

# Correlations of surface ocean pCO<sub>2</sub> to satellite chlorophyll on monthly to interannual timescales

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## Key points

- Relationships between in-situ pCO<sub>2</sub> and satellite chlorophyll are analyzed on timescales from monthly to interannual for 1998-2014
- Except in the equatorial Pacific, pCO<sub>2</sub> is negatively correlated to chlorophyll, but underlying mechanisms differ across timescales
- Only in the Southern Ocean do correlations indicate that the biological pump influences carbon uptake on all timescales

## ABSTRACT

On the mean, ocean carbon uptake is linked to biological productivity, but how biological variability impacts carbon uptake is poorly quantified. Our ability to diagnose past change, understand present variability and predict the future state of the global carbon cycle requires improving mechanistic understanding in this area. Here, we make use of co-located pCO<sub>2</sub> and temperature data, a merged surface ocean color product, and physical fields from an ocean state estimate to assess relationships between surface ocean biology and the carbon cycle on seasonal, monthly anomaly, and interannual timescales over the period 1998-2014. Using a correlation analysis on spatial scales from local to basin-scale biomes, we identify the timescales on which ocean productivity could be directly modifying ocean carbon uptake. On seasonal timescales outside of the equatorial Pacific, biome-scale correlations are negative between chlorophyll and pCO<sub>2</sub>. Though this relationship is pervasive, the underlying mechanisms vary across timescales and biomes. Consistent with previous findings, biological activity is a significant driver of pCO<sub>2</sub> seasonality only in the subpolar biomes. For monthly anomalies acting on top of the mean seasonality, productivity and pCO<sub>2</sub> changes are significantly correlated in the subpolar North Pacific and Southern Ocean. Only in the Southern Ocean are correlations consistent with a dominant role for biology in the surface ocean carbon cycle on all timescales.

## 1. Introduction

Variability in the air-sea flux of CO<sub>2</sub> is controlled primarily by surface ocean partial pressure of carbon dioxide (pCO<sub>2</sub>) [Lovenduski *et al.*, 2008; McKinley *et al.*, 2004; Takahashi *et al.*, 2002; Feely *et al.*, 2001], and thus understanding pCO<sub>2</sub> variability is critical if

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/2016GB005563

variability in the ocean carbon sink is to be quantified [McKinley *et al.*, 2017; Landschutzer *et al.*, 2015; Fay and McKinley, 2013; Schuster *et al.*, 2013; McKinley *et al.*, 2011; Schuster *et al.*, 2009]. Variability in oceanic pCO<sub>2</sub> is complex, being influenced by sea surface temperature (SST), salinity, dissolved inorganic carbon (DIC) and alkalinity. DIC and alkalinity, in turn, are influenced by the production of organic carbon in phytoplankton; production is controlled by surface nutrient concentrations and light availability, both set by the physical environment. Both variability in biological productivity, for which the surface ocean chlorophyll concentration can be used as a proxy, and physical variability, associated with temperature, salinity and mixed layer depths, govern the evolution of pCO<sub>2</sub> in the surface ocean.

Satellite retrievals of surface ocean chlorophyll clearly indicate variability in biological production; however, how this variability affects surface ocean pCO<sub>2</sub> is poorly understood. For the long-term mean, it is clear that the ocean's capacity to hold carbon is linked to biological productivity, with the biological pump acting as a critical mediator of large vertical gradients of carbon [McKinley *et al.*, 2017; Sarmiento and Gruber, 2006], though detailed quantification of these processes remains an area of active research [Mouw *et al.*, 2016; Behrenfeld *et al.*, 2015; Siegel *et al.*, 2014]. And though significant temporal variability in productivity has been observed globally with satellites [Martinez *et al.*, 2009, 2011, 2016; Polovina *et al.*, 2008; Behrenfeld *et al.*, 2006], we know little about how this variability impacts carbon uptake [Bennington *et al.*, 2009].

Variability and trends in ocean carbon uptake are of significant interest in the context of the global carbon budget, particularly since Le Quéré *et al.* [2007] and Canadell *et al.* [2007] suggested a long-term decline in the fraction of emitted anthropogenic CO<sub>2</sub> absorbed by the ocean. Reduced efficacy of the Southern Ocean carbon sink, linked to circulation changes through the mid-2000s, has been suggested [Takahashi *et al.*, 2012; Lenton *et al.*,

2012; *Le Quéré et al.*, 2009; *Lovenduski et al.*, 2008], however more recently, a recovery toward a greater sink subsequent to the mid-2000s has been identified from observations [*Munro et al.*, 2015; *Landschutzer et al.*, 2015; *Fay et al.*, 2014; *Fay and McKinley*, 2013] and models [*Lovenduski et al.*, 2015]. Both increasing and decreasing trends in carbon uptake have been reported in the North Atlantic for recent decades [*McKinley et al.*, 2017; *Breeden and McKinley*, 2016; *Fay and McKinley*, 2013; *McKinley et al.*, 2011; *Schuster et al.*, 2009]. Climate variability has been cited as a driver in most studies, though the precise mechanisms remain in debate.

Likewise, there has been substantial debate in the literature about variability and change in global ocean productivity. Some analyses of satellite data reveal significant declines in productivity between the El Nino of 1998 and the mid-2000s [*Polovina et al.*, 2008; *Behrenfeld et al.*, 2006; *Gregg et al.*, 2005; *McClain et al.*, 2004], with the proposed mechanism being an increase in stratification due to climate warming [*Doney*, 2006]. This mechanism has been much debated and other mechanisms proposed [*Martinez et al.*, 2011, 2016; *Dave and Lozier*, 2013; *Lozier et al.*, 2011; *Dave and Lozier*, 2010]. With continued satellite records, it has also been made clear that these changes, identified with barely a decade of continuous satellite observations, are consistent with climate variability and should not be interpreted as indicative of long-term, anthropogenic trends. *Kahru et al.* [2010] find both positive and negative correlations between chlorophyll concentration and wind speed, a regulating factor of wind-driven turbulent mixing, throughout various ocean regions. *Henson et al.* [2010] use global biogeochemical models to confirm that observed changes in trends are consistent with decadal variability and cannot be attributed to global climate change.

Climate model projections of the expected future impacts of warming on ocean productivity suggest that productivity in the subtropics will decrease with warming and associated stratification, while higher-latitude waters could become more productive due to

enhanced stratification and reduced light stress [Krumhardt *et al.* 2016; Bopp *et al.*, 2013; Sarmiento *et al.*, 2004]. However, Behrenfeld *et al.* [2009] cast doubt on these predictions by using a merged SeaWiFS/MODIS-Aqua record to show that warming has been associated with less productivity everywhere, even at high latitudes.

Global ocean pCO<sub>2</sub> trends analyzed by Fay and McKinley [2013] reveal substantial interannual to decadal timescale variability. In this study, we make progress on discerning how much of the observed pCO<sub>2</sub> variability may be biologically driven. Given the available data, the seasonal cycle and monthly anomalies around this seasonality can be considered in the most detail.

As has been previously described, physical change can modify both productivity and pCO<sub>2</sub> without a direct linkage between these changes. For example, wintertime low pCO<sub>2</sub> in the subtropics can be attributed to cool water temperatures [Koch *et al.*, 2009; Takahashi *et al.*, 2002, 2009]. Biological carbon drawdown is not believed to be large enough to significantly modify pCO<sub>2</sub> in this “temperature dominated” region [Gruber *et al.*, 2002]. At higher latitudes, vertical mixing that supplies carbon from depth to the surface increases pCO<sub>2</sub> in winter at a time when light is insufficient for biological productivity, while in summer, stratification and greater insolation leads to a phytoplankton bloom that draws down pCO<sub>2</sub> [Kortzinger *et al.*, 2008a,b]. These regions are “non-temperature dominated” [Takahashi *et al.*, 2002, 2009]. Takahashi *et al.* [2002, 2009] described these seasonal relationships at gyre-scale, across the globe, based on a gridded climatological estimate of surface ocean pCO<sub>2</sub>. Here, we provide a next step in this understanding by directly assessing these relationships with co-located data and also by expanding the timeframe of analysis to higher frequency (monthly anomalies) and lower frequency (interannual).

We utilize satellite-based observations of ocean color since the late 1990s and a newly updated in-situ pCO<sub>2</sub> dataset to investigate the relationship between co-located observations

of surface ocean pCO<sub>2</sub> and satellite chlorophyll over large-scale ocean biomes at frequencies ranging from monthly to interannual. This analysis focuses on qualitative, correlative relationships between seasonal, monthly anomaly, and interannual variability in pCO<sub>2</sub> and chlorophyll. The potential for impact of the biological pump on surface ocean carbon cycling is identified when surface ocean chlorophyll increases occur coincidently with the lowering of pCO<sub>2</sub> via the non-temperature (chemical/biological) component of pCO<sub>2</sub> [Takahashi *et al.*, 2002], and vice-versa. Of course, it is well-understood that chlorophyll is not synonymous with the biological pump, given the myriad of upper ocean ecosystem processes that connect primary production to carbon export to depth [Mouw *et al.* 2016; Siegel *et al.*, 2014; Buesseler and Boyd, 2009], as well as variations in both phytoplankton community structure and the chlorophyll content of individual phytoplankton [Behrenfeld *et al.*, 2015; Siegel *et al.*, 2013]. Nonetheless, chlorophyll is the primary globally-available indicator of surface ocean primary production, and offers the potential for a global-scale assessment of the potential links between productivity and drawdown of carbon from the atmosphere at multiple spatial and temporal scales.

To complement this analysis of pCO<sub>2</sub> and chlorophyll data, an investigation of one-dimensional (vertical) physical mechanisms is provided through the analysis of variability in sea surface temperature (SST) and mixed layer depths (MLDs). Horizontal advection is not accounted for with this analysis when performed at 1x1 degree spatial resolution. However, within-biome advection effects are indirectly incorporated when biome-scale aggregated timeseries are analyzed.

## **2. Data and Methods**

This analysis considers relationships between satellite chlorophyll-a concentration (Chl) and in-situ surface ocean pCO<sub>2</sub> observations from SOCAT, each averaged temporally to

monthly means. Spatially, we consider both co-located chlorophyll and  $p\text{CO}_2$  at  $1\times 1$  degree resolution and grouped into gyre-scale biomes [Fay and McKinley, 2013, 2014]. SST data collected along with the  $p\text{CO}_2$  observations is also included in the analysis. MLDs are taken from an ocean state estimate.

## Chlorophyll

Beginning in 1998, satellite records of ocean color provide estimates of chlorophyll concentration in the surface ocean. The SeaWiFS satellite remained in operation from 1998-2010, however, missing months of retrieval during 2008 and 2009 limit its consecutive timeseries. In 2002 the MODIS AQUA satellite was deployed to complement and ultimately replace the SeaWiFS satellite. A trio of satellites including MODIS, MERIS, and VIIRS provide chlorophyll estimates beginning in 2010. Merging these satellite retrievals to obtain a continuous timeseries of chlorophyll concentration is a complex and sensitive project. The merged satellite chlorophyll product utilized in this study was obtained from the Ocean Color MEaSUREs project at UCSB (<http://wiki.icess.ucsb.edu/measures/Products>). This merged product employs the Garver-Seigel-Maritorena (GSM) model [Maritorena *et al.*, 2002] to combine retrievals from different satellites. When multiple sensors are available, the model uses the remote sensing reflectance to calculate the merged value before computing chlorophyll concentration. Increased coverage, both temporally and spatially, is gained from this merged product. Compared to data from a single sensor, the merged products have roughly twice the mean global coverage and lower uncertainties for monthly chlorophyll concentrations due to an increase in available observations [Maritorena *et al.*, 2010]. Underestimations of chlorophyll concentrations using current ocean color algorithms have been reported for the high latitudes, specifically for the Southern Ocean. However, improvements are found and underestimations are minimized when using merged sensor

products [Johnson *et al.*, 2013], as done here. By incorporating the knowledge of parent sensor errors and biases, estimates for the high latitudes can be corrected for.

