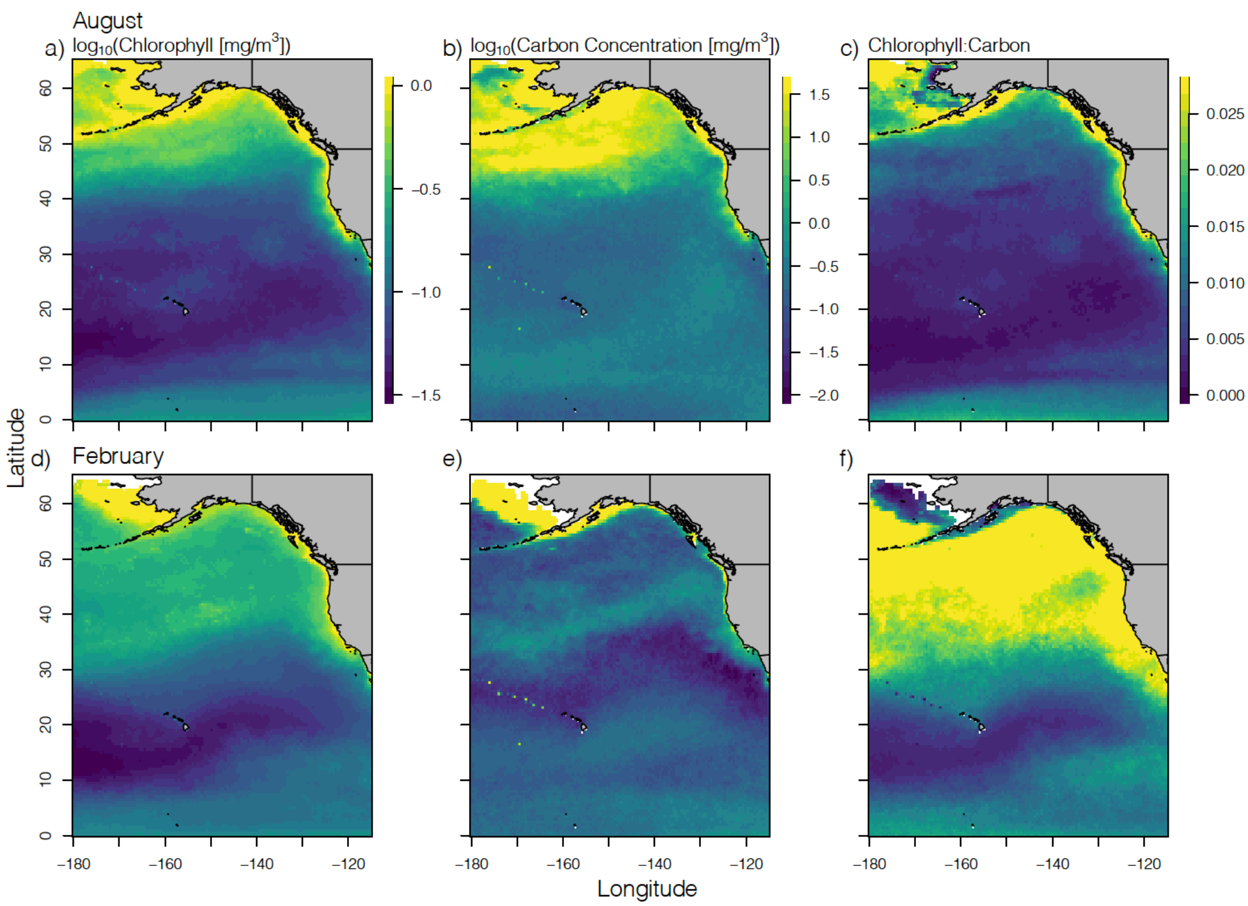

Figure 1. Satellite-estimated climatology for surface chlorophyll concentrations, carbon concentrations, and their ratio for the months of August and February in the Northeast Pacific. Panels a-c give the climatological chlorophyll, carbon, and chlorophyll:carbon ratio distributions for August, respectively. Panels d-f give the same respective fields for February.

