

## Interannual Variation in Phytoplankton Class-specific Primary Production at a Global Scale

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**Abstract:** We used the NASA Ocean Biogeochemical Model (NOBM) combined with remote sensing data via assimilation to evaluate the contribution of 4 phytoplankton groups to the total primary production. First we assessed the contribution of each phytoplankton groups to the total primary production at a global scale for the period 1998-2011. Globally, diatoms were the group that contributed the most to the total phytoplankton production (~50%, the equivalent of ~20 PgC y<sup>-1</sup>). Coccolithophores and chlorophytes each contributed to ~20% (~7 PgC y<sup>-1</sup>) of the total primary production and cyanobacteria represented about 10% (~4 PgC y<sup>-1</sup>) of the total primary production. Primary production by diatoms was highest in high latitude (>45°) and in major upwelling systems (Equatorial Pacific and Benguela system). We then assessed interannual variability of this group-specific primary production over the period 1998-2011. Globally the annual relative contribution of each phytoplankton groups to the total primary production varied by maximum 4% (1-2 PgC y<sup>-1</sup>). We assessed the effects of climate variability on the class-specific primary production using global (i.e. Multivariate El Niño Index, MEI) and ‘regional’ climate indices (e.g. Southern Annular Mode (SAM), Pacific Decadal Oscillation (PDO) and North Atlantic Oscillation (NAO)). Most interannual variability occurred in the Equatorial Pacific and was associated with climate variability as indicated by significant correlation ( $p < 0.05$ ) between the MEI and the class-specific primary production from all groups except coccolithophores. In the Atlantic, climate variability as indicated by NAO was significantly correlated to the primary production of 2 out of the 4 groups in the North Central Atlantic (diatoms/cyanobacteria) and in the North Atlantic (chlorophytes and coccolithophores). We found that climate variability as indicated by

SAM had only a limited effect on the class-specific primary production in the Southern Ocean. These results provide a modeling and data assimilation perspective to phytoplankton partitioning of primary production and contribute to our understanding of the dynamics of the carbon cycle in the oceans at a global scale.

**Keywords:** Primary production; Phytoplankton composition; Chl-a; remote sensing; MODIS; SeaWiFS; biogeochemical models

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## 1. Introduction

Phytoplankton is responsible for over half of the net primary production on earth [1]. The venue of satellite coincided with the improvement of our knowledge on global dynamics of phytoplankton through the development of ocean color algorithms. More recently, progress has been made in discerning phytoplankton types using algorithms [e.g. 2,3-6] and models [e.g. 7,8-11]. The knowledge on the contribution of various phytoplankton groups to the total primary production is still poorly understood. Data from satellite observations [i.e. 12] suggest that for upwelling regions, photosynthetic rates by microplankton is higher than that of nanoplankton but that when the spatial extent is considered, the production by nanoplankton is comparable or even larger than microplankton. Climate variability has been shown to drive phytoplankton composition shifts in some regions [13-16]. These changes are likely to have an effect on primary production. The contribution of each group to the total primary production and how their contribution changes on seasonal and interannual scales remains very poorly characterized. To our knowledge, there have been few attempts so far at estimating size-specific primary productivity at a global scale [i.e. 17,18,19]. Uitz et al. [5] used the primary production model of Morel [20] to derive size-specific phytoplankton primary production over the upper water column. This approach estimated the contribution of pico-, nano- and microphytoplankton to the total primary production.

Although there has been few attempts at estimating size-specific primary production, to our knowledge this paper represents the first attempt at estimating taxonomic/functional class-specific primary production at a global scale. We use the NASA Ocean Biogeochemical Model (NOBM) combined with ocean color remote sensing data assimilation to (1) assess the climatological class-specific primary production globally and (2) assess the contribution of each group to the total primary production on an interannual scale for the period 1998-2011. Class-specific primary production is reported globally and in 12 major oceanographic regions for total chlorophyll, diatoms, chlorophytes, coccolithophores and cyanobacteria.

## 2. Results and Discussion

### 2.1. Climatology of primary production and comparison with VGPM

Globally, the total primary production was of 39 PgC y<sup>-1</sup> with the majority of this total production coming from the Equatorial Pacific (~17% or 6.5 PgC y<sup>-1</sup>) and the South and North Central Pacific (~12%, Table 1). Antarctic contributed the fourth most to the global primary production with 4.5 PgC

(~11%) produced annually. This estimate of total primary production at a global scale fits in the lower range of values previously reported by Carr et al. [21] in an intercomparison of 24 models for which total primary production ranged between 40 and 60 PgC y<sup>-1</sup>. This discrepancy can be explained by the fact that the northernmost latitude covered by NOBM is 72°N. Similarly to the spatial distribution of primary production in the NOBM, Carr et al. [21] found that most total primary production occurred in the Pacific Ocean (a total of 21 PgC y<sup>-1</sup> or 44% for the entire basin compared to 17 PgC y<sup>-1</sup> or 44% for the entire Pacific Ocean using the NOBM).