With the merged chlorophyll product, a near-continuous timeseries spanning years 1998-2014 is available. Averaging the chlorophyll product to a 1x1 degree spatial resolution allows for a more direct comparison to the available pCO<sub>2</sub> product. Quality control on the chlorophyll dataset is accomplished by removing data outside of 3 $\sigma$  from the 1x1 degree gridcell mean over each available month. This removes less than 2% of the data, largely from higher latitudes and coastal areas. Chlorophyll variables analyzed here are log-10 transformed to avoid amplifying the influence of a few highly productive sites in our global biome study [Siegel *et al.*, 2013]. Histograms of available chlorophyll observations within each biome have been checked to verify normality.

## **pCO<sub>2</sub>**

This analysis utilizes the quality-controlled, oceanic pCO<sub>2</sub> dataset Surface Ocean CO<sub>2</sub> Atlas (SOCAT) version 3, released in 2015 (available at [www.socat.info](http://www.socat.info)). SOCATv3 includes roughly 10 million global observations spanning years 1957-2014 [Bakker *et al.*, 2016]. Individual observations for years 1998-2014 are spatially averaged at 1x1 degree resolution and temporally averaged to a monthly resolution. Concurrent SST observations included in the SOCAT dataset are treated in the same manner as pCO<sub>2</sub> to obtain 1x1 degree monthly values. The pCO<sub>2</sub> data are also decomposed into a temperature-driven component (pCO<sub>2</sub>-T) and the remainder (pCO<sub>2</sub>-nonT) that is potentially biologically-driven through influence on DIC and ALK. This decomposition follows Takahashi *et al.* [2002]. For simplicity and direct comparison to Takahashi *et al.* [2002], we use these equations rather than the updated equations [Takahashi *et al.*, 2009], but note that differences are minimal with the alternative choice.



## Mixed Layer Depth

The ECCO (Estimating the Circulation and Climate of the Ocean) version 4 model (available at <http://www.ecco-group.org/products.htm>) [Forget *et al.*, 2015] is a dynamically consistent ocean state estimate model based on the MITgcm [Marshall *et al.*, 2007a,b]. By utilizing an inverse estimate of parameterized physics, this adjoint model is able to adjust its estimates to the whole system in order to best fit all of the available data. With global coverage, this state estimate provides mixed layer depths (MLDs) for years 1992-2011. Thus, when correlations of variables to MLD are presented, the timeframe covered is 1998-2011.

## Analysis

All datasets are sub-sampled to include only observations for months and 1x1 degree gridcells where all sparsely sampled variables (pCO<sub>2</sub>, chlorophyll, and SST) have reported values. This relatively coarse temporal and spatial scale allows for comparison of observations that were collected on different days or locations, but is appropriate for the study of large-scale seasonal and interannual timescale relationships.

In addition to the analysis presented at 1x1 degree, we also aggregate timeseries to gyre-scale regions, or “biomes” (Figure 1) [Fay and McKinley, 2014]. A consistent pattern emerges that if biome correlations are weaker, there also tend to be weaker and/or more varied correlations apparent at 1x1 degree resolution. If a biome encompasses significant numbers of negative and positive correlations, these relationships will cancel out in the aggregated timeseries and the biome mean correlation will tend to be insignificant. In Figures 6-7 and 9-10, correlations are presented on both spatial scales so as to allow for direct inspection of both 1x1 and biome scale relationships. Consideration of biome-scale timeseries and their correlations includes the impacts of horizontal advection within the gyres, a factor not allowed for in the 1x1 analysis.

When averaging to biome scale analysis, it is important to consider the background



latitudinal variability of these observations [Fay *et al.*, 2014]. In order to account for this, we remove a background climatological value for each variable at 1x1 degree resolution before averaging variables to biome scale: pCO<sub>2</sub> [Landschutzer *et al.*, 2014], SST (NOAA\_OI\_SST\_V2 data provided by the NOAA/OAR/ESRL PSD; Reynolds *et al.*, 2002), Chl (NASA Ocean Color Data group available at [http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/Monthly\\_Climatology/9km/chlor\\_a](http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/Monthly_Climatology/9km/chlor_a)) and MLD climatologies calculated from the observations introduced above. For presentation clarity, each biome-mean value is added back to the resulting anomalies for timeseries figures.

The atmospheric pCO<sub>2</sub> trend for 1998-2014 [Dlugokencky and Tans, NOAA/ESRL, [www.esrl.noaa.gov/gmd/ccgg/trends/](http://www.esrl.noaa.gov/gmd/ccgg/trends/)] is subtracted out from the monthly pCO<sub>2</sub> timeseries. On long timescales, oceanic pCO<sub>2</sub> largely tracks atmospheric pCO<sub>2</sub> [Fay and McKinley, 2013], so by removing this trend we are able to consider relationships between chlorophyll and ocean carbon that deviate from this first-order relationship.

Northern hemisphere ICE biomes have very limited data, both due to poor satellite coverage at high latitudes and the difficulties involved with obtaining in-situ observations in these ocean regions. In order for a biome to be considered in this study, we require there to be at least 34 observations over 17 years (an average of 2 observations per year). Neither the North Atlantic or North Pacific ICE biomes meet this criterion and are thus removed from this analysis.

We have also conducted this analysis with the LDEOv2014 pCO<sub>2</sub> dataset [Takahashi *et al.*, 2015] and the SeaWiFS-only chlorophyll product (<http://oceancolor.gsfc.nasa.gov/cgi/l3>) and find consistent results. For our primary analysis, the SOCATv3 dataset and merged chlorophyll product are selected as they contain more observations with consistent quality control, and also span the longest time period.

Correlations are calculated between log10-chlorophyll and pCO<sub>2</sub>, SST, MLD, as well as the decomposed components of pCO<sub>2</sub> (pCO<sub>2</sub>-T and pCO<sub>2</sub>-nonT) using the Pearson correlation, which assumes linear relationships between the variables. Correlations at 1x1 degree gridcells and at biome scale are shown side by side to confirm that averaging available data to the biome scale does not substantially impact findings. Significant correlations are determined at the 95% confidence level using a p-value calculation and figures only show correlations with a p-value less than or equal to 0.05.

In this analysis we consider results on various timescales. The full dataset includes a clear seasonal cycle for each variable, and thus correlations of the full timeseries are interpreted as representing the seasonal cycle. To remove this seasonal cycle for the consideration of monthly anomalies, a harmonic cycle fit to the timeseries of biome-scale monthly means is removed [Fay and McKinley, 2013]; we acknowledge the regional heterogeneities within a biome and therefore tested the biome mean harmonic against local harmonic fits (for each 1x1 gridcell) as well as monthly climatological means and the impacts on results were found to be negligible. High frequency relationships at 1x1 or in the biomes are investigated using the resulting monthly anomalies. By calculating 12-month running means of the full timeseries, interannual variations can begin to be diagnosed, however data are only sufficient to do this at the biome scale. Data are insufficient at 1x1 degree to estimate 12-month running means. To limit the impact of very sparse data for interannual correlations, only biomes with at least 5 years worth of 12-month running mean values are included. It is important to note that the interannual variability discussed here should be attributed only to natural variability, as a minimum three decades of data would be required before anthropogenic trends could begin to be detected [McKinley *et al.*, 2016; Lovenduski *et al.*, 2015; Fay and McKinley, 2013; Henson *et al.*, 2010].

### 3. Results

Example timeseries for  $p\text{CO}_2$  and chlorophyll in four subtropical and tropical biomes (Figure 2) and two subpolar biomes (Figure 3) illustrate some of the challenges with respect to data availability. Prior to 2005, this is primarily due to limited  $p\text{CO}_2$ , and in high latitude wintertime, sparsity is due to limited satellite chlorophyll. Clear seasonality in  $p\text{CO}_2$  and chlorophyll is most evident in the subtropical gyre (STPS) and subpolar (SPSS) biomes, but is harder to clearly identify in the equatorial and subtropical transitional (STSS) biome. At the biome scale for all biomes, analysis of the mean seasonal amplitudes illustrates high wintertime chlorophyll in the subtropics and high summertime chlorophyll in the subpolar regions (Figure 4a). Everywhere,  $p\text{CO}_2\text{-T}$  is lower in wintertime while  $p\text{CO}_2\text{-nonT}$  is always higher in winter (Figure 4c,d); and the magnitudes of these cycles are generally amplified at high latitudes (Figure 4d). The magnitude of  $p\text{CO}_2\text{-nonT}$  dominates over  $p\text{CO}_2\text{-T}$  in subpolar regions, while  $p\text{CO}_2\text{-T}$  dominates in the subtropics (Figure 4b). For all variables, seasonality is limited in equatorial biomes.

The analysis focusing on correlations between seasonal, monthly anomaly, and interannual variability allows for the determination of where and when correlations indicate that the biological pump could be a primary driver of variability in surface ocean  $p\text{CO}_2$ , and thus ocean carbon uptake (Table 1). It is worth clarifying that identification of temperature variability ( $p\text{CO}_2\text{-T}$ ) as dominant, does not preclude a secondary biological driver. Future research will be needed to fully elucidate both the primary relationships identified here, as well as any secondary drivers.

The correlative relationships between chlorophyll and  $p\text{CO}_2$  that we identify can be separated into five regimes based on controlling factors for chlorophyll production and the dominating component of  $p\text{CO}_2$  change ( $p\text{CO}_2\text{-T}$  or  $p\text{CO}_2\text{-nonT}$ ), and also MLD relationships to chlorophyll which indicate either nutrient limitation (MLD and chlorophyll positively

correlated) or light limitation (MLD and chlorophyll anti-correlated). In Figure 5, the horizontal axis indicates the dominant control on  $p\text{CO}_2$  variability ( $p\text{CO}_2$ -T dominated,  $p\text{CO}_2$ -nonT dominated, or cancellation of  $p\text{CO}_2$ -T and  $p\text{CO}_2$ -nonT responses), and the vertical axis indicates light limited or nutrient limited. In addition to these five regimes, there is an additional layer of complexity in the sign of the  $p\text{CO}_2$  to chlorophyll correlation. If  $p\text{CO}_2$  is negatively (positively) correlated with chlorophyll change, a net drawdown of carbon is (is not) occurring coincident with productivity (Figure 5, plus and minus signs).

The regimes found in the observational analysis, starting from top left and moving clockwise in Figure 5, are:

- *Nutrient limitation with  $p\text{CO}_2$ -T domination leads to a negative correlation between  $p\text{CO}_2$  and chlorophyll.* In these regions, mostly the subtropics, cooling drives down  $p\text{CO}_2$  as it deepens MLDs; this same mixing causes nutrient supply and chlorophyll increases (Figure 5, top left).
- *Nutrient limitation with  $p\text{CO}_2$ -nonT domination leads to a positive correlation between  $p\text{CO}_2$  and chlorophyll.* This occurs when equatorial upwelling brings up high DIC waters and nutrients that support productivity (Figure 5, top middle, top).
- *Nutrient limitation with  $p\text{CO}_2$ -nonT domination leads to a negative correlation between  $p\text{CO}_2$  and chlorophyll.* Negative relationships occur when high latitude MLD deepening or upwelling delivers nutrients to the surface, and the resulting biologically-mediated carbon drawdown is strong enough to drive a net  $p\text{CO}_2$  decrease (Figure 5, top middle, bottom).
- *Nutrient limitation with  $p\text{CO}_2$ -T and  $p\text{CO}_2$ -nonT relationships cancelling such that  $p\text{CO}_2$  and chlorophyll are not correlated.* This occurs only in the subtropics for anomalies and interannual variability, with the interpretation being that cool anomalies drive down  $p\text{CO}_2$

while coincident mixing supplies DIC to the surface to raise  $p\text{CO}_2$ ; at the same time, productivity responds to anomalies of nutrient supply (Figure 5, top right).