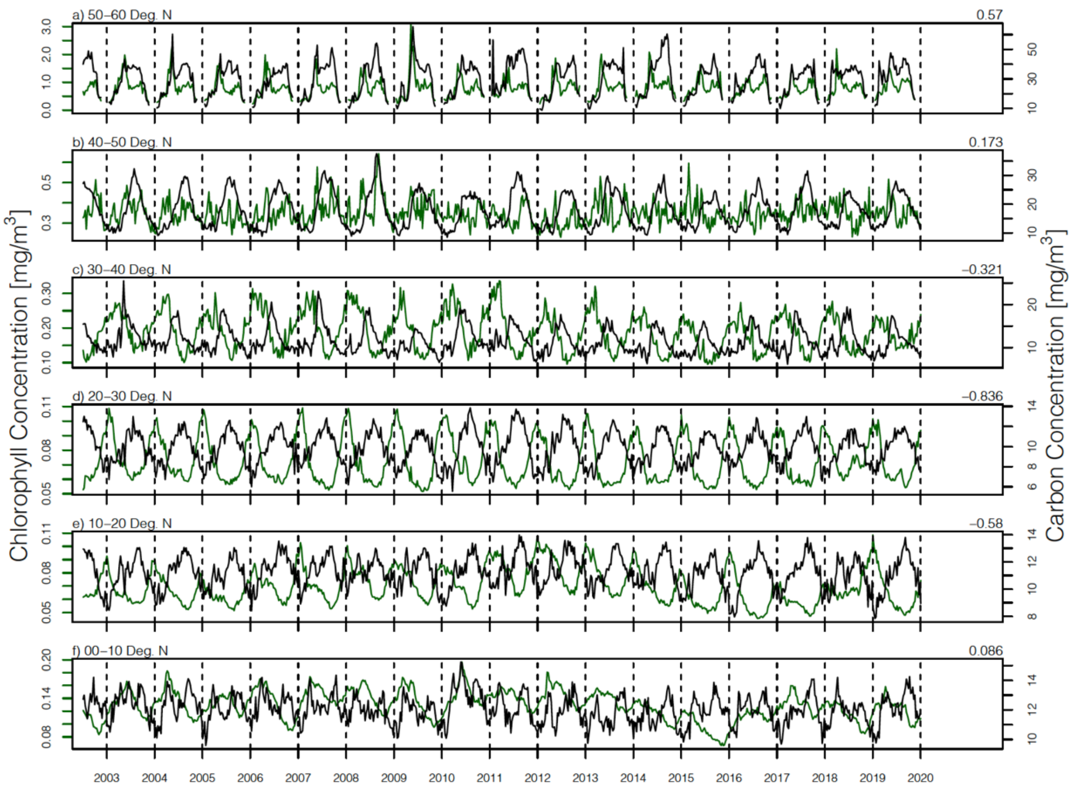

Figure 2. Latitudinal time series of chlorophyll and carbon concentrations. Chlorophyll is given with green lines and carbon is given with black. Rows represent different latitude bands. Latitudinal range is given in the top left of each panel. Correlation coefficient between the two series is given in the top right of each panel. Vertical dashed lines show January 01 of each year. Note the differing axis limits across panels.

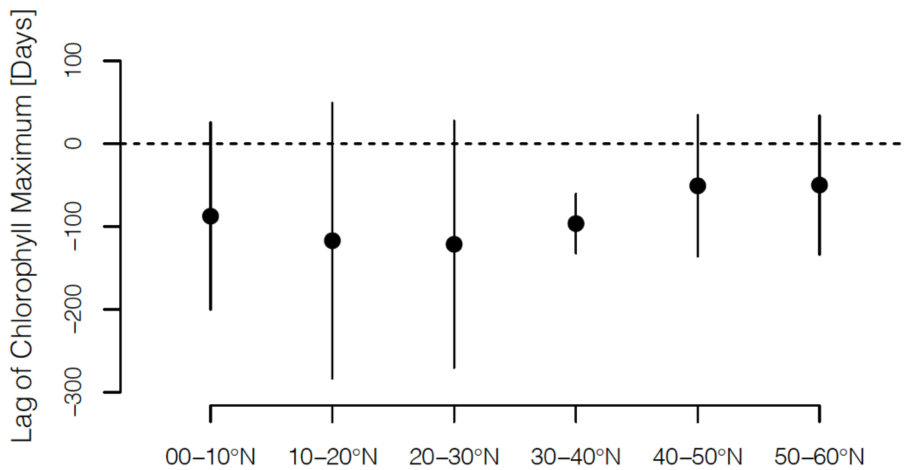

Figure 3. Means and standard deviations of the lag between seasonal chlorophyll and carbon maxima. Maxima are taken within individual years according to latitudinal time series in Figure 2. Mean and standard deviations are calculated across years. Negative values indicate that chlorophyll peaks before carbon in the seasonal cycle.