Carr et al. [21] compared the global primary production fields corresponding to 8 months of 1998 and 1999. Comparing one satellite-based approach with the NOBM for a longer period (1998-2011), we found that the primary production from the model was greater than that of the satellite-based approach (VGPM) by ~6 PgC y<sup>-1</sup> (Figure 1). Within the 12 regions, annual regional means from both approaches was always within ~2 PgC y<sup>-1</sup>. The greatest difference was observed in the Equatorial regions (model between 1.4 and 2.3 PgC y<sup>-1</sup> higher than VGPM) and in Antarctic (VGPM 1.2 PgC y<sup>-1</sup> higher than the model). In all regions except Antarctic, the North Pacific and North Atlantic, i.e., the high latitudes, the primary production from the model was greater than the one from the satellite-based approach.

Globally, diatoms were the group that contributed the most to the total phytoplankton production (~50%, the equivalent of ~20 PgC y<sup>-1</sup>, Figure 2). Coccolithophores and chlorophytes each contributed to ~20% (~7 PgC y<sup>-1</sup>) of the total primary production. Cyanobacteria represented about 10% (~4 PgC y<sup>-1</sup>) of the total primary production. Primary production by diatoms was highest in high latitudes (>40°) and in major upwelling systems (Equatorial Pacific and Benguela system, Figure 3a). In Antarctic and the North Pacific, diatoms contributed more than 85% to the total primary production. The only region where diatoms contributed to <40% of the primary production was in the Equatorial Atlantic and the North Central Atlantic. Maximum primary production for chlorophytes occurred in regions directly adjacent to those regions where maximum primary production from diatoms was encountered (i.e. Equatorial Pacific and Benguela systems, Figure 3b) and in the Equatorial Indian. Coccolithophores contributed considerably to the total primary production in the North Central Atlantic (38%, see Table 1 for an equivalence in PgC y<sup>-1</sup> for all regions and groups) and Western Equatorial Pacific (31%). In the regions along 40°S (South Indian, South Pacific, South Atlantic), primary production by coccolithophores was ~20-30% of the total primary production. Some local high primary production by coccolithophores led to average >20% in the North Atlantic and North Central Pacific (Figure 3c). Finally, although globally cyanobacteria only contributed to ~10% of the total primary production, their contribution reached ~80% in the ocean gyres (Figure 3d).

Using a satellite-derived approach, Uitz et al. [17] estimated the global total primary production to be ~7 PgC y<sup>-1</sup> higher than the NOBM (~46 PgC y<sup>-1</sup> compared to 39 PgC y<sup>-1</sup> for NOBM). Except for the primary production by microphytoplankton, a similar tendency (satellite-derived approach higher than the NOBM) was found for the class-specific primary production: ~15 PgC y<sup>-1</sup> for microphytoplankton (~20 PgC y<sup>-1</sup> for NOBM), 20 PgC y<sup>-1</sup> (~8 PgC y<sup>-1</sup> for NOBM) for nanophytoplankton and 11 PgC y<sup>-1</sup> (~11 PgC y<sup>-1</sup> for NOBM) for picophytoplankton. In the satellite-derived approach, microphytoplankton is identified as 'mostly diatoms' and therefore is very close to the classification of the NOBM. In Uitz et al. [17], nanophytoplankton includes prymnesiophytes, pelagophytes and cryptophytes and is therefore compared to coccolithophores (prymnesiophytes) from the NOBM.

Picophytoplankton of the Uitz et al. [17] approach includes cyanobacteria, prochlorophytes, chlorophytes and are therefore compared to the sum of cyanobacteria and chlorophytes from the NOBM. The group of nanophytoplankton, and to a lesser extent picophytoplankton, in the satellite-derived approach encompasses more groups than in the NOBM. It is therefore expected that the estimates of primary production from the satellite-derived approach for this group would be greater than the one from the NOBM. Some of the differences between the two approaches can also be attributed to the difference in the depth of integration: primary production in the NOBM is calculated over the entire water column whereas the satellite-derived approach integrates over the upper water  $y^1$  column (0-1.5  $Z_{eu}$ ). This would lead to a higher primary production in the model than in the satellite-derived approach.

Uitz et al. [17] divided the global ocean into 6 basins and provided the size-specific primary production for those 6 basins as well as the breakdown numbers for the north and south of each basin. We can therefore compare these regions with the class-specific primary production from the NOBM. Regionally, the greatest difference (4.3  $\text{PgC y}^{-1}$ ) was observed for nanophytoplankton in the Pacific Ocean and is most likely directly related to the fact that the satellite-derived approach encompasses more group than the NOBM for this size class. For all the other regions (Atlantic, Pacific, Equatorial, Indian and Southern Ocean), the size/class-specific primary production from the two approaches was always within 3.5  $\text{PgC y}^{-1}$  of each other. By looking at individual regions, we can attempt to narrow down the reasons, other than the classification difference as described earlier, for the satellite-derived approach being globally higher than the NOBM. If we compare the latitudes between 10°S and 10°N, we find that except for nanophytoplankton, the total and the primary production by micro- and picophytoplankton using the NOBM was higher than those from the satellite-derived approach (by 2.3-2.4  $\text{PgC y}^{-1}$ ). This is the opposite of what was observed at a global scale. This suggests that the reasons behind the global satellite-derived approach having larger estimates than the NOBM may be related to the difference in coverage. The northernmost latitude covered by the NOBM being 72°N would lead to a global underestimate of total and class-specific primary production using NOBM, as was observed for total, nano- and picophytoplankton primary production. Some of the discrepancies between the two approaches may also be linked to the inherent sampling bias resulting from clouds, thick aerosols, interorbit gaps, sunglint and high solar zenith angle in the satellite-derived approach. This sampling bias can lead to 6-8% annual mean bias [22] with the largest bias caused by the exclusion of data with high solar zenith angle. This would occur in regions such as North Indian, Equatorial Atlantic, etc which unfortunately were not regions for which Uitz et al. [17] reported size-specific primary production values.