- *Light limitation with  $p\text{CO}_2$ -nonT domination leads to a negative correlation between  $p\text{CO}_2$  and chlorophyll.* In these regions, mostly subpolar seasonally stratified biomes (SPSS), shoaling of MLDs leads to increased productivity that strongly draws down DIC. The resulting change in  $p\text{CO}_2$ -nonT governs the total  $p\text{CO}_2$  response (Figure 5, bottom middle).
- *Light limitation with  $p\text{CO}_2$ -T domination leads to a negative correlation between  $p\text{CO}_2$  and chlorophyll.* In these regions, MLD shoaling is, surprisingly, associated with SST cooling that drives down  $p\text{CO}_2$  through the  $p\text{CO}_2$ -T term. At the same time, shoaling leads to chlorophyll increases and a small decrease of  $p\text{CO}_2$ -nonT. This categorization only applies to some seasonally stratified (SPSS and STSS) biomes for monthly anomalies and interannual variability (Figure 5, bottom left).

For some biomes, correlations exist for variable pairs, but not for all of the variables that are required to place the biomes in the above regimes. The discussion below is focused on biomes where  $p\text{CO}_2$  drivers can be determined with  $p\text{CO}_2$ -T and  $p\text{CO}_2$ -nonT and where also nutrient vs. light limitation is indicated via MLD to chlorophyll correlations.

## Seasonality

### *Subtropical Biomes (STPS and STSS)*

Subtropical waters are  $p\text{CO}_2$ -T dominated for carbon (Figure 4, 6a-d) and nutrient limited for chlorophyll (Figure 7a,b). The negative correlation between chlorophyll and  $p\text{CO}_2$  (Figure 6a,b) occurs because warming raises  $p\text{CO}_2$  when stratification limits nutrient supply and productivity in summer, vice versa in winter [Follows and Dutkiewicz, 2002; Dutkiewicz

*et al.*, 2001]. In all STPS and the North Pacific STSS, MLDs are negatively correlated with both  $p\text{CO}_2$  and SST (Figure 7c-f) indicating cooler waters are associated with deeper mixing that supplies DIC to the surface. Though the  $p\text{CO}_2$ -nonT and chlorophyll correlation is strong (Figure 6e,f), the small amplitude of the seasonal cycle as compared to  $p\text{CO}_2$ -T (Figure 4) indicates that the biological pump is not driving the carbon cycle here (Figure 5, top left).

### *Subpolar (SPSS)*

In the subpolar oceans,  $p\text{CO}_2$  is reduced via biological drawdown in summer and increased in winter due to vertical mixing of high DIC subsurface waters to the surface [Takahashi *et al.*, 2002, 2009]. The summertime portion of this cycle is quite clear in the raw timeseries, with a clear inverse relationship between  $p\text{CO}_2$  and chlorophyll (Figure 3). The negative MLD to chlorophyll correlation (Figure 7a,b) indicates all three subpolar biomes (SPSS) are, to first order, light-limited environments [Thomalla *et al.* 2015; Swart *et al.* 2015; Thomalla *et al.* 2011; Fauchereau *et al.* 2011; Dutkiewicz *et al.*, 2001; Follows and Dutkiewicz, 2002]. Certainly, a full description of bloom dynamics is more nuanced, including submesoscale shoaling events that allow for patchy blooms early in the spring and intermittent wind-induced entrainment of nutrients that could maintain summertime productivity [Thomalla *et al.* 2015; Swart *et al.* 2015; Carranza and Gille, 2015; Mahadevan *et al.*, 2012]. These subpolar biomes also have chlorophyll to  $p\text{CO}_2$  relationships that are  $p\text{CO}_2$ -nonT dominated (Figure 6). Thus for seasonality, all SPSS biomes are considered light limited and  $p\text{CO}_2$ -nonT dominated (Figure 5, bottom middle), which is consistent with the biological pump having a significant impact on the ocean carbon uptake. That seasonal change in surface  $p\text{CO}_2$  is biologically-driven is further supported by the large seasonal amplitudes for  $p\text{CO}_2$ -nonT (Figure 4d) that govern the total  $p\text{CO}_2$  cycle (Figure 4b). Temperature effects in these biomes, though strong, are secondary in amplitude ( $p\text{CO}_2$ -T, Figure 4c) and do not show a significant correlation with chlorophyll except in the North

Atlantic subpolar and Southern Ocean ICE (Figure 6c,d) where weak positive correlations occur because of spring warming coincident with productivity increases.

The Southern Ocean is to first order light-limited and is also a HNLC region where iron availability limits productivity [Song *et al.*, 2016; Gervais *et al.*, 2002; Falkowski *et al.*, 1998]. This may be why  $p\text{CO}_2\text{-nonT}$  has a smaller seasonal amplitude in the Southern Ocean SPSS biome than in northern SPSS biomes (Figure 4d). As in the northern SPSS, MLDs are positively correlated with  $p\text{CO}_2$  (Figure 7d), with the scattered negative correlations at 1x1 degree (Figure 7c) potentially attributable to mesoscale activity [Song *et al.*, 2016].

Chlorophyll and  $p\text{CO}_2$  are strongly negatively correlated, due to  $p\text{CO}_2\text{-nonT}$  (Figure 6). In SO SPSS, there is also a weak negative correlation of MLDs and chlorophyll (Figure 7b), indicating light limitation. Though data are sparse and biased to austral summer (Figure 3), these overall relationships remain consistent with Southern Ocean productivity being light-limited and  $p\text{CO}_2\text{-nonT}$  dominated (Figure 5, bottom middle), again consistent with the biological activity significantly driving surface ocean  $p\text{CO}_2$ , and thus ocean carbon uptake.

#### *Equatorial Pacific Biomes*

The two equatorial Pacific biomes exhibit nutrient-controlled,  $p\text{CO}_2\text{-nonT}$  dominated characteristics on seasonal timescales (Figure 5, top middle, top - positive correlation of  $p\text{CO}_2$  to chlorophyll). Seasonal amplitudes are small in the equatorial biomes for all variables (Figure 2c, Figure 4). Positive correlations between chlorophyll and  $p\text{CO}_2$  in the equatorial Pacific biomes are dominated by  $p\text{CO}_2\text{-nonT}$  (Figure 6). These relationships are consistent with an outgassing of carbon upwelled from below the thermocline [Takahashi *et al.*, 2009; McKinley *et al.*, 2004; Feely *et al.*, 1997].



## Monthly Anomalies

Correlation of monthly anomalies (seasonal cycle removed) of chlorophyll and  $p\text{CO}_2$  indicate high-frequency relationships that are best interpreted as short-term responses to local physical anomalies or a modification of the mean seasonal cycle, such as an early or late phytoplankton bloom. These high-frequency perturbations are significant in magnitude, typically about half of the mean seasonal amplitude (Figure 4, Figure 8). With the exception of the equatorial Pacific and subpolar North Pacific, biome-aggregated mechanisms analyzed from monthly anomalies are different than those relationships found for seasonality (Figure 5).

### *Subtropical Permanently Stratified Biomes (STPS)*

In the subtropics, monthly anomalies of chlorophyll and  $p\text{CO}_2$  have significant correlations in some locations at  $1 \times 1$  degree, but there is no significant relationship when averaged to the biome (Figure 9a,b). Similar to the signal at seasonal timescales,  $p\text{CO}_2\text{-T}$  and  $p\text{CO}_2\text{-nonT}$  anomalous correlations of  $p\text{CO}_2$  to chlorophyll are opposed to each other (Figure 9c-f). Chlorophyll anomalies are negatively correlated with  $p\text{CO}_2\text{-T}$  anomalies (Figure 9c,d) and positively correlated with MLD (Figure 10a,b), indicating that anomalous cooling and mixing promotes productivity, i.e. nutrient limitation [Follows and Dutkiewicz, 2002]. Chlorophyll and  $p\text{CO}_2\text{-nonT}$  are positively correlated in the subtropics (Figure 9e,f), consistent with the same mixing supplying carbon to the surface ocean. The two components of  $p\text{CO}_2$  cancel each other, indicating no net impact on surface ocean carbon (Figure 5, top right). This contrasts with clear  $p\text{CO}_2\text{-T}$  domination for the seasonal cycle in this region (Figure 6; Figure 5, top left).

### *Subtropical Seasonally Stratified Biomes (STSS)*

In STSS biomes, transitional zones between the subtropical and subpolar gyres, there are strong negative correlations between chlorophyll and  $p\text{CO}_2$  for monthly anomalies

(Figure 9a,b). Though this correlation is of the same sign as for seasonality, the mechanism is different: the anomalous relationship of MLD to chlorophyll in all three STSS regions is negative, indicating light limitation (Figure 10), contrasting to nutrient limitation on the seasonal timescale (Figure 7). This contrast is consistent with these regions experiencing co-limitation by nutrients and light [Dutkiewicz *et al.*, 2001], with this analysis suggesting distinct timescales on which each limitation is dominant.

In the North Atlantic, the negative relationship of  $p\text{CO}_2$  anomalies to chlorophyll anomalies is due only to  $p\text{CO}_2\text{-T}$ ; in the North Pacific, both  $p\text{CO}_2\text{-T}$  and  $p\text{CO}_2\text{-nonT}$  are significantly negative, with  $p\text{CO}_2\text{-T}$  showing a stronger negative correlation (Figure 9c-f). In the Southern Ocean, the negative relationship of  $p\text{CO}_2$  anomalies to chlorophyll anomalies is only attributable to  $p\text{CO}_2\text{-nonT}$  at the biome scale (Figure 9b,f).

The negative relationship for anomalies of  $p\text{CO}_2$  to chlorophyll in the northern STSS biomes, with  $p\text{CO}_2\text{-T}$  as the driver indicates that warm excursions (high  $p\text{CO}_2\text{-T}$ ) are associated with low chlorophyll. At first glance, this appears counter to expectations if productivity is light limited. This conundrum is resolved by noting that monthly anomalies in MLD have a counter-intuitive positive correlation with SST – i.e. warm SSTs with deep MLDs and cold SSTs with shallow MLDs in all STSS and the North Atlantic SPSS biome (Figure 10e,f) [Martinez *et al.*, 2011, 2016; Carton *et al.*, 2008]. This same relationship is found with unsampled ECCO model output for SST and MLD, confirming it is not a result of sampling bias. In all STSS biomes, MLDs are negatively correlated with chlorophyll (Figure 10a,b) and in the northern STSS biomes, MLDs are positively correlated to  $p\text{CO}_2$  (Figure 10c,d). In summary, warming increases  $p\text{CO}_2$  while anomalous deep MLDs limit chlorophyll production due to light limitation (Figure 10a,b; Figure 5, bottom left).

In the Southern Ocean STSS biome, SST and MLD anomalies are also positively correlated (Figure 10f). With cooling and shoaling, relief of light limitation promotes

productivity [Thomalla et al. 2015; Swart et al. 2015; Thomalla et al. 2011; Fauchereau et al. 2011] and draws down  $p\text{CO}_2$  (Figure 9a,b,e,f). That the Southern Ocean and North Pacific STSS anomaly relationship of chlorophyll to  $p\text{CO}_2$  comes primarily through  $p\text{CO}_2\text{-nonT}$  is consistent with anomalies in biological activity directly driving anomalies in ocean carbon uptake (Figure 5, bottom middle).