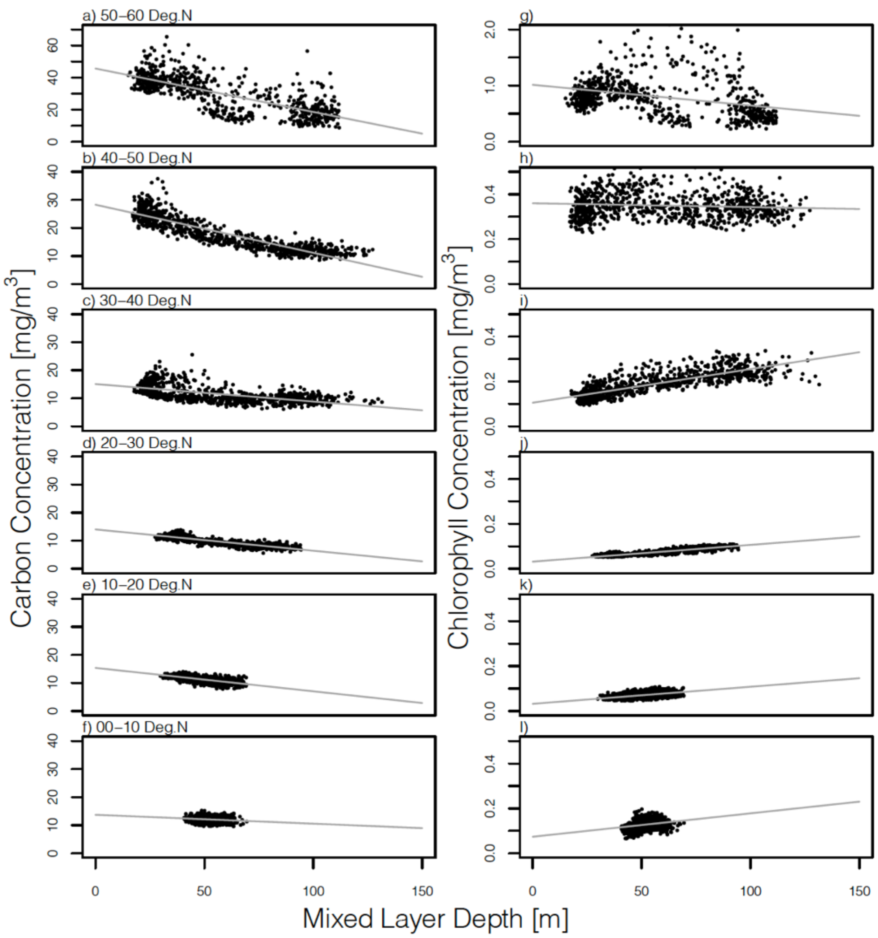

Figure 4. Latitudinal relationships between carbon and chlorophyll concentrations with respect to mixed layer depth. Left column (panels a-f) gives the relationships between carbon and mixed layer depth. Right column (panels g-l) gives the relationships with chlorophyll. Rows are latitude bands as in Figure 2. Latitude range is given in the top left of left column panels. Grey lines give the ordinary least squares regression line.

