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Marco Bellacicco, G. Volpe, N. Briggs, V. Brando, J. Pitarch, et al.. Global Distribution of Non-algal Particles From Ocean Color Data and Implications for Phytoplankton Biomass Detection. *Geophysical Research Letters*, 2018, 45 (15), pp.7672-7682. 10.1029/2018GL078185 . hal-03505053

**HAL Id: hal-03505053**

**<https://hal.science/hal-03505053>**

Submitted on 31 Dec 2021

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## RESEARCH LETTER

10.1029/2018GL078185

## Key Points:

- A new pixel-scale method is developed to compute backscattering of non-algal particles from ocean color data
- The backscattering of non-algal particles has geographical variability from northern to southern hemispheres
- The backscattering of non-algal particle variability has to be taken into account in phytoplankton biomass models

## Supporting Information:

- Supporting Information S1

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## Citation:

Bellacicco, M., Volpe, G., Briggs, N., Brando, V., Pitarch, J., Landolfi, A., et al. (2018). Global distribution of non-algal particles from ocean color data and implications for phytoplankton biomass detection. *Geophysical Research Letters*, 45, 7672–7682. <https://doi.org/10.1029/2018GL078185>

Received 17 APR 2018

Accepted 16 JUL 2018

Accepted article online 24 JUL 2018

Published online 11 AUG 2018

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## Global Distribution of Non-algal Particles From Ocean Color Data and Implications for Phytoplankton Biomass Detection

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**Abstract** In the last few decades, phytoplankton biomass has been commonly studied from space. However, satellite analysis of non-algal particles (NAPs), including heterotrophic bacteria and viruses, is relatively recent. In this work, we estimate the backscattering coefficient associated with the NAP fraction that does not covary with chlorophyll based on satellite particulate backscattering coefficient and chlorophyll ( $b_{bp}NAP$ ).  $b_{bp}NAP$  is computed at 100-km resolution using 19 years of monthly satellite data. We find clear differences in  $b_{bp}NAP$  between northern and southern oceans. High  $b_{bp}NAP$  values are found in the Arctic and Southern Oceans, the North Atlantic area influenced by the Gulf Stream current, as well as shelf regions (i.e., Patagonian shelf) affected by upwelling regimes. Low correlation between chlorophyll and backscattering prevents precise  $b_{bp}NAP$  estimations in oligotrophic areas (e.g., subtropical gyres). These  $b_{bp}NAP$  estimations lead to a reduction to half in satellite-based phytoplankton biomass estimates respect to previously published results.

**Plain Language Summary** In the ocean, there are different seawater constituents that contribute to the inherent optical properties: Phytoplankton is a major constituent and one of the most studied in the last decade. Other important constituents are the colored dissolved organic matter and non-algal particles (NAPs). NAP includes (i) heterotrophic organisms such as bacteria, micrograzers, and viruses; (ii) detrital organic particles such as fecal pellets and cell debris; and (iii) mineral particles of both biogenic (e.g., calcite liths and shells) and terrestrial origin (e.g., clays and sand). This study is the first attempt to define the NAP from space, and its spatial variability, and how it contributes to refine the phytoplankton carbon biomass estimation. We estimate the backscattering coefficient associated with the NAP fraction that does not covary with chlorophyll from the satellite particulate backscattering coefficient and chlorophyll ( $bbpNAP$ ). Our main results evidence a geographical variability of  $bbpNAP$  from northern to southern oceans with two distinct regimes: one associated with the productive areas in which  $bbpNAP$  and biomass are anticorrelated and another in which  $bbpNAP$  high values are in regions dominated by inorganic origin. We demonstrate that the spatial variability of  $bbpNAP$  should not be ignored.