### *Subpolar Biomes (SPSS)*

North Pacific and Southern Ocean SPSS biomes are, to first order, light limited and  $p\text{CO}_2\text{-nonT}$  dominated as on seasonal timescales (Figure 5, bottom middle). Amplitudes of monthly anomalies in chlorophyll and  $p\text{CO}_2$  are higher in these biomes than elsewhere (Figure 8), which is consistent with the substantial variability in bloom timing that has been found in these regions [Cole et al., 2015; Thomalla et al. 2011]. Negative correlations of monthly anomalies in chlorophyll and  $p\text{CO}_2$  are attributable to  $p\text{CO}_2\text{-nonT}$  (Figure 9), as for the seasonal (Figure 6). Shoaling MLDs lead to increased chlorophyll and reduced  $p\text{CO}_2$  (Figure 10a-d).

The North Atlantic SPSS, however, has an anomaly mechanism that differs from the seasonal mechanism. This region is light-limited and  $p\text{CO}_2\text{-T}$  dominated (Figure 5, bottom left, Figure 9), similar to the northern hemisphere STSS biomes. As in all STSS biomes, anomalous MLDs and anomalous SSTs are positively correlated – i.e. warm SST with deep MLD (Figure 10) [Martinez et al. 2016; Carton et al., 2008]. Deep MLD anomalies are associated with decreased chlorophyll and increased  $p\text{CO}_2$  (Figure 10). However, this is not indicative of a biologically-mediated response because it is  $p\text{CO}_2\text{-T}$ , not  $p\text{CO}_2\text{-nonT}$ , that dominates the negative correlation between chlorophyll and  $p\text{CO}_2$  (Figure 9). Warm anomalies raise  $p\text{CO}_2$  via direct temperature control (Figure 9b,d), and at the same time are associated with deeper MLDs that limit chlorophyll (Figure 10).

### *Equatorial Biomes*

Monthly anomalies in the equatorial Pacific indicate a nutrient-limited,  $p\text{CO}_2$ -nonT dominated situation as on seasonal timescales (Figure 5, top middle, positive correlation of  $p\text{CO}_2$  to chlorophyll).  $p\text{CO}_2$ -nonT controls the relationship of  $p\text{CO}_2$  to chlorophyll (Figure 9a,b,e,f). Though  $p\text{CO}_2$ -T has a significant relationship, it is not dominant (Figure 9c,d). In the western equatorial Pacific, a positive correlation is also evident between anomalies in chlorophyll and MLD (Figure 10a-b). In both equatorial Pacific biomes, anomalously deep MLDs occur with cooling and lead to increased  $p\text{CO}_2$  (Figure 10c-f).

### **Interannual**

In all biomes, data availability makes it difficult to draw conclusions for interannual timescales (Figure 2). First, limited data means that only biome-mean analyses are possible. Second, at higher latitudes, winter observations of chlorophyll are very rare. Summer-only means in the SPSS biomes (Figure 3, stars) are an alternative way to consider interannual variability at high latitudes, but variability in bloom timing [Bennington *et al.*, 2009; Thomalla *et al.*, 2011, 2015] could quite likely be aliased when only a subset of months are considered. Even at lower latitudes, limited  $p\text{CO}_2$  data prior to 2005 leads to sparse timeseries (12-month smoothed timeseries; bold lines in Figure 2). Thus, for interannual timeseries, only biomes with 12-month running means that span at least 5 years are considered. This limits analysis to the North Atlantic and both Pacific STPS, all three STSS and the two equatorial Pacific biomes.

#### *Subtropical Permanently Stratified Biomes (STPS)*

In the North Atlantic STPS, the strong positive correlation of  $p\text{CO}_2$  and chlorophyll (Figure 11a) is different from the strong negative seasonal relationship (Figure 6b) and the lack of relationship for monthly anomalies (Figure 9b). The  $p\text{CO}_2$  to chlorophyll relationship is clearly due to  $p\text{CO}_2$ -nonT (Figure 11a,c). This suggests that years of higher chlorophyll

occur with years of greater nutrient supply that is accompanied by greater DIC supply.

However, correlations are not significant between interannual variability in MLD and chlorophyll (Figure 12a), and thus nutrient or light limitation cannot be clearly determined, and we do not place this biome on the grid of Figure 5. Horizontal advective supply of nutrients and DIC could be driving this positive association between interannual change in chlorophyll and  $p\text{CO}_2\text{-nonT}$  on these timescales [Dave *et al.*, 2015; Lozier *et al.*, 2011].

In the North Pacific STPS, there is also a positive correlation of  $p\text{CO}_2$  and chlorophyll, again differing from the strong negative seasonal relationship (Figure 6b).

Shoaling MLDs are associated with warming (Figure 12c) and increased  $p\text{CO}_2$  (Figure 12b).

In contrast to the North Atlantic STPS, the chlorophyll to  $p\text{CO}_2$  relationship is due to  $p\text{CO}_2\text{-T}$  and is damped by  $p\text{CO}_2\text{-nonT}$  (Figure 11). Though together this suggests a light-limitation mechanism, there is no relationship of MLD to chlorophyll (Figure 12a). As in the North Atlantic STPS, horizontal advection may be important [Dave and Lozier, 2013; Ayers and Lozier, 2010, 2012; Dave and Lozier, 2010]. In the South Pacific STPS, there is no correlation of  $p\text{CO}_2$  to chlorophyll, but chlorophyll is positively related to  $p\text{CO}_2\text{-T}$ , and negatively to  $p\text{CO}_2\text{-nonT}$  (Figure 11) and MLDs and chlorophyll are positively related (Figure 12), indicating nutrient limitation; thus this biome falls in the same regime as for its monthly anomalies (Figure 5, top right).

#### *Subtropical Seasonally Stratified Biomes (STSS)*

Interannual relationships in the North Pacific STSS are the same as for the seasonal cycle (Figure 5, top left). Negative correlations between  $p\text{CO}_2$  and chlorophyll are driven more by  $p\text{CO}_2\text{-T}$  than  $p\text{CO}_2\text{-nonT}$  (Figure 11), and interannual variability in MLDs is positively associated with chlorophyll (Figure 12a), indicating nutrient limitation. In the North Atlantic STSS, there is a negative correlation between  $p\text{CO}_2$  and chlorophyll that is also driven more by  $p\text{CO}_2\text{-T}$  than  $p\text{CO}_2\text{-nonT}$  (Figure 11). However, here interannual

variability in MLDs is negatively associated with chlorophyll (Figure 12a), indicating light limitation, the same finding as for monthly anomalies in this biome (Figure 5, bottom left).

Interannual relationships in the Southern Ocean STSS are different from any other region on any timescale. Here, a negative correlation between  $p\text{CO}_2$  and chlorophyll is driven by  $p\text{CO}_2\text{-nonT}$  and damped by  $p\text{CO}_2\text{-T}$  (Figure 11) and MLDs are positively correlated with chlorophyll (Figure 12a), indicating nutrient limitation. Warming is associated with deeper mixing, and for this biome, also likely greater upwelling (Figure 12c), and thus nutrient supply to the surface. Despite likely increased DIC supply from depth, and warming raising  $p\text{CO}_2$  (Figure 11b), the  $p\text{CO}_2\text{-nonT}$  term is negative which is consistent with an increased biological pump being strong enough to cause a net carbon drawdown (Figure 11a,c). This provides evidence that the biological activity is directly important to interannual variability of the carbon cycle in SO STSS (Figure 5, top middle, bottom - anti-correlation of  $p\text{CO}_2$  to chlorophyll). The underlying driver for these interannual anomalies is likely variable atmospheric forcing [Landschutzer *et al.*, 2016; Lovenduski *et al.*, 2007, 2008].

#### *Equatorial Biomes*

In the west and east equatorial Pacific, the positive  $p\text{CO}_2$  to chlorophyll correlation is consistent with previous findings that El Niño / Southern Oscillation variability governs interannual change – i.e. during El Niño, less upwelling of carbon and nutrients leads to both lower  $p\text{CO}_2$  and reduced productivity [Sutton *et al.*, 2016; McKinley *et al.*, 2004; Feely *et al.*, 1997].

## **4. Discussion**

Seasonal relationships between the carbon cycle and ocean primary productivity that are identified here have been inferred previously based on climatological estimates of  $p\text{CO}_2$  seasonality [Takahashi *et al.*, 1993, 2002, 2009], with satellite chlorophyll and numerical

models [Cole *et al.*, 2015; Bennington *et al.*, 2009; Dutkiewicz *et al.*, 2001; Follows and Dutkiewicz, 2002], and in situ data [Kortzinger *et al.*, 2008a,b]. We have re-evaluated these associations with co-located in-situ pCO<sub>2</sub> and satellite chlorophyll observations for the longest available record (1998-2014). These data provide further support for the seasonal mechanisms previously proposed in all biomes with sufficient data. For higher (monthly anomaly) and lower frequencies (interannual), this analysis offers a first global assessment of these relationships. The focus here is on qualitative indications with respect to correlation significance and sign, with future work needed to fully elucidate driving mechanisms.

These data provide further evidence of a counter-intuitive link in some northern subpolar and subtropical / subpolar transition regions of cool temperatures, shoaling MLDs, chlorophyll increase and reduced pCO<sub>2</sub> via pCO<sub>2</sub>-T (bottom left, Figure 5). This relationship is found only for monthly anomalies in the North Atlantic SPSS and STSS, and North Pacific STSS; and for interannual variability also in the North Atlantic STSS. Horizontal advective processes have been shown to contribute significantly to carbon and nutrient supply in the subtropical North Atlantic [Dave *et al.*, 2015] and North Pacific [Ayers and Lozier, 2010, 2012]. There is also evidence of strong horizontal advective signals in the North Atlantic SPSS [Martinez *et al.*, 2016; Thomas *et al.*, 2008; Carton *et al.*, 2008; Hakkinen and Rhines, 2004]. In the North Atlantic, multi-decadal variability associated with the North Atlantic Oscillation (NAO) and/or Atlantic Multi-decadal Oscillation (AMO) may need to be considered [Breedon and McKinley, 2016; Martinez *et al.*, 2016]. Future work will likely need to expand on the 1-dimensional physical framework used here.

There are caveats worthy of note in this global-scale, multi-timescale study. First, is that data sparsity remains an issue, particularly for the interannual timescale. For monthly anomaly and seasonal timescales, the 1x1 degree correlations illustrated alongside the biome correlations provide confidence that the biome scales are representative of the majority of



local correlations. Nonetheless, the 1x1 correlations also indicate many instances of correlations opposite to the biome mean in many locations, with a variety of potential causes. In the Southern Ocean, positive chlorophyll to MLD correlations have been attributed to peak chlorophyll occurring before mixed layer depths have fully shoaled combined with limited winter data [Fauchereau *et al.* 2011]. Submesoscale features can cause temporary restratification events and support blooms even when large-scale mixed layer depths remain deep [Thomalla *et al.* 2015; Swart *et al.* 2015; Mahadevan *et al.*, 2012]. Mesoscale features have several effects on chlorophyll, including stirring of the background chlorophyll field, trapping and horizontally translating chlorophyll, and modifying vertical nutrient supply at the eddy center [Gaube *et al.* 2014]. Second, as noted before, satellite chlorophyll is not a direct measure of organic matter export, and thus the biological carbon pump. This connection is modified by both phytoplankton physiology [Behrenfeld *et al.*, 2015; Dave *et al.*, 2015; Siegel *et al.*, 2013] and complex processing through the upper ocean food web [Mouw *et al.* 2016; Siegel *et al.* 2014; Cermeno *et al.*, 2008]. Since we find the strongest links between biological activity and pCO<sub>2</sub> at high latitudes, this concern is at least partially mitigated. Chlorophyll primarily represents biomass change, not photoadaptation, in these regions [Gaube *et al.* 2014; Siegel *et al.*, 2013].