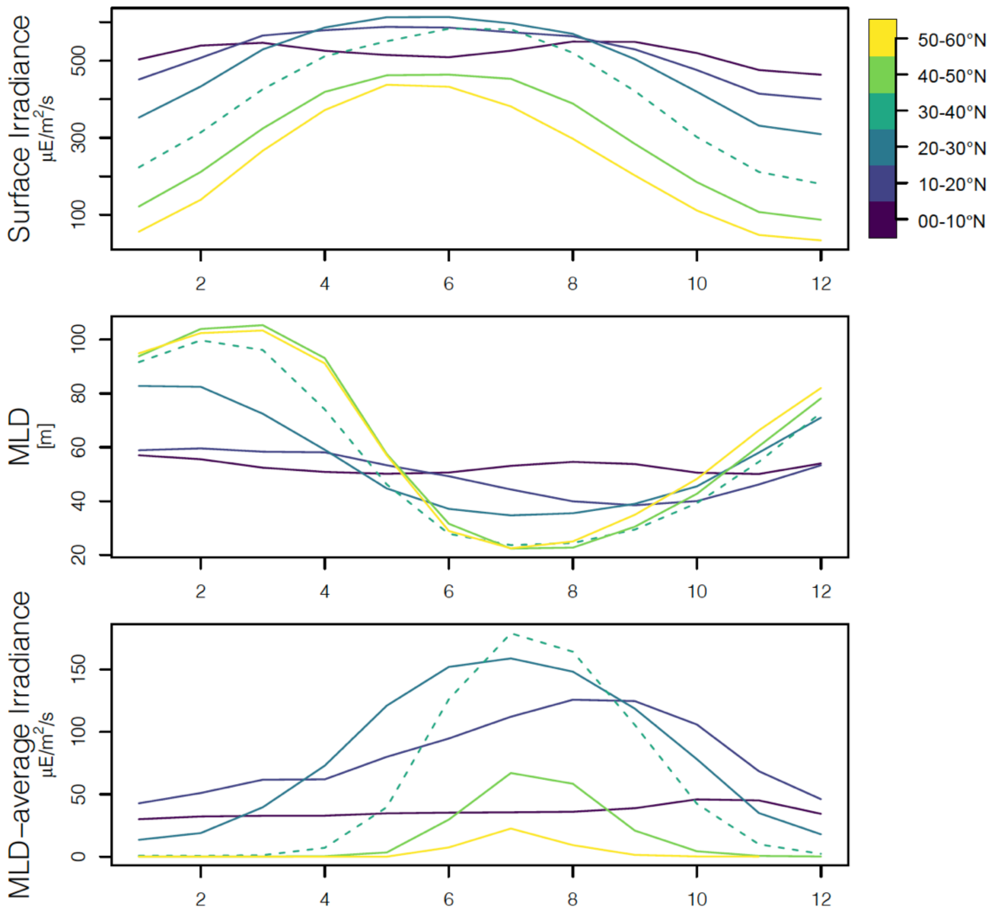

Figure 5. Seasonal climatology of surface irradiance (top), mixed layer depth (middle), and mixed layer-averaged irradiance (bottom) for ten-degree latitude bands in the Northeast Pacific. Color bar gives the latitude bands for each line. Dashed line indicates the transition zone (30-40°N).