### 1. Introduction

In the ocean, there are different seawater constituents that contribute to the inherent optical properties. Phytoplankton is a major constituent and one of the most studied in the last decade (e.g., its space-temporal variability, physiology, and ecology; Siegel et al., 2013; Halsey & Jones, 2015). Other important constituents are colored dissolved organic matter (CDOM) and non-algal particles (NAPs). NAP includes (i) heterotrophic organisms such as bacteria, micrograzers, and viruses; (ii) detrital organic particles such as fecal pellets and cell debris; and (iii) mineral particles of both biogenic (e.g., calcite liths and shells) and terrestrial origin (e.g., clays and sand; Sosik, 2008, and references therein). While phytoplankton and CDOM are quite well studied at global scale, the optical properties of these particles are not well known. In particular, the total NAP absorption spectrum tends to monotonically increase with decreasing wavelengths, similar to that observed for CDOM (e.g., Iturriaga & Siegel, 1989; Nelson et al., 1998; Roesler et al., 1989; Sosik & Mitchell, 1995). Several studies have investigated the absorption of NAP (Bricaud et al., 2010; Sosik, 2008, and reference therein), but

patterns of NAP backscattering in the surface ocean are not fully studied (Cho & Azam, 1990; Stramski & Kiefer, 1991) because direct measurements of fractionated  $b_{bp}$  in the field are not possible using current technology. However, we can gain some insight into the constituents of particulate backscattering  $b_{bp}$  by separating the fraction that covaries with phytoplankton from the fraction that does not covary.

In this context, a first attempt to define the backscattering due to NAP from space was suggested by Behrenfeld et al. (2005), who proposed an equation for phytoplankton carbon biomass estimation from satellite, based on a linear relationship between particulate backscattering coefficient ( $b_{bp}$ ) and chlorophyll (Chl). In their model, the  $b_{bp}$ NAP coefficient, which is defined as the fraction of backscattering due to non-algal particles (e.g., stable heterotrophic and detrital components of the surface particle population in open ocean) that does not covary with Chl, is assumed constant in space and time (Behrenfeld et al., 2005; for more details on the  $b_{bp}$ NAP computation see paragraph 2.2.). Behrenfeld's method has been applied in many recent works: Westberry et al. (2008), Siegel et al. (2013), Mignot et al. (2014), Behrenfeld et al. (2016), Westberry et al. (2016), Thomalla et al. (2017), among others.

This method has been used to estimate phytoplankton carbon biomass in terms of  $\text{mg C m}^{-3}$  and the Chl:C ratio in photoacclimation studies (Behrenfeld et al., 2016; Bellacicco et al., 2016; Halsey & Jones, 2015; MacIntyre et al., 2002) and applied in phytoplankton physiology studies from space as well as biogeochemical models (Arteaga et al., 2014; Bellacicco et al., 2016; Halsey & Jones, 2015; Siegel et al., 2013).

Recently, Bellacicco et al. (2016) computed  $b_{bp}$ NAP in a 3-month window in predefined bioregions of the Mediterranean Sea (Lavigne et al., 2013) and found both marked seasonal and regional  $b_{bp}$ NAP variabilities. Their results supported in situ observations in the Mediterranean Sea (Siokou-Frangou et al., 2010), suggesting that the heterotrophic and detrital components of the surface particle pool are neither negligible (Morel, 1988) nor stable, but highly dynamic in both space and time. In Bellacicco et al. (2016) the Chl- $b_{bp}$  relationship was found to be highly dependent on the season and on the biogeochemistry of the area, similarly as in Antoine et al. (2011, their Figure 10). These findings suggest that the use of the global  $b_{bp}$ NAP constant coefficient (Behrenfeld et al., 2005) can result in an overestimation of phytoplankton biomass, in the Mediterranean Sea.

High covariability between Chl and  $b_{bp}$  is expected because phytoplankton cells contain Chl and also act as light scatterers. In addition, the unpigmented NAP also contributes to the  $b_{bp}$  signal and is known to exhibit patterns of variability similar to that of phytoplankton biomass (Bellacicco et al., 2016). The degree of covariability between Chl and  $b_{bp}$  provides a means for assessing the role that the physiological state of phytoplankton cells plays in modulating the biomass concentration and how it is perceived from remote sensing observations (Bellacicco et al., 2016, and references therein). High Chl- $b_{bp}$  covariability is a clear indication that particles (and biomass) covary also with phytoplankton abundance, with the physiological photoacclimation process playing a negligible role in the Chl detection from space. On the other hand, when the range of variability of  $b_{bp}$  is narrower than that of Chl, covariability is low and Chl detected from space is dominated by the photoacclimation process (Barbieux et al., 2018; Behrenfeld et al., 2005; Bellacicco et al., 2016; Halsey & Jones, 2015).