Despite these caveats, this analysis supports notable mechanistic findings. With Figure 13, we summarize these across timescales and in the context of the regimes outlined above (Figure 5). Outside the tropics, pCO<sub>2</sub> and chlorophyll are negatively correlated or uncorrelated, but the driving mechanisms vary across timescales. For seasonality, the subtropical (STPS and STSS) carbon cycle is temperature dominated and nutrient limited. At subpolar latitudes (SPSS), light limitation with a pCO<sub>2</sub>-nonT domination is consistent with a substantial role for the biological pump in carbon cycle seasonality. For monthly anomalies, the subtropics (STPS only) experience a cancellation of pCO<sub>2</sub> drivers coupled with nutrient

limitation. Anomalies in the Southern Ocean STSS and North Pacific SPSS biomes are characterized by nutrient limitation and  $p\text{CO}_2$ -nonT dominance, indicating that biological pump anomalies could drive carbon uptake anomalies. For interannual variability, northern STSS carbon variability is temperature dominated. Southern Ocean STSS is the only biome where the biological pump appears to be strong enough to drive interannual carbon cycle variability. These relationships are consistent with the biological pump being dominant to carbon uptake only at high latitudes and for select timescales (dots, Figure 13).

That we find the biological pump drives carbon cycle change on all timescales in the Southern Ocean is consistent with previous studies suggesting an important role for this region's biological pump in glacial-interglacial shifts in the partitioning of carbon between the atmosphere and ocean [Martinez-Garcia *et al.*, 2014; Sigman *et al.*, 2010; Kohfeld *et al.*, 2005]. The Southern Ocean's unique ability to influence the global inventory of "preformed" nutrients, which are nutrients returned from the surface to the deep ocean before being biologically utilized has been frequently invoked in this context [Marinov *et al.*, 2006; Ito *et al.*, 2005]. An important caveat is that the longest timescales that can be investigated in this study are orders of magnitude shorter than those of glacial-interglacial change. Nevertheless, this consistency makes for a tantalizing connection that deserves further study.

## 5. Conclusions

A primary thrust of this investigation is to determine when and where the available data provide evidence that surface ocean primary productivity, a proxy for the biological carbon pump, may act directly to control ocean carbon uptake. Future studies will be needed to further quantify the relationships identified herein.

The locations where these data support a direct biological pump influence on the ocean carbon sink are indicated on Figure 13 (dots). In the Northern Hemisphere on seasonal

timescales, only in SPSS biomes does the biological pump control  $p\text{CO}_2$  and drive ocean carbon uptake. For monthly anomalies in the Northern Hemisphere, the biological pump is only found to be a driver in the North Pacific SPSS and Southern Ocean STSS. It is only in the Southern Ocean where this analysis indicates that the biological pump may drive the carbon cycle on all timescales analyzed (SO SPSS for seasonal, SO STSS for anomaly and interannual). This finding for the Southern Ocean is intriguing both for current and future climate studies, as well as in the context of glacial-interglacial change.

This analysis, as summarized in Figure 13, indicates that well-established seasonal mechanisms that link the carbon cycle and biological productivity [Sarmiento and Gruber, 2006; Takahashi *et al.*, 1993, 2002, 2009; Sverdrup, 1958] cannot be assumed to be applicable at other timescales. This finding adds a direct link to the ocean carbon cycle from recent studies of ocean productivity that have shown that seasonal mechanisms cannot be invoked to explain variability on longer timescales [Martinez *et al.*, 2016, Barton *et al.*, 2014; Dave and Lozier, 2013; Lozier *et al.*, 2011; Dave and Lozier, 2010]. Looking forward, this suggests that the impacts of ocean productivity on the ocean carbon cycle in a warmer climate are likely to be significantly more complex than what can be gleaned from seasonal relationships that are well established [Takahashi *et al.*, 2002, 2009] and further confirmed with this study.

Continued satellite ocean color satellites, improved ocean color algorithms, and in-situ monitoring of  $p\text{CO}_2$  from ships and with autonomous technologies are critical to refine the relationships identified here. Improved process understanding of the links between remotely sensed ocean color and the export of carbon from the surface ocean is also essential. High-frequency observation efforts, especially in the Southern Ocean, will allow for further research on this topic. For example, the Drake Passage observation effort provides monthly observations of simultaneous fluorometry and  $p\text{CO}_2$  data since 2012. These observations,

coupled with ever-improving mechanistic models, will allow for better understanding of the influence of the biological pump on the past, present and future ocean carbon cycle.

## Acknowledgments

We would like to thank the scientists working on the ECCO model for making the output publically available to a wide-community (<http://www.ecco-group.org/products.htm>). The Surface Ocean CO<sub>2</sub> Atlas (SOCAT) is an international effort, endorsed by the International Ocean Carbon Coordination Project (IOCCP), the Surface Ocean Lower Atmosphere Study (SOLAS) and the Integrated Marine Biogeochemistry and Ecosystem Research program (IMBER), to deliver a uniformly quality-controlled surface ocean CO<sub>2</sub> database. The many researchers and funding agencies responsible for the collection of data and quality control are thanked for their contributions to SOCAT. This data can be accessed at [www.socat.info](http://www.socat.info). The chlorophyll product is available at <http://wiki.icess.ucsb.edu/measures/Products>. We thank NASA (NNX/13AC53G) for funding this research.

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Table 1: Correlations of logChl and pCO<sub>2</sub> by biome for seasonal, monthly anomaly, and interannual variability timescales. Bold values designate significant correlations (p-value ≤ 0.05). 'Not reported' values are due to insufficient available data. These values correspond to the map in Figure 6b, 9b, and 11a.

Biome	Seasonal	Monthly Anom	12-mon Running Means
NP SPSS	<b>-0.4</b>	<b>-0.36</b>	Not reported
NP STSS	<b>-0.87</b>	<b>-0.65</b>	<b>-0.51</b>
NP STPS	<b>-0.66</b>	<b>-0.05</b>	<b>0.26</b>
West EQU Pac	<b>0.41</b>	<b>0.43</b>	<b>0.72</b>
East EQU Pac	<b>0.42</b>	<b>0.41</b>	<b>0.46</b>
SP STPS	<b>-0.47</b>	-0.01	Not reported
NA SPSS	<b>-0.55</b>	<b>-0.25</b>	Not reported
NA STSS	<b>-0.62</b>	<b>-0.6</b>	<b>-0.67</b>
NA STPS	<b>-0.66</b>	<b>0.14</b>	<b>0.73</b>
Atl EQU	-0.1	0.15	Not reported
SA STPS	<b>-0.32</b>	0.11	Not reported
IND STPS	<b>-0.56</b>	<b>0.22</b>	Not reported
SO STSS	<b>-0.51</b>	<b>-0.5</b>	<b>-0.33</b>
SO SPSS	<b>-0.56</b>	<b>-0.35</b>	Not reported
SO ICE	<b>-0.48</b>	<b>-0.39</b>	Not reported

Figure 1

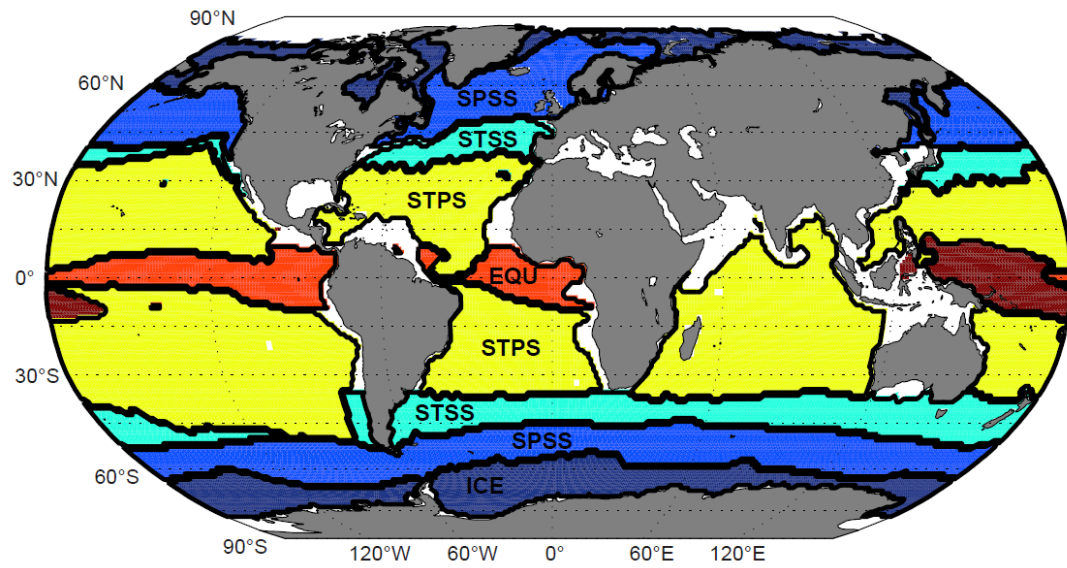


Figure 1: Global ocean biome map. ICE: seasonally covered ice biome; SPSS: subpolar seasonally stratified biome; STSS: subtropical seasonally stratified biome; STPS subtropical permanently stratified biome; EQU: equatorial biome.



Figure 2

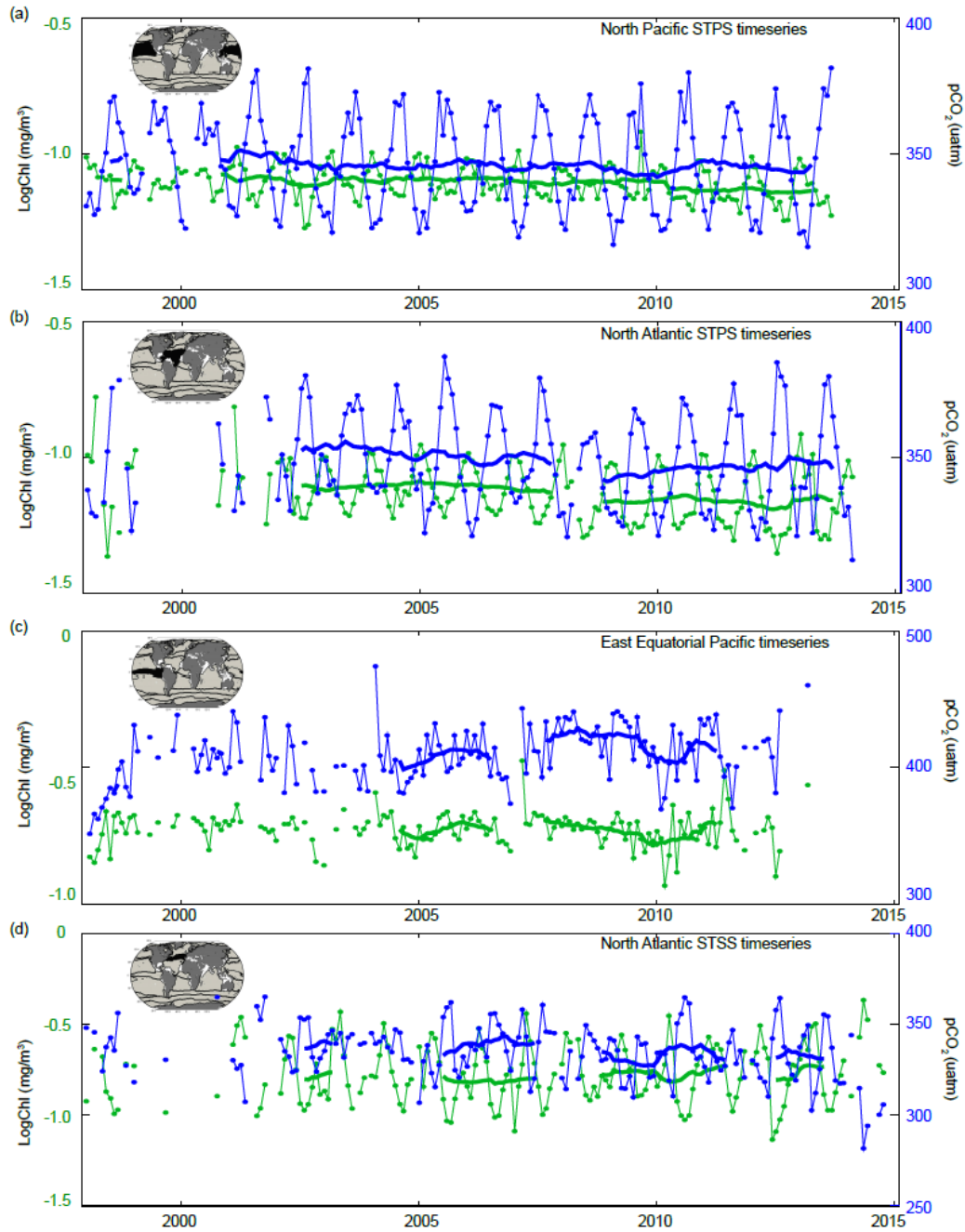


Figure 2: Timeseries of biome monthly means of logChl (green) and pCO<sub>2</sub> (blue) for years 1998-2014 for: (a) North Pacific subtropical permanently stratified biome, (b) North Atlantic subtropical permanently stratified biome, (c) East Equatorial Pacific biome, and (d) North Atlantic subtropical seasonally stratified biome. Biome locations are highlighted in black on inset maps. Bold lines are 12-month running means where 12 continuous months of observations are available.