## 2.2. Interannual variability

Globally the magnitude of interannual variability was of maximum 3  $\text{PgC y}^{-1}$  which compares favorably with the previous estimates of an average magnitude of 2  $\text{PgC y}^{-1}$  based on a period from 1992 to 2010 [23]. Over the period 1998-2011, the relative contribution of each phytoplankton group to the total primary production varied by ~4% except for cyanobacteria for which the highest interannual variability was of only ~2%. This was the equivalent of ~2  $\text{PgC y}^{-1}$  for diatoms and chlorophytes and ~1  $\text{PgC y}^{-1}$  for cyanobacteria and coccolithophores. In both the Atlantic and the

Pacific, the interannual variability in class-specific primary production increased at low latitude (Figure 4).

The region where all groups displayed the greatest interannual variation was the Equatorial Pacific (Figure 4). In the Equatorial Pacific, the magnitude of interannual variability in primary production by diatoms and chlorophytes was of  $\sim 1 \text{ PgC y}^{-1}$  and  $0.3\text{--}0.4 \text{ PgC y}^{-1}$  for cyanobacteria and coccolithophores. In this region, the phytoplankton composition is known to be strongly influenced by climate variability. There has been numerous studies that have indicated the impact of climate variability in this region [e.g. 24,25–27]. Rousseaux & Gregg [15] showed a phytoplankton composition shift in this region during transition from El Niño to La Niña conditions. The class-specific primary production follows a similar pattern (Figure 4) with diatoms and chlorophytes reaching their maximum primary production in 1999 while primary production by cyanobacteria is maximum in 1998. Interannual variability in class-specific primary production was also high in the North Central Pacific (Figure 4). Here, the magnitude over which the primary production varied was comparable to that found in the Equatorial Pacific for diatoms ( $\sim 0.85 \text{ PgC y}^{-1}$ ) but was lower for the other 3 groups ( $0.10\text{--}0.30 \text{ PgC y}^{-1}$ ).

By using climate indices, we can assess the factors driving this interannual variability. Globally all groups except coccolithophores were significantly correlated with the Multivariate El Niño Index (MEI). Behrenfeld et al. [28] showed that for the permanently stratified ocean (between  $40^\circ\text{S}$  and  $40^\circ\text{N}$ ) there was a significant correlation between primary production and MEI. Regionally, there was a significant correlation between the MEI and the primary production from the NOBM for 2 phytoplankton groups or more in 7 out of the 12 regions (Table 2). In the Equatorial Pacific for example, primary production by cyanobacteria was significantly ( $p < 0.05$ ) positively correlated while primary production by diatoms and chlorophytes were negatively correlated. In the North Central Pacific, primary production by chlorophytes and diatoms were significantly correlated with MEI but here diatoms were positively correlated while chlorophytes were negatively correlated. This is similar to what was observed using the PDO and is discussed later on. In the Atlantic Ocean, all 4 regions except the Equatorial Atlantic had two or more phytoplankton groups whose primary production was significantly correlated to MEI. In the South Atlantic, diatoms and chlorophytes were negatively correlated and cyanobacteria positively correlated with MEI. In the North and North Central Atlantic primary production by coccolithophores was significantly positively correlated to MEI while primary production by cyanobacteria was significantly negatively correlated with the MEI.

Some of the regions such as the North Atlantic, the Pacific Ocean and the Antarctic have well established climate indices. In the Antarctic for example, the Southern Annular Mode (SAM) is the dominant climate pattern. It is defined as the leading mode of Empirical Orthogonal Function analysis of monthly atmospheric pressure gradient. It has been suggested that a positive SAM, characterized by stronger westerly wind anomaly would intensify the upwelling therefore resulting in an increase in phytoplankton biomass [29]. Arrigo et al. [30] found a significant correlation between SAM and SST in the Southern Ocean. In this region, the MEI was not correlated to the primary production for any groups (Table 2) and SAM was only correlated to chlorophytes (Table 3). Similarly, Arrigo et al. [30] found that only 31% of the variation in annual primary production could be explained by SAM index. Instead, Arrigo et al. [30] found that most of the interannual variability in primary production was driven by changes in sea ice cover. Although changes in surface nutrient induced by processed



associated with atmospheric variability (e.g. SAM) are also likely to play a role, especially at regional scales through enhanced upwelling, it seems that its effect is relatively limited on both the total and class-specific primary production in this region.