There can be a number of reasons for which the Chl- $b_{bp}$  relationship will vary both in space and time. These include the ratio of NAP to phytoplankton biomass, variability in phytoplankton carbon-to-Chl ratio (Bellacicco et al., 2016), and the species composition and diversity (e.g., size and shape) of phytoplankton cells and nature of the NAP itself (Dall'Olmo et al., 2009, 2012; Stramski et al., 2004).

When this intrinsic variability dominates over the variability in biomass, null or negative correlations can be obtained violating the assumptions for the calculation of  $b_{bp}$ NAP (i.e., in the ultraoligotrophic oceanic areas).

Filling the knowledge gap about the global scale  $b_{bp}$ NAP variability can surely improve our understanding of its main components and enhancing the estimation of the phytoplankton carbon from space. Heterotrophic bacteria, part of  $b_{bp}$ NAP, are the crucial connection among detritus, dissolved organic matter, and higher trophic levels (Bellacicco et al., 2016; Siokou-Frangou et al., 2010). Similarly, the ecological role of calcifying phytoplankton has been widely documented in certain oceanic regions (e.g., Southern Ocean; Balch, 2018; Balch et al., 2016, and references therein) where the impact of their calcium carbonate coccoliths, also part of  $b_{bp}$ NAP, may be assessed via space-born observations of the backscattering coefficient (Balch et al., 1999). Open research questions on  $b_{bp}$ NAP estimates from space are as follows:

- i Does  $b_{bp}NAP$  vary in space on a global scale?
- ii Does  $b_{bp}NAP$  spatial variability impact phytoplankton carbon biomass estimation?

In this paper, we aim to answer these questions by extending the Behrenfeld et al. (2005) and Bellacicco et al. (2016) methodologies to develop a global map of mean  $b_{bp}NAP$  along with a first evaluation of its potential impact on phytoplankton carbon biomass estimation.

## 2. Data and Methods

### 2.1. Satellite Data

The full European Space Agency (ESA) Ocean Color-Climate Change Initiative version 3 monthly Chl ( $mg\ m^{-3}$ ) and  $b_{bp}$  ( $m^{-1}$ ; 443 nm) data time series at 4-km resolution for the period 1997–2015 over the global ocean was downloaded from the ESA-CCI website (<http://www.esa-oceancolour-cci.org/>). ESA-CCI products are the results of the merging between Sea-Viewing Wide Field-of-View Sensor, Medium-Resolution Imaging Spectrometer, Moderate Resolution Imaging Spectroradiometer-Aqua, and Visible Infrared Imaging Radiometer Suite time series (Brewin et al., 2015; Mélin & Sclep, 2015; Mélin et al., 2017; Sathyendranath et al., 2017). Chl was estimated with a blending of the OCI (as implemented by NASA, itself a combination of CI and OC4), the OC5 (NASA, 2010), and the OC3 algorithms ([http://www.esa-oceancolour-cci.org/?q=webfm\\_send/684](http://www.esa-oceancolour-cci.org/?q=webfm_send/684)). The Quasi Analytical Algorithm was used to compute  $b_{bp}$  (Lee, 2014; Lee et al., 2002). The accuracy of the Quasi Analytical Algorithm was demonstrated in Brewin et al. (2015), and also by Pitarch et al. (2016) and Bellacicco et al. (2016), and previous works of Mélin et al. (2005, 2011). A thorough analysis on the uncertainties of both parameters is available on the ESA OC-CCI website or on the Product User Guide. Both data sets were remapped at 100-km resolution, enough to resolve the broader oceanographic scales of variability.

### 2.2. $b_{bp}NAP$ Computation

The  $b_{bp}NAP$  model is based upon the approach of Behrenfeld et al. (2005), who estimated global  $b_{bp}NAP$  as the intercept of the least square linear regression fit between Chl and  $b_{bp}$ ; that is,  $b_{bp}NAP$  is  $b_{bp}$  when Chl is zero. They estimated a unique constant value ( $0.00035\ m^{-1}$ ; their Figure 1) using the entire multiyear global data set.