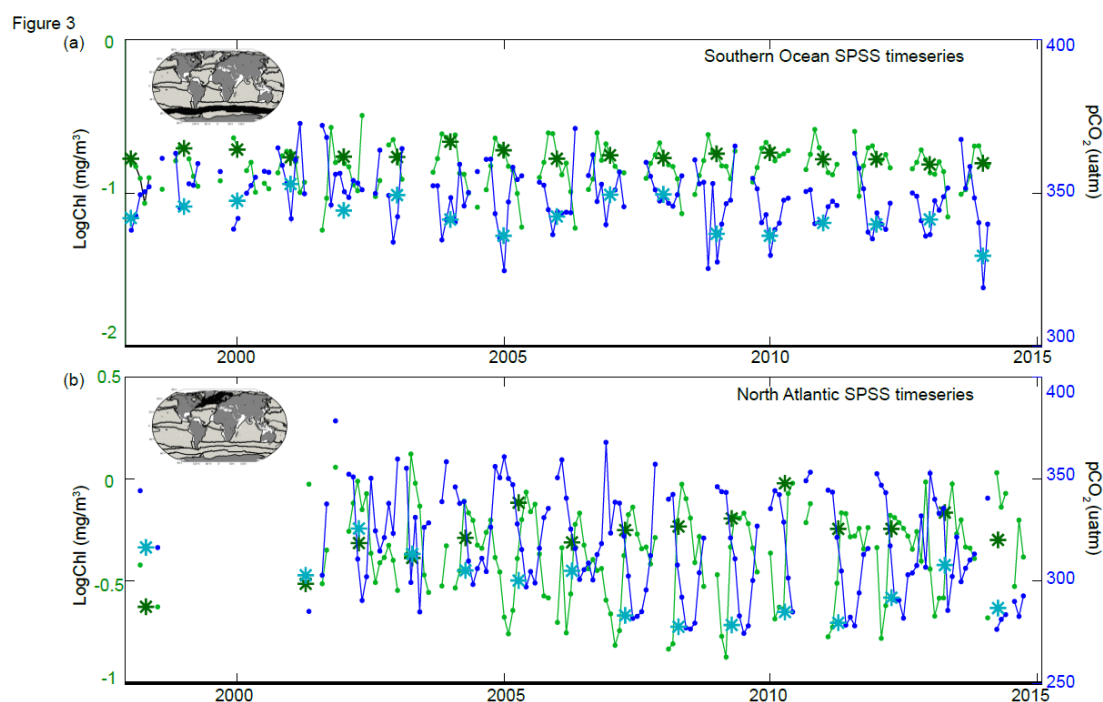


Figure 3: Timeseries of biome monthly means of logChl (green) and pCO<sub>2</sub> (blue) for years 1998-2014 for: (a) Southern Ocean subpolar seasonally stratified biome, and (b) North Atlantic subpolar seasonally stratified biome. Biome locations are highlighted in black on inset maps. Stars are summer averages (DJF or JJA depending on hemisphere).

Figure 4

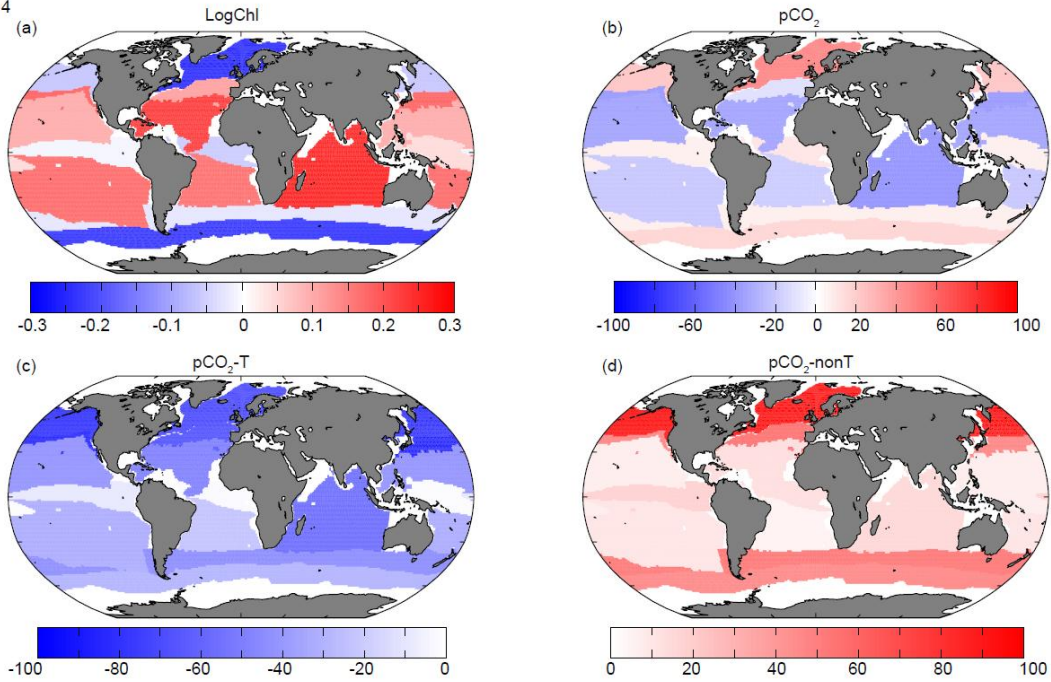


Figure 4: Maps of seasonal amplitudes by biome, calculated from harmonic fit to biome means: (a) logChl ( $\text{mg}/\text{m}^3$ ), (b) pCO<sub>2</sub> (uatm), (c) pCO<sub>2</sub>-T (uatm), and (d) pCO<sub>2</sub>-nonT (uatm). Seasonal amplitudes are calculated as winter minus summer so that northern and southern hemisphere can be compared directly. The intensity of the color represents the amplitude of the seasonal cycle.

Figure 5

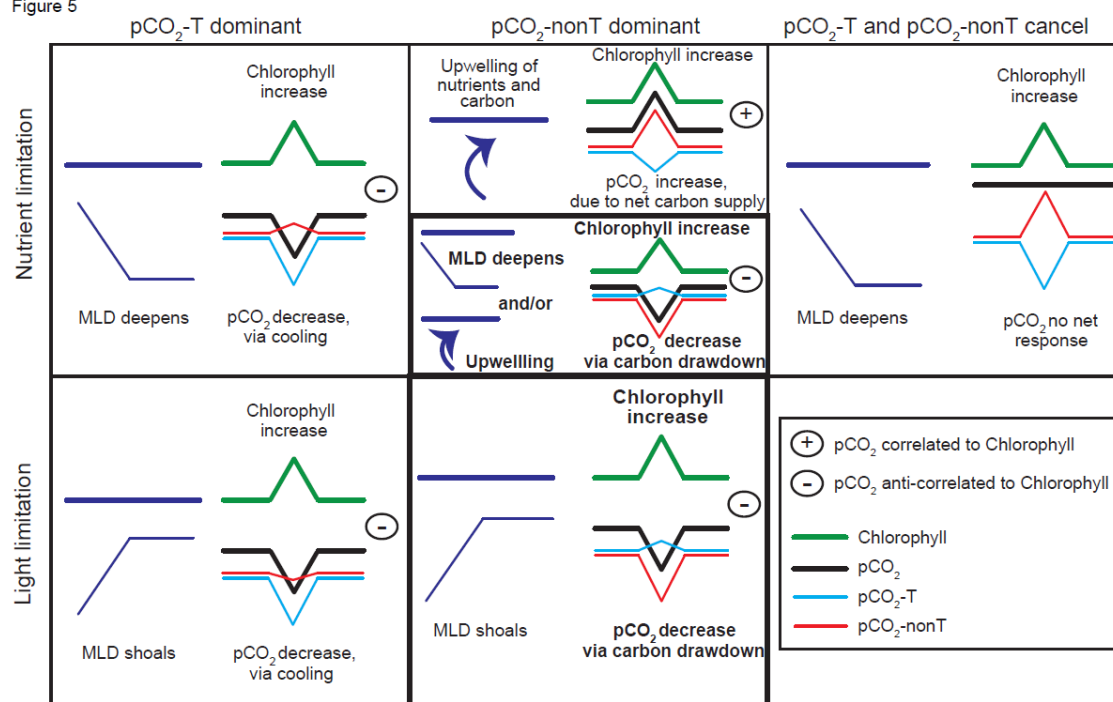


Figure 5: Grid showing dominant controls on  $p\text{CO}_2$  variability (horizontal axis) and the limiting factor (vertical axis). Each box includes schematics of relationships between chlorophyll,  $p\text{CO}_2$ , and MLDs. Plus and minus signs indicate correlation or anti-correlation of  $p\text{CO}_2$  and chlorophyll.

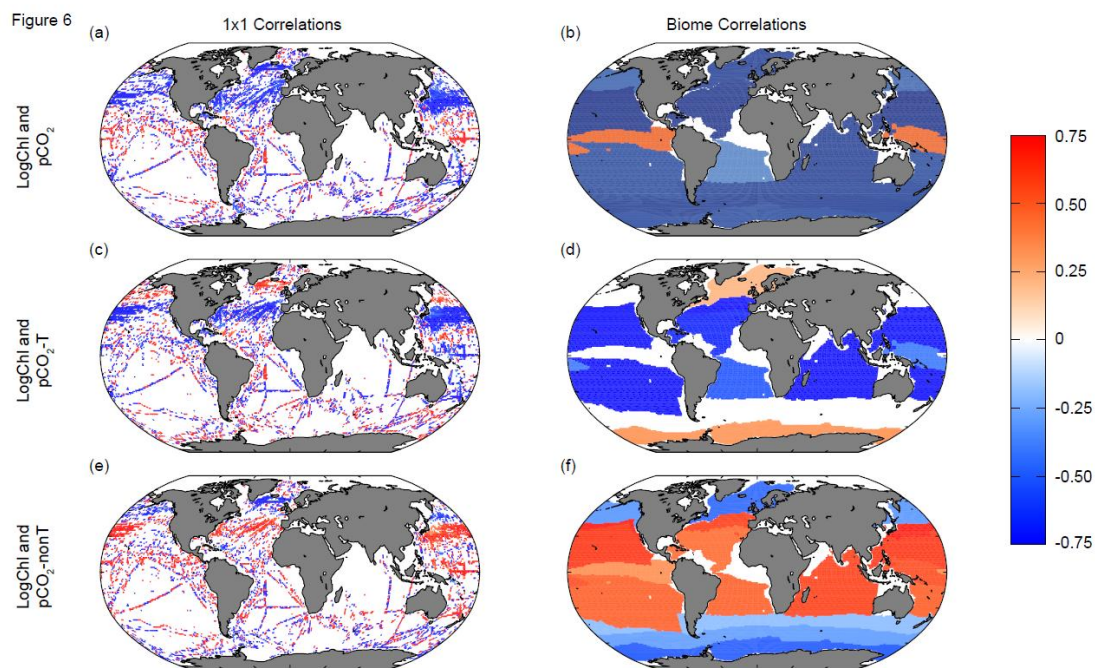


Figure 6: Map of monthly mean correlations at 1x1 degree (a,c,e) and biome scales (b,d,f) for (a-b) logChl and  $pCO_2$ , (c-d) logChl and  $pCO_2-T$ , and (e-f) logChl and  $pCO_2-nonT$ .