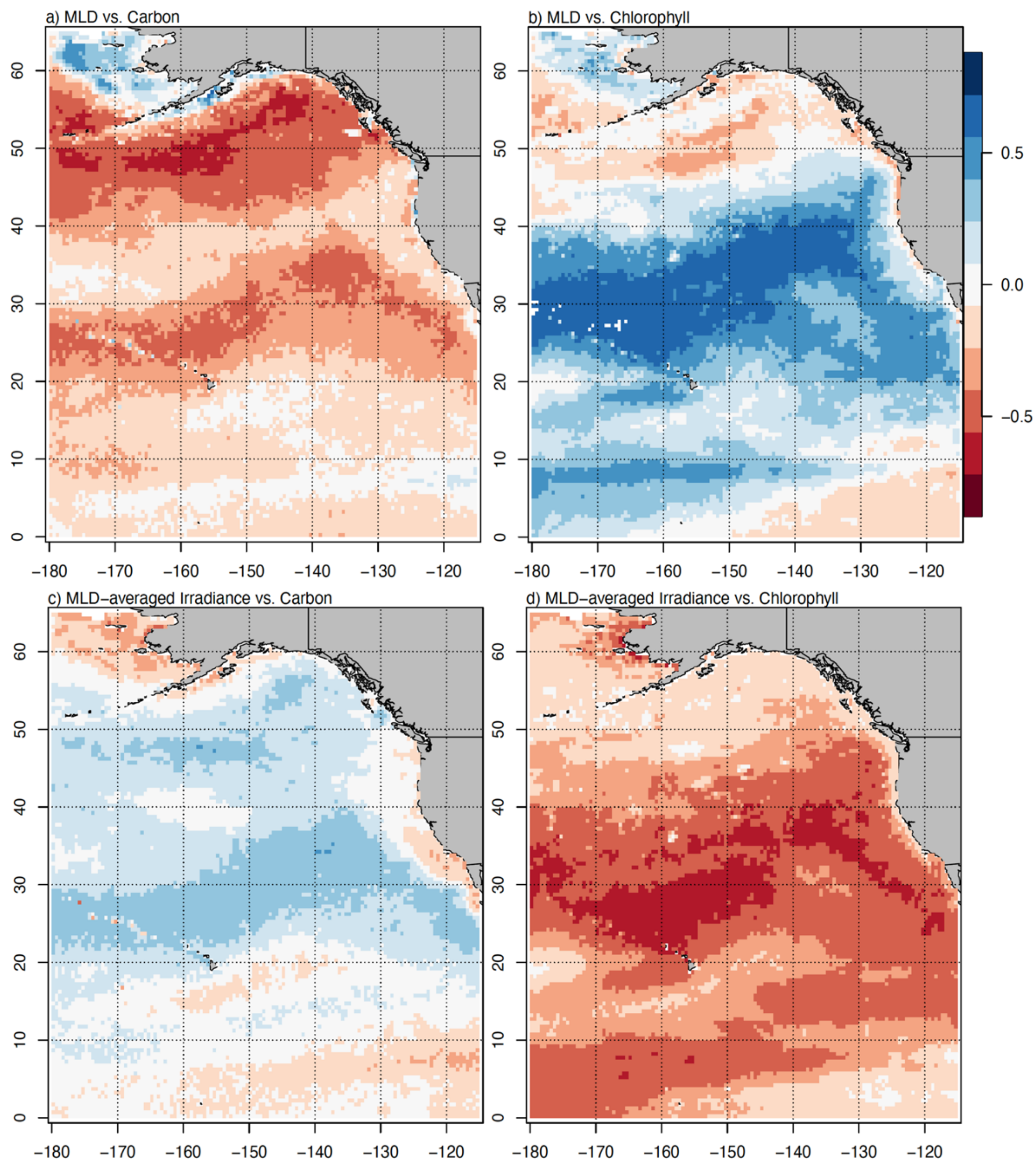

Figure 6. Time series correlation coefficients between mixed layer depth (MLD) vs. carbon concentration (a), MLD vs. chlorophyll concentration (b), MLD-averaged irradiance vs. carbon concentration (c), and MLD-averaged irradiance vs. chlorophyll concentration (d). Correlations are calculated interannually at each grid cell over the 20-year satellite record.

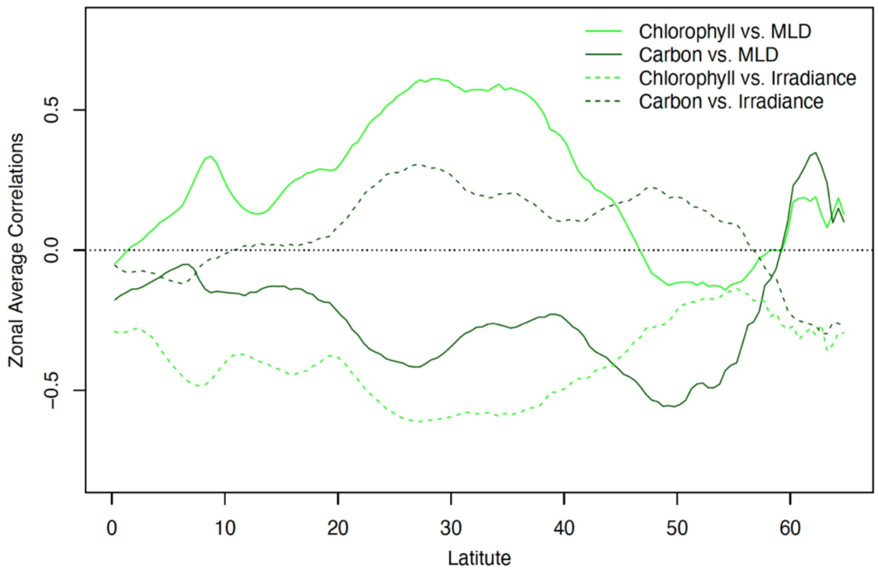

Figure 7. Zonally averaged correlations of the maps presented in Figure 6. Chlorophyll vs. mixed layer depth (MLD) and chlorophyll vs. MLD-averaged irradiance are given in solid and dashed light green lines, respectively. Carbon vs. mixed layer depth (MLD) and carbon vs. MLD-averaged irradiance are given in solid and dashed dark green lines, respectively. Horizontal dashed line gives the zero-correlation line.