The North Atlantic Oscillation index (NAO) is calculated as the normalized sea level pressure difference between the Azores and Iceland [31]. When the NAO is high, the westerlies are stronger than average, which in turn transport warm and moist air toward Europe. Using the NAO, a significant negative correlation was found in the North Atlantic for chlorophytes and coccolithophores. In the North Central Atlantic, a positive NAO was associated with significantly less primary production by diatoms and significantly more by cyanobacteria (Table 3). A few local scale studies have shown a positive correlation between NAO and phytoplankton concentration [32-35] as well as a phytoplankton composition shift from a diatom-dominated community during positive NAO to a dinoflagellates-dominated community during negative phase of NAO in the North Atlantic [36]. At a basin scale, Leterme et al. [37] showed that the influence of NAO on diatoms and dinoflagellates abundance was highly mixed across the North Atlantic basin. Similarly, Barton et al. [38] found that there was no statistical relationship between the detrended NAO and the results from the continuous plankton recorder. These studies suggest that the effects of NAO on phytoplankton composition and production remain unclear. Further studies are necessary to understand the impact of the NAO on the phytoplankton composition and primary production. Finally, although both the MEI and NAO agreed on the limited effect of climate variability on class-specific primary production in the Equatorial Atlantic, both index diverged on the effect of climate variability on the class-specific primary production in the North, North Central and South Atlantic (Table 2 & Table 3). This is not totally unexpected since in contrast to the MEI, the NAO is largely an atmospheric mode.

The Pacific Decadal Oscillation [PDO, 39] is an index of oceanic climate variability with a similar expression to El Niño, but acting on a longer time scale. It is defined as the leading principal component of surface temperature variability north of 20°N. During the positive phase of the PDO, trade winds generally weaken reducing the upwelling of nutrient-rich water. Using the PDO, we found that the groups that were significantly correlated with this index in the North Central Pacific were the same as the ones for the MEI (positive for diatoms and negative for chlorophytes). In the North Pacific however, the PDO was negatively correlated with chlorophytes and cyanobacteria whereas there was no significant correlation between the MEI and any of the class-specific primary production. These two climate phenomenon can vary independently and exhibit variable strength in both the warm and cold phase [40,41]. Several studies have shown a correlation between climate variability and chlorophyll concentration as well as primary production in the Pacific [e.g. 42,43-45]. Chiba et al. [46] found a significant correlation between PDO and the timing of the annual bloom in the western North Pacific (average date occurring in mid-May) but could not find a relationship between the interannual variation of the summertime phytoplankton community structure and the PDO. Karl et al. [44,47] found that during a positive phase of the PDO (1965-1977), the plankton community composition shifted with prokaryotes becoming more dominant and coincided with changing new and export production, nutrient supply and fisheries yields. In the Equatorial Pacific, there was a significant positive correlation between both MEI and PDO and the primary production by cyanobacteria and a negative correlation for the production by diatoms. Climate variability seemed to have only a limited effect on the primary production in the South Pacific. Here there was only a significant correlation

between the PDO and the primary production by diatoms. The effects of climate variability in the South Pacific remains poorly characterized. For this region, Thomas et al. [42] suggested some correlation between PDO and coastal chlorophyll at least at specific latitudes. The effects that PDO has on the phytoplankton composition and productivity remain poorly characterized. Furthermore, since the PDO is a decadal scale phenomena, the satellite observations currently available do not cover a period long enough to identify possible relationships between PDO and phytoplankton dynamics (whether in terms of composition or primary production).

**Table 1.** Climatological Primary Production for the four phytoplankton groups in PgC y<sup>-1</sup> and relative contribution and total primary production in PgC y<sup>-1</sup>.

	Diatoms		Chloro		Cyano		Cocco		Total
	PgC y <sup>-1</sup>	%	PgC y <sup>-1</sup>	%	PgC y <sup>-1</sup>	%	PgC y <sup>-1</sup>	%	PgC y <sup>-1</sup>
Ant	4.0	89	0.2	5	0.0	0	0.3	7	4.5
SIND	1.7	51	0.4	13	0.5	13	0.8	23	3.4
SPAC	2.2	46	0.6	13	0.6	12	1.4	29	4.7
SATL	1.2	51	0.4	19	0.2	10	0.5	20	2.3
EIND	1.9	52	1.0	28	0.5	14	0.2	6	3.7
EPAC	2.8	43	1.1	16	0.7	10	2.0	31	6.5
EATL	1.1	36	1.2	42	0.2	8	0.4	13	2.9
NIND	0.7	48	0.6	38	0.2	12	0.0	2	1.5
NCPAC	2.4	51	0.5	10	0.7	14	1.2	25	4.7
NCATL	0.6	26	0.4	16	0.5	19	0.9	39	2.4
NPAC	1.1	86	0.1	10	0.0	0	0.1	4	1.3
NATL	0.6	51	0.2	20	0.0	1	0.3	28	1.1
Global	20.3	52	6.8	17	4.0	10	8.0	21	39.0