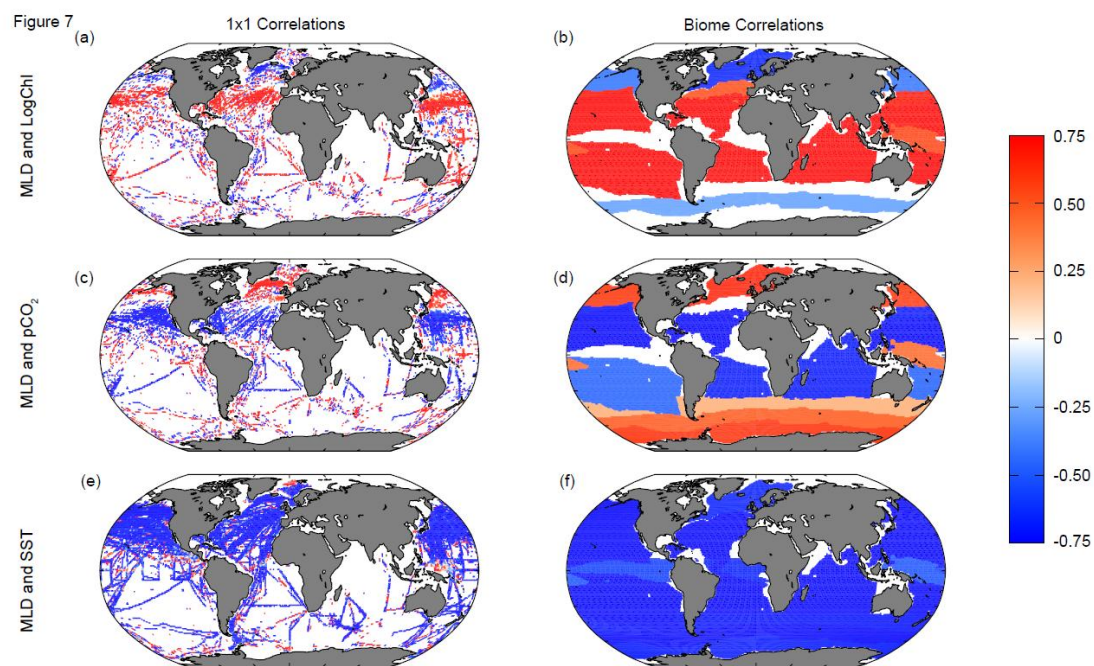


Figure 7: Map of monthly mean correlations at 1x1 degree (a,c,e) and biome scales (b,d,f) for (a-b) MLD and logChl, (c-d) MLD and pCO<sub>2</sub>, and (e-f) MLD and SST. MLDs are positive down.



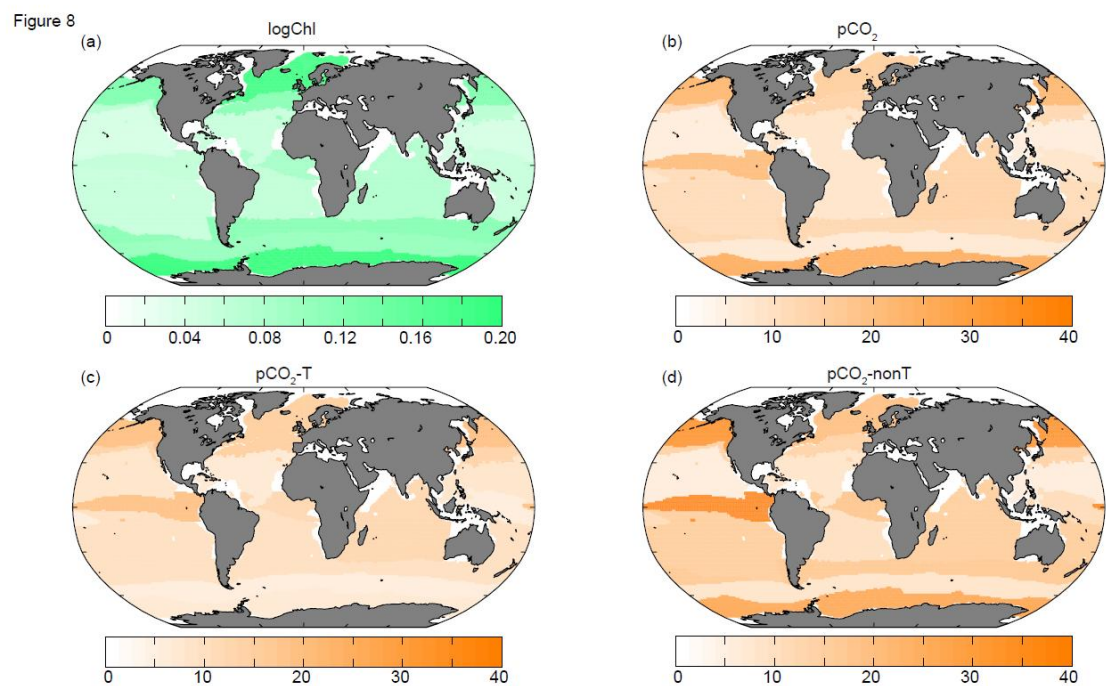


Figure 8: Maps showing standard deviation of biome monthly anomalies for (a) log-Chl ( $\text{mg/m}^3$ ), (b)  $\text{pCO}_2$  (uatm), (c)  $\text{pCO}_2\text{-T}$  (uatm) and (d)  $\text{pCO}_2\text{-nonT}$  (uatm).

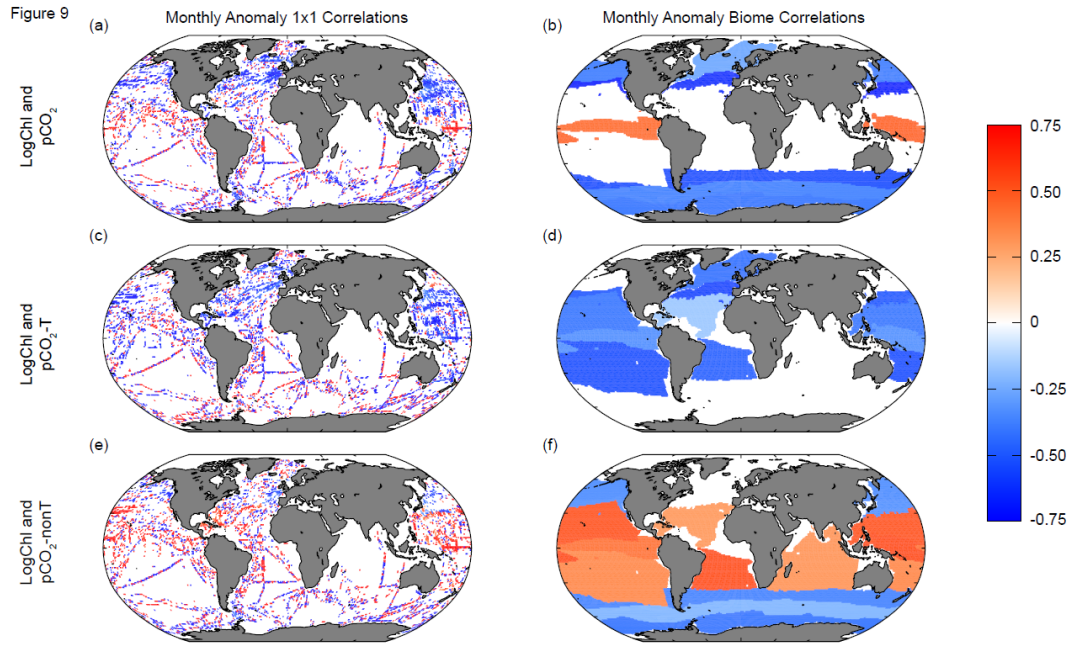


Figure 9: Correlation maps of monthly mean anomalies at 1x1 degree (a,c,e) and biome scales (b,d,f) for (a-b) logChl and  $pCO_2$ , (c-d) logChl and  $pCO_2-T$ , and (e-f) logChl and  $pCO_2-nont$ .



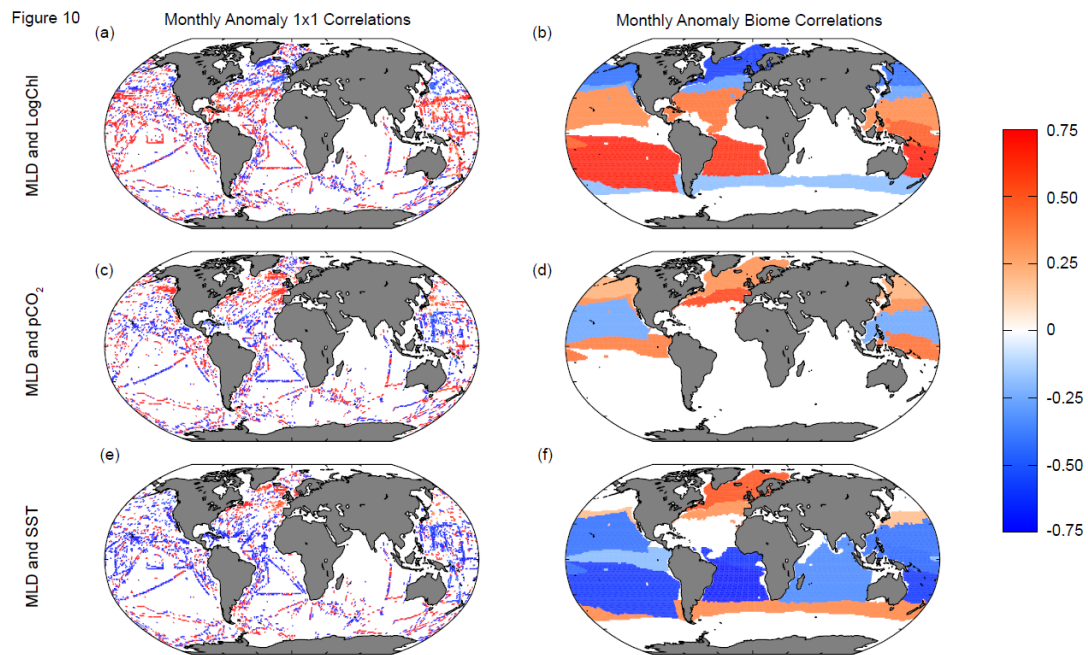


Figure 10: Correlation maps of monthly mean anomalies at 1x1 degree (a,c,e) and biome scales (b,d,f) for (a-b) MLD and logChl, (c-d) MLD and  $p\text{CO}_2$ , and (e-f) MLD and SST. MLDs are positive down.