In this work, the technique developed by Bellacicco et al. (2016) is extended to compute  $b_{bp}NAP$  at the scale of the satellite pixel, rather than using predefined bioregions, allowing the analysis of its spatial variability along the entire global ocean. The proposed equation for  $b_{bp}NAP$  is

$$b_{bp}NAP = b_{bp} - k\ Chl \quad (1)$$

with  $k$  being the slope of the least square regression fit between Chl and  $b_{bp}$  single-pixel time series.  $b_{bp}$ , Chl, and hence  $b_{bp}NAP$  are resolved at pixel scale. The term  $kChl$  is the fraction of  $b_{bp}$  that covaries with Chl. The  $b_{bp}NAP$  was computed using a broader  $3 \times 3$  pixel spatial window to increase statistical robustness of the regression fit. A quality control was applied to the data before computing the fit, and the outliers were discarded using three standard deviation confidence limit.

The  $b_{bp}NAP$  pixel-based estimations (Figure S1 in the supporting information), obtained from a regression between Chl and  $b_{bp}$  on a pixel scale with a statistical significance ( $S$ ) less than 0.95 (computed through the Student  $t$  test), were not considered in the analysis and were masked out. In addition, pixels in which the Pearson correlation coefficient,  $r$ , was lower than 0 were not considered in the computation of  $b_{bp}NAP$  and  $b_{bp}NAP:b_{bp}$  ratio (hereafter  $b_{bp}NAP\sim$ ).  $\sigma_{bbp}NAP$  is estimated as the standard deviation of the intercept for each regression. The coefficient of variation is then  $CV = \sigma_{bbp}NAP/b_{bp}NAP$  at pixel scale to show the relative uncertainty of the  $b_{bp}NAP$  estimates. Figure S2 shows the robustness of  $b_{bp}NAP$  estimate at 99% confidence level.

The  $b_{bp}NAP$  pixel-based estimates are then used to compute phytoplankton carbon biomass ( $mg\ C\ m^{-3}$ ; Figure 3a) following Behrenfeld et al. (2005, see their paragraph 3.1) and Bellacicco et al. (2016, see their equation (1)), but using the  $b_{bp}NAP$  spatially resolved (Figure 2a) instead of a single constant value ( $0.00035\ m^{-1}$ ):

$$Carbon = [b_{bp} - b_{bp}NAP] * SF \quad (2)$$

where  $SF$  is the scaling factor chosen for satellite Chl:C ratio values to be consistent with laboratory results, and for the average contribution of phytoplankton to total particulate organic carbon to be consistent with field estimate: It is equal to  $13,000\ mg\ C\ m^{-2}$  (Behrenfeld et al., 2005).

Finally, we calculate the relative percentage difference (RPD) between phytoplankton carbon computed with single  $b_{bp}$ NAP coefficient (Behrenfeld et al., 2005) and the carbon as computed in equation (2):

$$RPD = 100 * \frac{[\text{Carbon}_{\text{single } b_{bp}\text{NAP}} - \text{Carbon}]}{\text{Carbon}} \quad (3)$$

### 2.3. The Chl- $b_{bp}$ Relationship for $b_{bp}$ NAP Estimation

Here to guide the interpretation of the  $b_{bp}$ NAP distribution, the biogeochemical implications of the Chl- $b_{bp}$  relationship (equations (1) and (2)) are presented. Figures 1a and 1b show the climatological maps of  $b_{bp}$  and Chl, respectively. The  $b_{bp}$  and Chl patterns of variability are coherent in the productive areas like the polar regions, the coastal upwelling, and along the equatorial belts of the Atlantic and Pacific oceans. There are areas in which the Chl and  $b_{bp}$  maps show differences: In the equatorial Atlantic between 10°S and 10°N, Chl shows high values, but  $b_{bp}$  does not. North and south of this belt, the Chl map clearly displays the presence of the subtropical gyres, while the  $b_{bp}$  map presents a uniform area of low values which extends from the equator to 30°N/S. The oligotrophic pattern of the South Pacific Subtropical Gyre shows different spatial extent when observed through Chl and  $b_{bp}$ . Figure 1b shows that South Pacific Subtropical Gyre extends more to the south toward the Antarctic Circumpolar Current than shown by Figure 1a. Similarly, in the Pacific Equatorial upwelling system, high Chl extends more to the west than  $b_{bp}$ , resulting in the latitudinal thickness of the Chl pattern to be more pronounced than  $b_{bp}$ . Globally, Chl and  $b_{bp}$  vary over more than 3 orders of magnitude, also showing similar geographical patterns (Figures 1a and 1b).