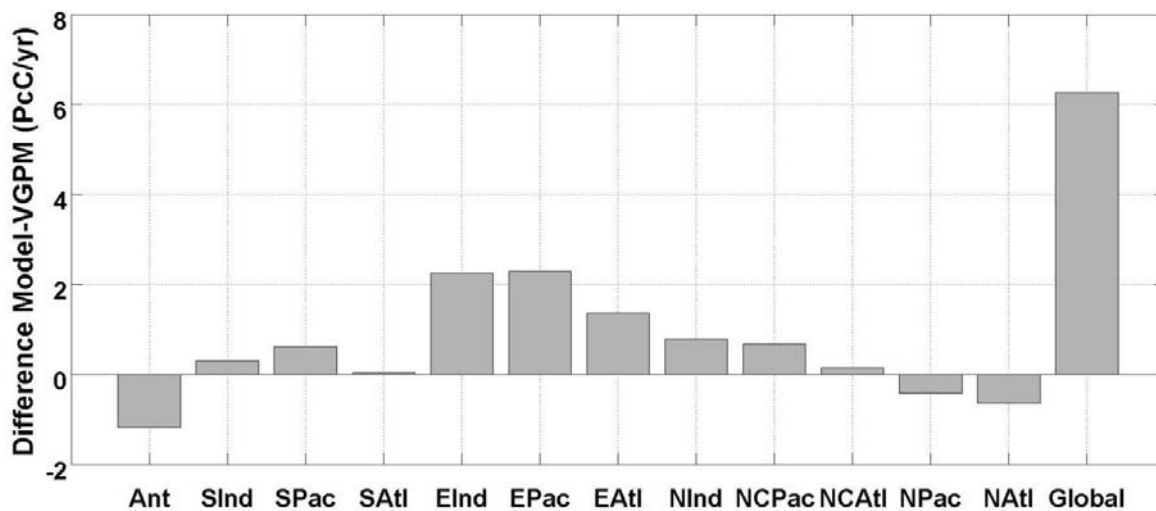
**Table 2.** Correlation Coefficient between class specific primary production and the Multivariate El Niño Index (MEI) in 12 major oceanographic basins. Bold and (\*) indicates statistical significance ( $p < 0.05$ ).

	Ant	SIND	SPAC	SATL	EIND	EPAC	EATL	NIND	NCPAC	NCATL	NPAC	NATL
Diatoms	-0.12	-0.14	-0.10	<b>-0.17*</b>	<b>-0.46*</b>	<b>-0.68*</b>	-0.05	-0.09	<b>0.21*</b>	0.10	0.13	<b>0.18*</b>
Chlorophytes	-0.13	-0.09	-0.06	<b>-0.17*</b>	<b>-0.38*</b>	<b>-0.28*</b>	-0.14	<b>-0.35*</b>	<b>-0.18*</b>	0.06	0.01	0.00
Cyanobacteria	-0.05	0.00	-0.07	<b>0.33*</b>	0.13	<b>0.61*</b>	0.10	<b>0.18*</b>	0.03	<b>-0.17*</b>	0.01	<b>-0.17*</b>
Coccolithophores	0.01	-0.13	-0.06	-0.14	0.09	0.12	-0.14	<b>0.18*</b>	0.08	<b>0.23*</b>	0.12	<b>0.15*</b>

**Table 3.** Correlation Coefficient between class specific primary production and several regions-specific climates indices: Antarctic Oscillation (AAO), North Atlantic Oscillation (NAO), and Pacific  $y^{-1}$ Decadal Oscillation (PDO). Bold and (\*) indicates statistical significance ( $p < 0.05$ ).