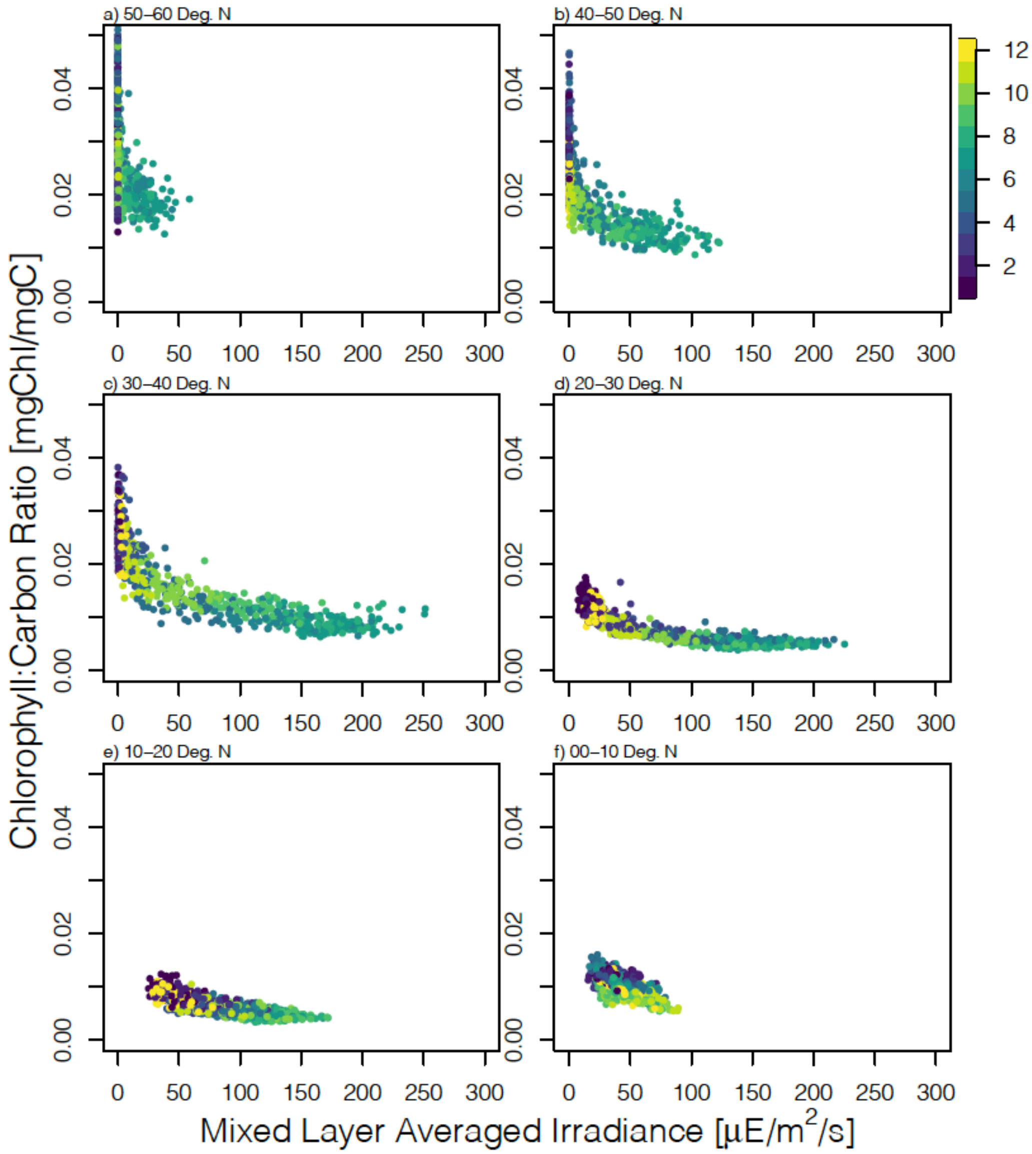

Figure 8. **Relationships between mixed layer-averaged irradiance and the satellite-estimated chlorophyll:carbon ratio.** Each box represents a ten-degree latitude band with the limits given in the upper left of each panel. Color represents month.