Figure 1c shows the Pearson coefficient ( $r$ ) between Chl and  $b_{bp}$  time series obtained using 19 years of satellite data. Two main considerations emerge: Nearly the entire global ocean presents significant positive correlation, and in most areas, this correlation is high, meaning that either  $b_{bp}$  or Chl can be used for determining the phytoplankton dynamics and distribution, as expected in case I waters. This type of relationship is the underpinning basis for the estimation of  $b_{bp}$ NAP. However, this Chl- $b_{bp}$  relationship falls short in the subtropical gyres, where  $r$  shows null or negative values. Two main reasons can contribute to this poor relationship: First, the photoacclimation process, known to be dominant in such areas (e.g., Barbieux et al., 2018; Siegel et al., 2013), introduces variability in Chl that is uncoupled with biomass, and second, ocean color can only sample the few upper meters of the water column, under the deep chlorophyll maximum conditions (Volpe et al., 2012), and thus, the phytoplankton vertical distribution is such that most of the algal biomass is out of the satellite detection. This in part explains the extremely oligotrophic character that these areas display when sampled through ocean color remote sensing (Volpe et al., 2007).

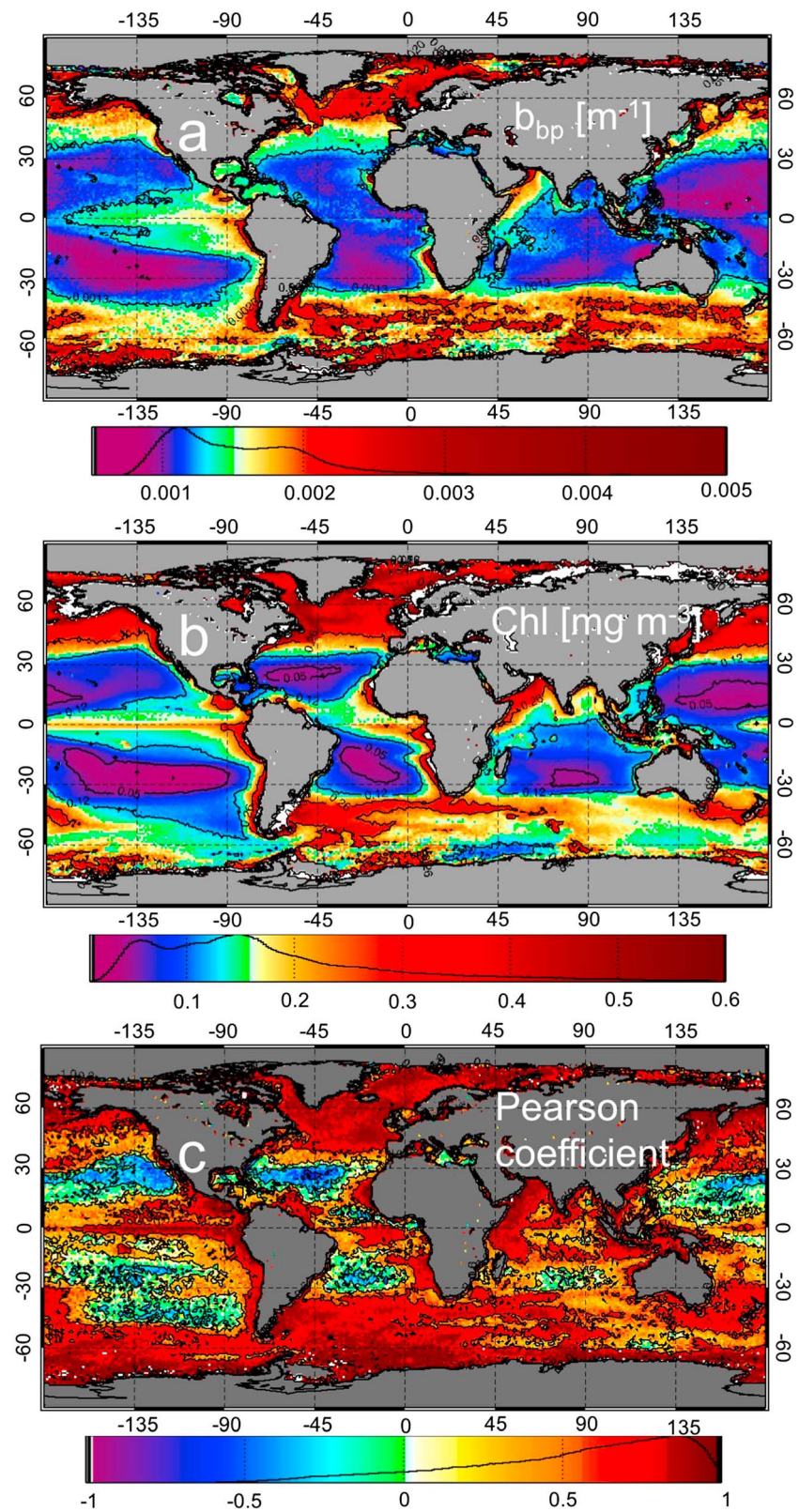
## 3. Results and Discussion

### 3.1. The Spatial Distribution of $b_{bp}$ NAP and CV

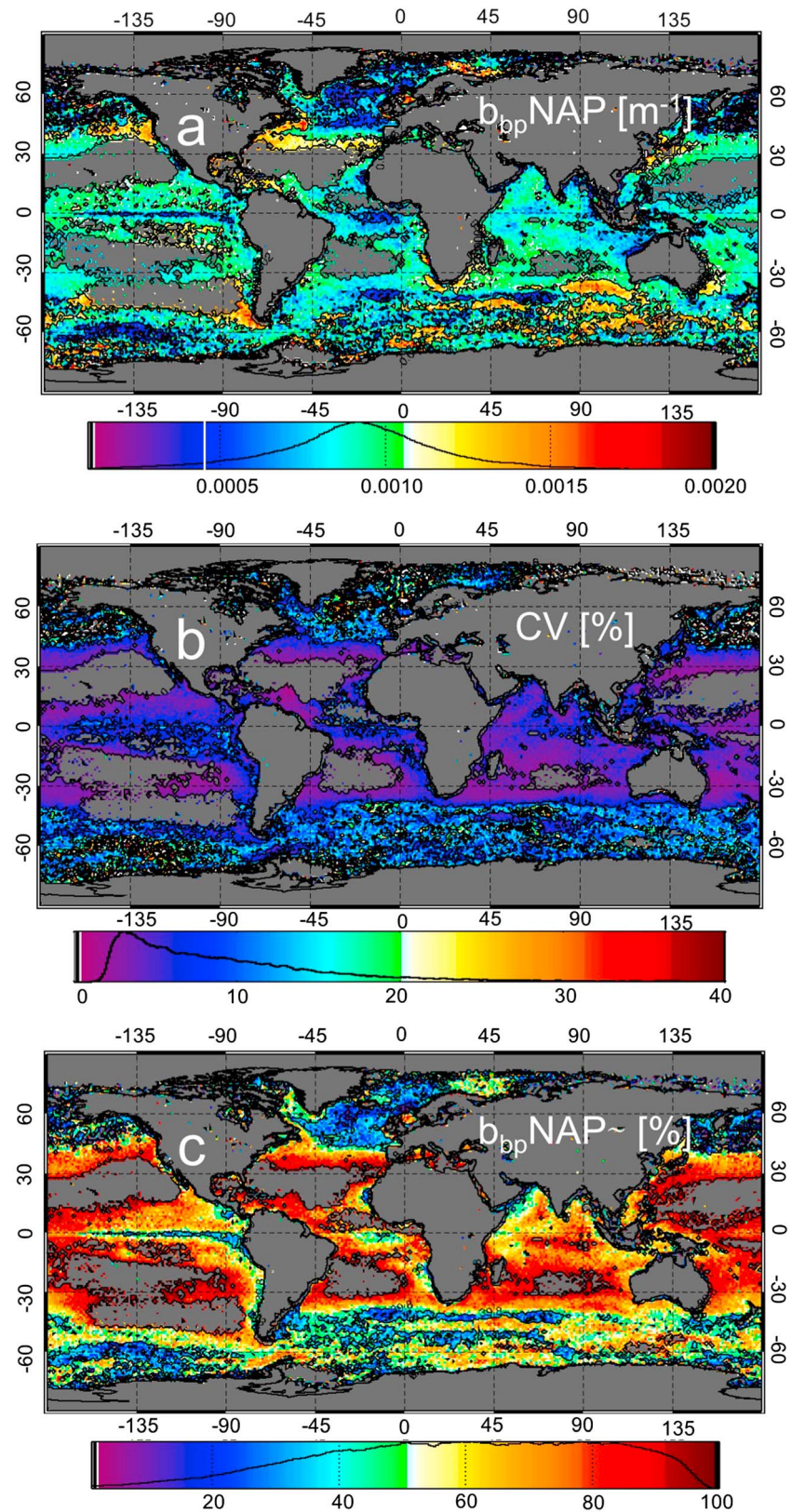
The pattern of  $b_{bp}$ NAP (Figure 2a) generally disagrees with the Chl geographical distribution, with lowest values in the most productive regions. For example, in the eastern portion of the productive subpolar North Atlantic,  $b_{bp}$ NAP is low relative to the area just south influenced by the Gulf Stream current. High  $b_{bp}$ NAP values are found in several hotspots around the globe, many with moderate or variable Chl, such as the north border of the North Atlantic subtropical gyre, in several bands across the Southern Ocean, the southeast coast of Australia, and the southwest tip of South America. Other  $b_{bp}$ NAP hotspots, however, do coincide with high Chl, including the eastern continental shelf of North America, the northern Benguela upwelling region, and the Barents and North Seas.