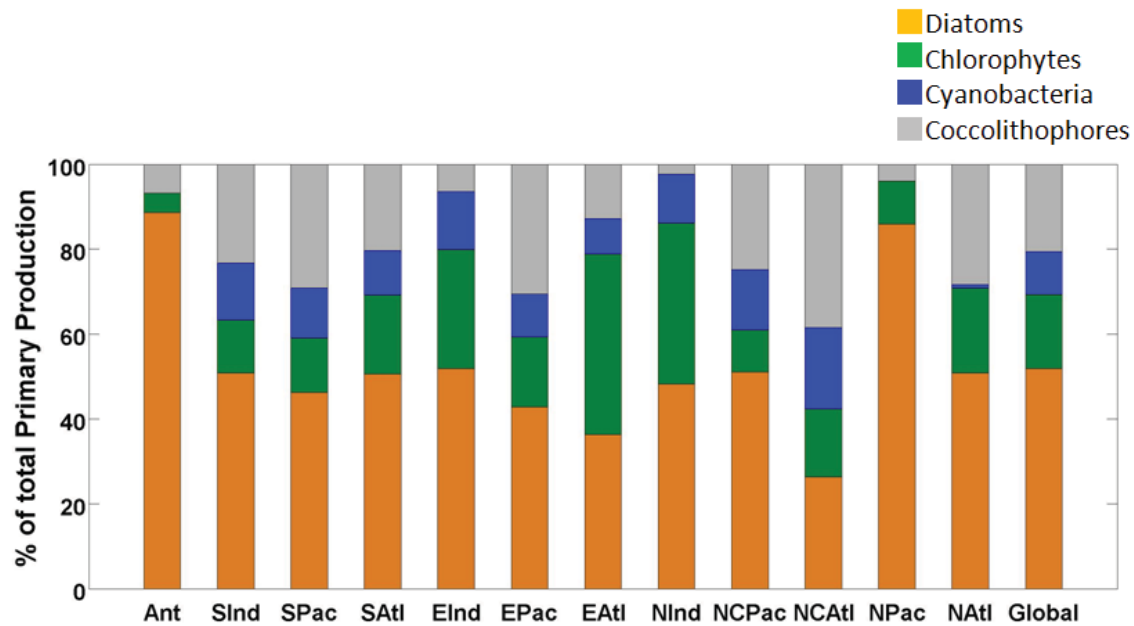
		Diatoms	Chlorophytes	Cyanobacteria	Coccolithophores
AAO	Antarctic	0.09	<b>0.16*</b>	0.08	0.14
NAO	North Atlantic	-0.11	<b>-0.22*</b>	-0.09	<b>-0.25*</b>
	North Central Atlantic	<b>-0.17*</b>	-0.05	<b>0.21*</b>	-0.12
	Equatorial Atlantic	-0.06	-0.05	0.00	0.06
	South Atlantic	-0.02	0.12	<b>-0.22*</b>	0.14
PDO	North Pacific	0.02	<b>-0.26*</b>	<b>-0.19*</b>	-0.07
	North Central Pacific	<b>0.40*</b>	<b>-0.25*</b>	0.03	-0.07
	Equatorial Pacific	<b>-0.24*</b>	-0.13	<b>0.45*</b>	<b>0.17*</b>
	South Pacific	<b>-0.20*</b>	0.04	0.09	0.00

**Figure 1.** Difference between total Primary production from the NOBM and those from the VGPM for the 12 regions and at the global scale ( $\text{PgC y}^{-1}$ ) averaged over the period from 1998 to 2011. [DifPPVGPM.m]