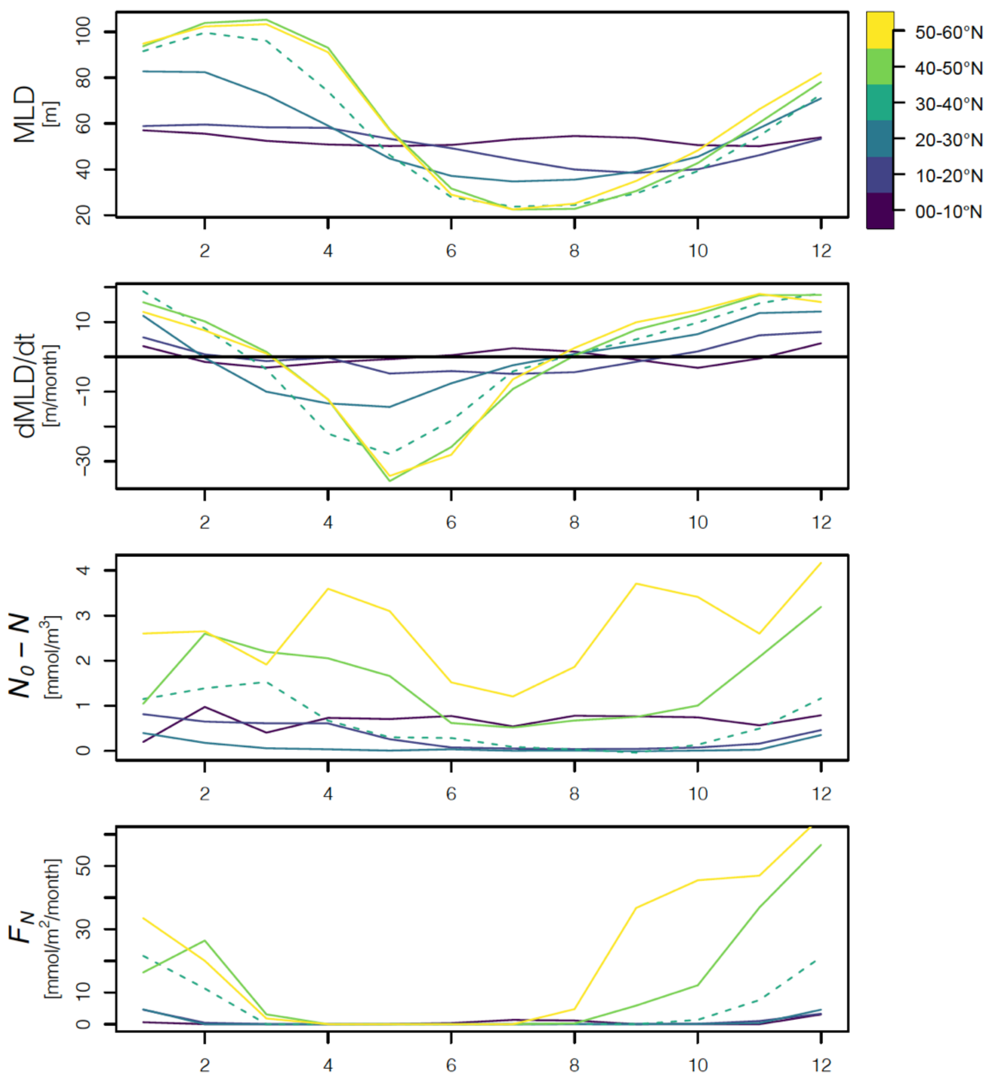

Figure 9. Climatological seasonal nitrate entrainment flux across latitudes. Colors represent ten-degree latitude bands as in Figure 5. Top panel gives the climatological seasonal cycle in mixed layer depth. Second panel gives the entrainment velocity (solid black gives the zero line). Third panel gives the nitrate gradient evaluated between the mixed layer and one meter below. Bottom panel gives the calculated entrainment flux. Dashed lines represent the transition zone (30-40°N).