The median  $b_{bp}$ NAP value computed using all the valid pixels of the global ocean is  $9.5 \cdot 10^{-4} \text{ m}^{-1}$ , very close to the median value found for the Mediterranean Sea ( $0.001 \text{ m}^{-1}$ ; Bellacicco et al., 2016). The coefficient of  $3.5 \cdot 10^{-4} \text{ m}^{-1}$  found by Behrenfeld et al. (2005) for  $b_{bp}$ NAP is much lower than this value and falls in the second percentile of the  $b_{bp}$ NAP frequency distribution (see histogram on Figure 2a; vertical white line). Despite the various possible sources of discrepancy between the two methods (ocean color algorithms and processing, length of data time series, and averaging aggregation methods), the distribution of the 99%  $b_{bp}$ NAP confidence interval (Figure S2) evidences that most of the  $b_{bp}$ NAP values computed here vary only ~5%. The  $b_{bp}$ NAP found here spans over more than 1 order of magnitude and is in line with the range of



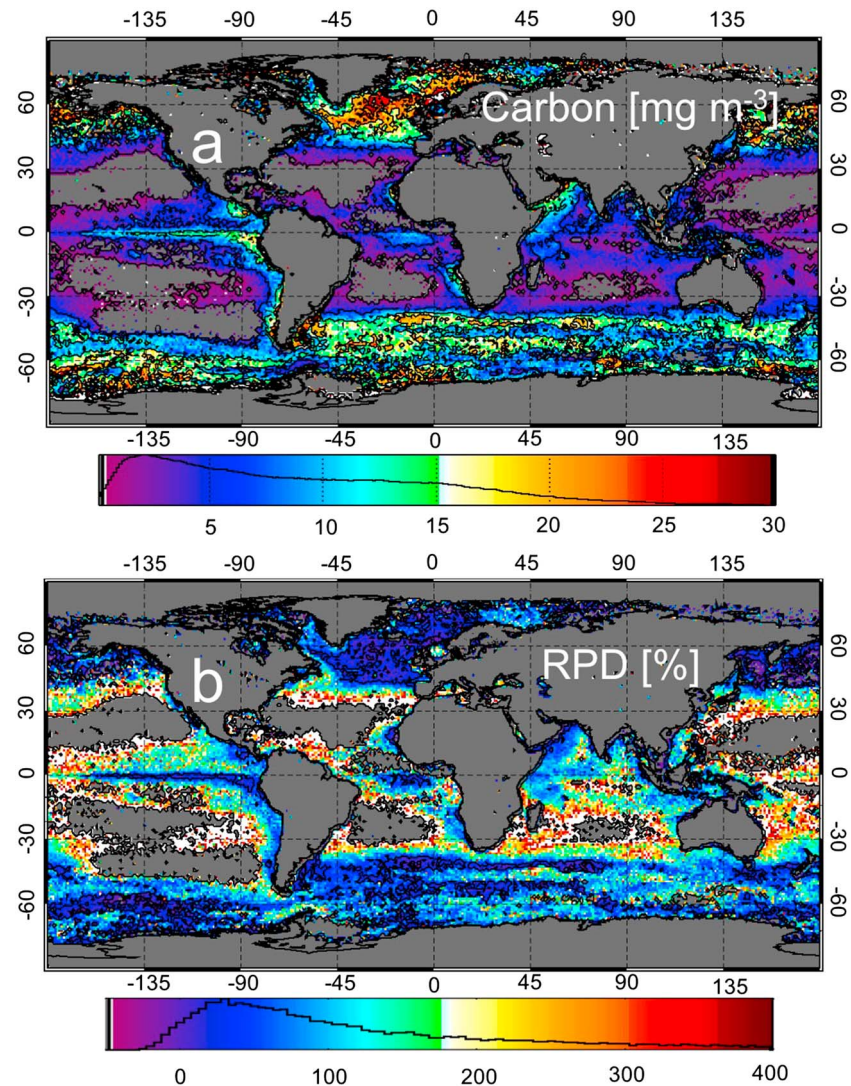


**Figure 1.** Annual climatology of (a)  $b_{bp}$ , (b) Chl, and (c) Pearson coefficient between Chl and  $b_{bp}$ . In case of the subtropical gyres, the Pearson coefficient is  $\leq 0$ , while in case of other areas of the global ocean, the coefficient is always  $> 0$  and close to 1. The frequency distribution histogram is overlaid in the three color bars.



**Figure 2.** Maps of (a)  $b_{bp} \text{ NAP}$ , (b)  $\text{CV}$ , and (c)  $b_{bp} \text{ NAP} \sim$ . The frequency distribution histogram is overlaid in the three color bars in order to show the recurrence of high values of each parameter. Pixels in which the Pearson coefficient ( $r$ ) was  $\leq 0$  and statistical significance ( $S$ ) was less than 0.95 were not considered in the analysis (gray areas).





**Figure 3.