Figure 11

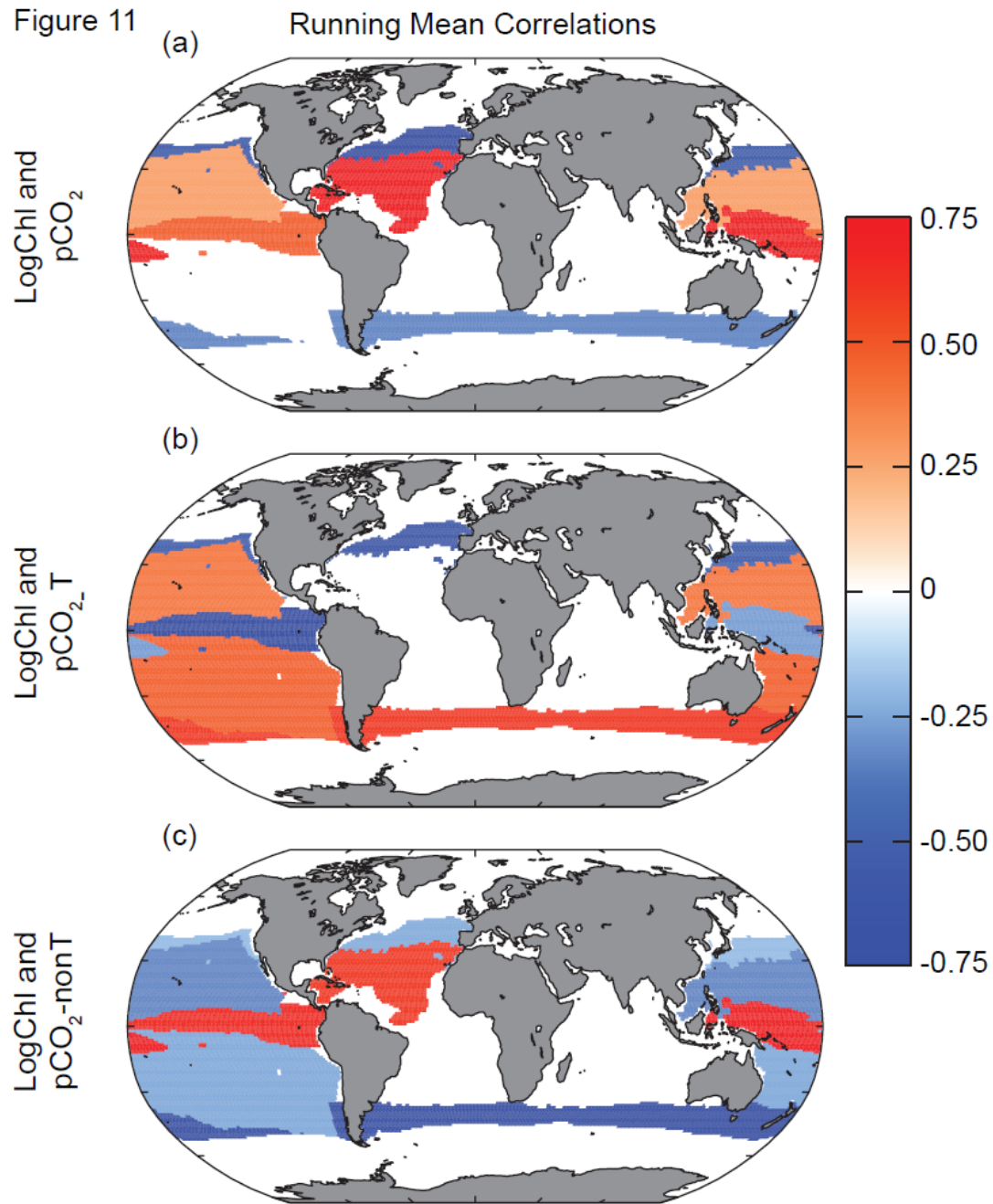


Figure 11: Correlation maps of interannual averages (12 month running means) at biome scales for (a) logChl and  $p\text{CO}_2$ , (b) logChl and  $p\text{CO}_2\text{-T}$ , and (c) logChl and  $p\text{CO}_2\text{-nonT}$ .

Figure 12

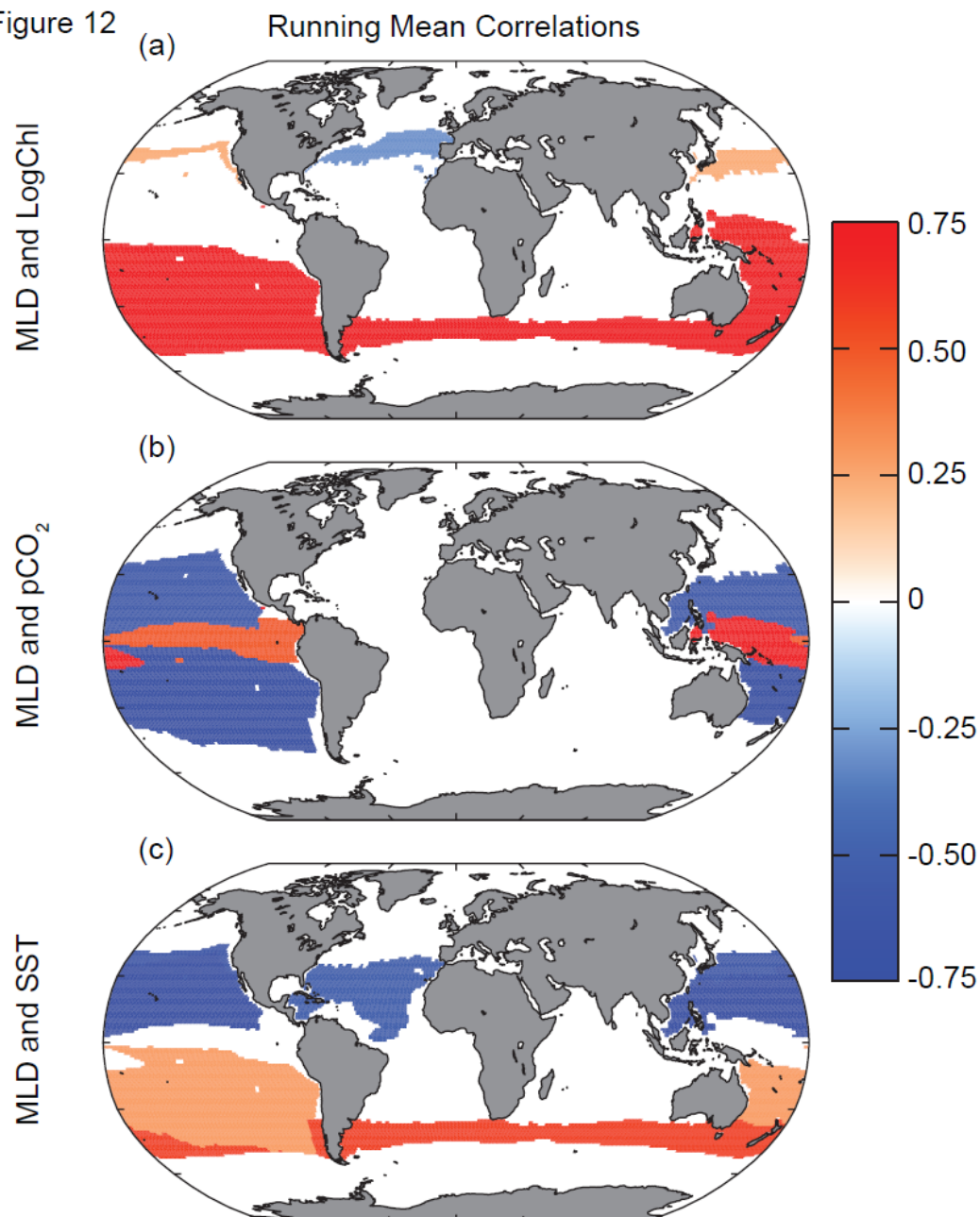


Figure 12: Correlation maps of interannual variability (12 month running means) at biome scales for (a) MLD and logChl, (b) MLD and  $p\text{CO}_2$ , and (c) MLD and SST. MLDs are positive down.

Figure 13 (a)

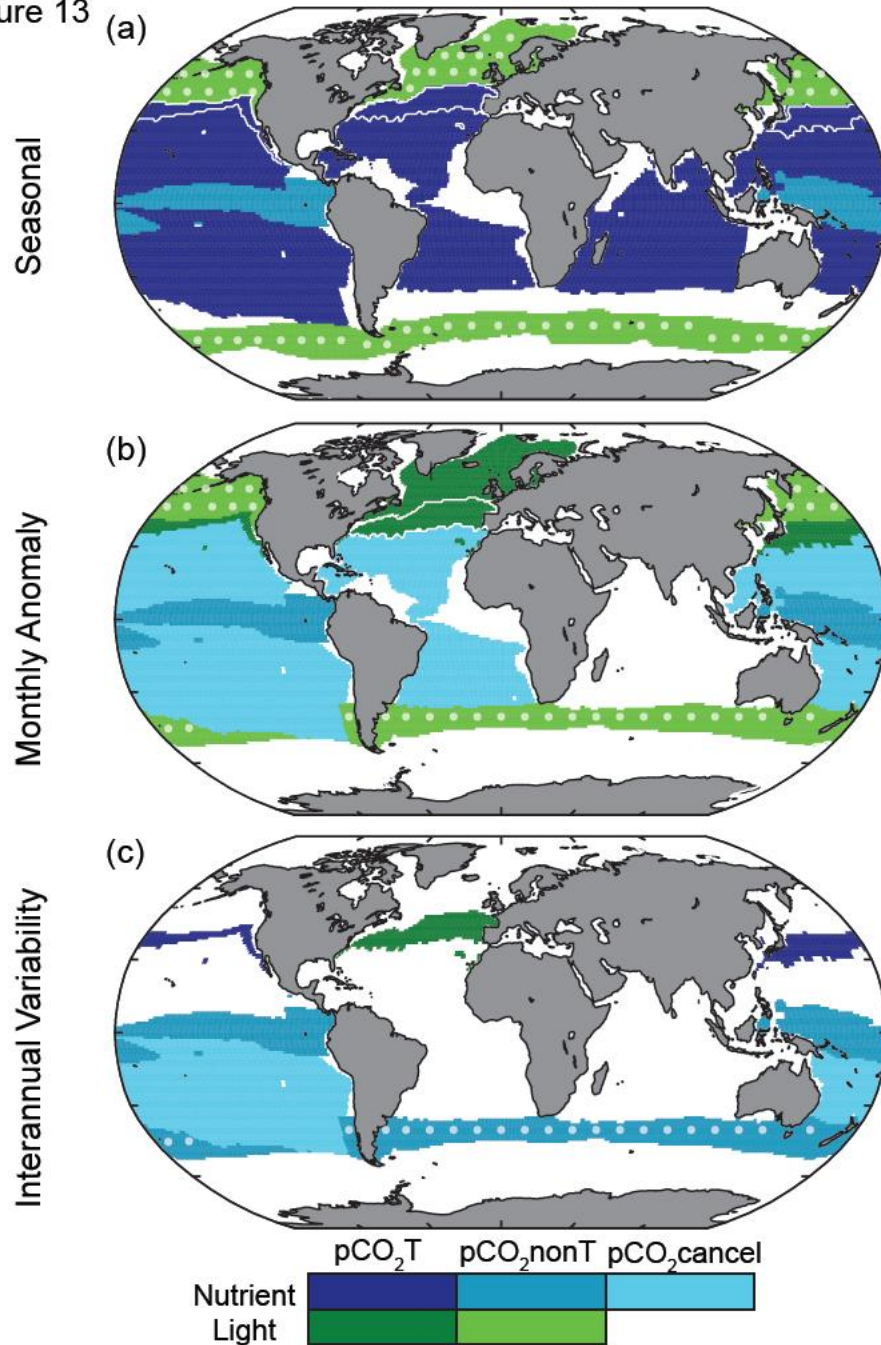


Figure 13: Maps of regime assignments corresponding to Figure 5. Regimes assigned by biome and timeseries: (a) seasonal, (b) monthly anomalies, and (c) interannual variability. Blue regions nutrient limitation and green regions are light limited. Dots highlight biomes where data are consistent with a direct biological pump influence on the surface ocean carbon cycle.