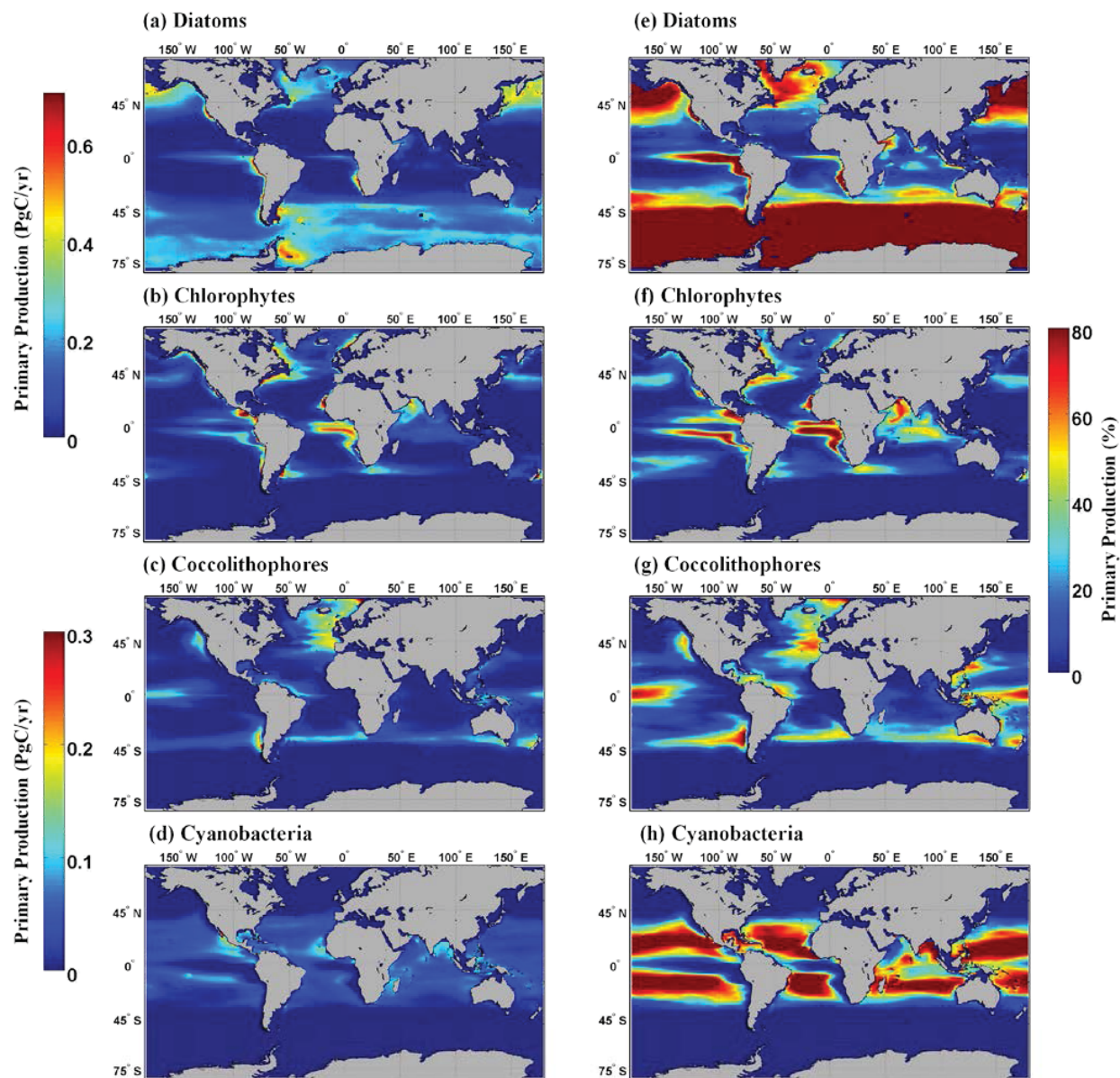




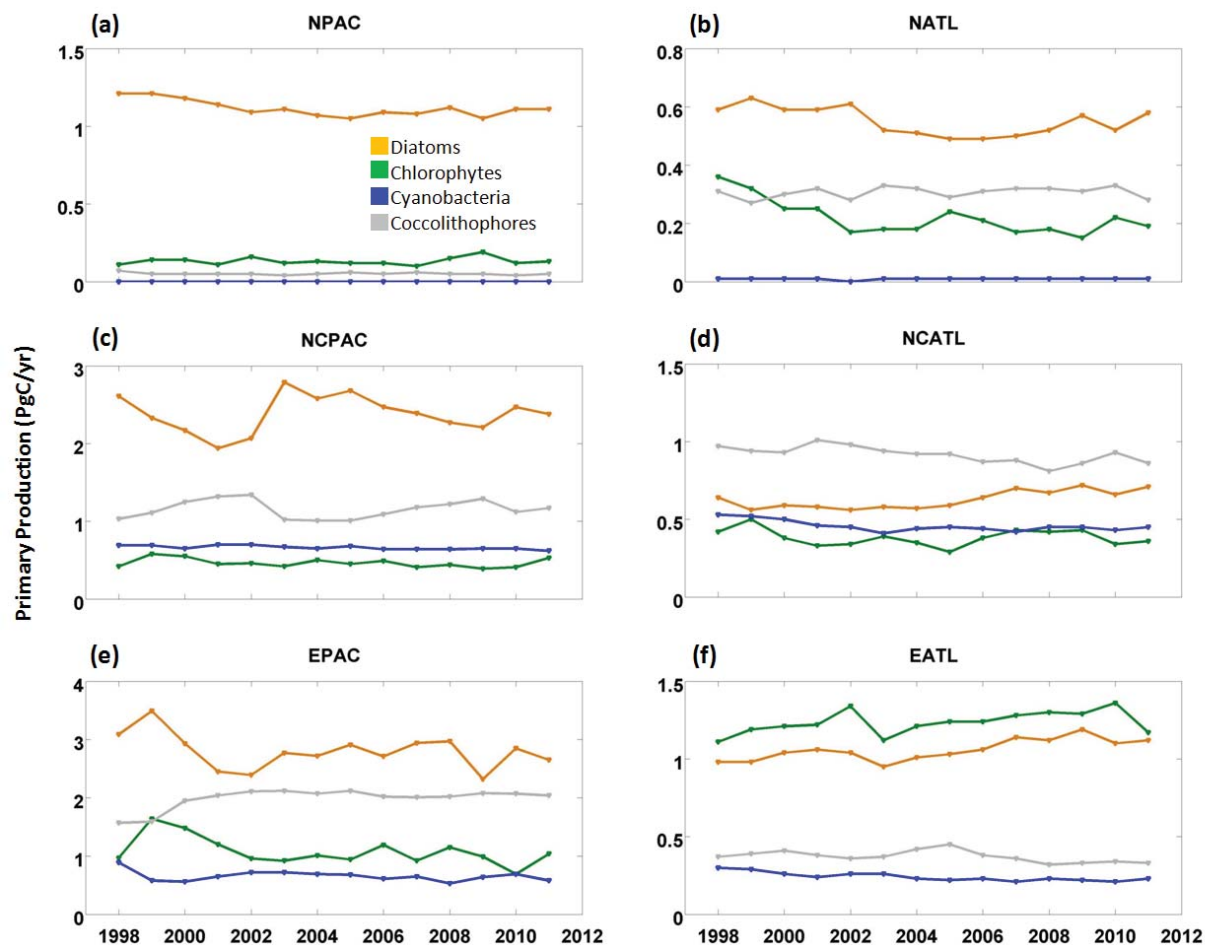
**Figure 2.** Relative contribution of the four phytoplankton group to total primary production at a global scale averaged over the period from 1998 until 2011. [InterannualPerc.m]



**Figure 3.** Climatology of class-specific primary production for the period from 1998 until 2011. The left-hand panels show the primary production in absolute units ( $\text{PgC y}^{-1}$ ). Note the difference of scale between diatoms/chlorophytes (scale from 0 to 0.7  $\text{PgC y}^{-1}$ ) and coccolithophores/cyanobacteria (scale from 0 to 0.3  $\text{PgC y}^{-1}$ ). The right-hand panels show the percent contribution of class-specific production to total primary production (same scale for all classes).



**Figure 4.** Interannual variation of class-specific primary production ( $\text{PgC y}^{-1}$ ) for diatoms, chlorophytes, cyanobacteria and coccolithophores in (a) North Pacific, (b) North Atlantic, (c) North Central Pacific, (d) North Central Atlantic, (e) Equatorial Pacific and (f) Equatorial Atlantic.



### 3. Experimental Section

Global primary production is derived from an established coupled ocean biogeochemical model, the NASA Ocean Biogeochemical Model [NOBM, 48]. It is a three-dimensional representation of circulation/biogeochemical/radiative process in a domain that spans from  $-84^{\circ}$  to  $72^{\circ}$  at a  $1.25^{\circ}$  resolution in water deeper than 200 m. NOBM is coupled with the Poseidon ocean general circulation model, which is driven by wind stress, sea surface temperature, and shortwave radiation [48]. The model includes 3 detrital pools (silica, N/C and iron detritus), 4 phytoplankton groups (diatoms, coccolithophores, chlorophytes and cyanobacteria) and 4 nutrients (ammonium, nitrate, iron and silicate). The phytoplankton groups differ in their maximum growth rates, sinking rates, nutrient requirements, and optical properties.

Satellite ocean chlorophyll from SeaWiFS and MODIS-Aqua for the years 1998-2012 is assimilated into NOBM following Gregg [49]. Multi-variate nutrient adjustments corresponding to the chlorophyll assimilation [15] are also included. Bias-correction of the satellite chlorophyll data is performed prior to assimilation using public in situ archives in the Empirical Satellite Radiance-In situ Data (ESRID) methodology [50]. The ESRID method also has the attribute of reducing discontinuities between the two satellite data sets [51]. The time series uses SeaWiFS data from 1998-2002, then switches to MODIS-Aqua data.

Primary production is computed in the model as a function of growth rate multiplied by the carbon:chlorophyll ratio:

$$PP = \int \sum \mu_i C_i \Phi dz$$

where  $\mu_i$  is the growth rate of phytoplankton component  $i$ ,  $C_i$  is the chlorophyll concentration of component  $i$ ,  $\Phi$  is the carbon:chlorophyll ratio, and the product is integrated over depth. It is a diagnostic variable in the model, representing the integral of net carbon uptake in the water column. Photoadaptation is simulated by stipulating three states: 50, 150, and 200 ( $\text{mmol quanta m}^{-2} \text{ s}^{-1}$ ). This is based on laboratory studies which typically divide experiments into low, medium, and high classes of light adaptation [48]. Carbon:chlorophyll ratios ( $\Phi$ ) correspond to the photoadaptation state, to represent the tendency of phytoplankton to preferentially synthesize chlorophyll in low light conditions, to enable more efficient photon capture. The three  $\Phi$  states corresponding to the three light states are 25, 50, and  $80 \text{ g g}^{-1}$ . For irradiance levels falling between the three light states, the C:chl ratios are linearly interpolated.

Irradiance data to drive phytoplankton growth is taken from the Ocean-Atmosphere Spectral Irradiance Model [OASIM; 52] for the years of interest. This model computes spectral irradiance in 33 bands for the domain 200 nm to  $4 \mu\text{m}$ , at the ocean surface as a function of atmospheric optical properties [52], and then propagates the spectral irradiance downward and upward through the water column as a function of ocean optical properties [53,54]. Surface spectral irradiance and photosynthetically available irradiance data are publicly available at [gmao.gsfc.nasa.gov/research/oceanbiology/data.php](http://gmao.gsfc.nasa.gov/research/oceanbiology/data.php).

Total primary production from NOBM has been evaluated along with multiple satellite-derived and numerical models in three intercomparison efforts [21,55,56]. However, for sanity purposes, we explicitly compare NOBM total primary production with a commonly used satellite-derived method,

that has the advantage of public availability (data downloaded from [www.science.oregonstate.edu](http://www.science.oregonstate.edu)) and heritage, the Vertically-Integrated Production Model [VGPM; 57]. The purpose of this comparison is not to validate per se, because there are many other models and we are not attributing an assessment of the quality of this particular one. However, we are interested in establishing a quantitative comparison of total primary production of NOBM with a common method that has been involved in many intercomparison efforts to place the NOBM total primary production estimates in perspective. Climate indices were downloaded from the NOAA Climate Prediction Center (<http://www.cpc.ncep.noaa.gov>).

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## Conflict of Interest

The authors declare no conflict of interest.

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