** (a) Map of phytoplankton carbon biomass computed using the  $b_{bpNAP}$  spatially resolved at pixel scale; RPD map between phytoplankton carbon biomass using the  $b_{bpNAP}$ , as computed in this work, and a single  $b_{bpNAP}$  coefficient. Pixels in which the Pearson coefficient ( $r$ ) was  $\leq 0$  and statistical significance ( $S$ ) was less than 0.95 were not considered in the analysis (gray areas). The frequency distribution histogram is overlaid in the two color bars in order to show the recurrence of high values of parameters. Note that RPD over 150 occurred at the boarder of the gyres and thus has to be interpreted with caution (see also the paragraph on spatial distribution of  $b_{bpNAP}$ ).

variability found by Brewin et al. (2012, their Table 3] from NOMAD, equatorial Pacific, and North Atlantic data set ( $3.6\text{--}7.2 \cdot 10^{-4} \text{ m}^{-1}$ ) and Graff et al. (2015, their Table 2 and Figure 3) from a data set in the equatorial Pacific and AMT cruises ( $3.9\text{--}10.8 \cdot 10^{-4} \text{ m}^{-1}$ ), but readers must be aware of the different temporal and spatial scales used to derive the former  $b_{bpNAP}$  estimates.

$b_{bpNAP}$  CV presents low values at low midlatitudes and higher values at high latitudes (Figure 2b). CV rarely exceeds 25% with the most frequent value below 5% in correspondence of the margins of the main ocean gyres. These areas are characterized both by high  $b_{bpNAP}$  and lower covariability in the Chl- $b_{bp}$  relationship. On the other hand, CV is higher at the high latitudes, which is due partly to higher variability in the Chl- $b_{bp}$  relationship (southern hemisphere) and partly to very low  $b_{bpNAP}$  (esp. in the North Atlantic). Figure S1 is a graphical representation of the method for the  $b_{bpNAP}$  determination, which is supported by statistical analysis of the Chl- $b_{bp}$  relationship.



One could argue that the  $b_{bp}NAP$  computation and assessment should be limited to the midrange of Chl values, avoiding the clear-water conditions (already limited by our criteria), and very high Chl values typical of the coastal waters. In this latter case, the relationship between Chl and  $b_{bp}$  tends again to flatten out, and consequently, the correlation is expected to be low, so our flagging criteria based on correlation value avoid  $b_{bp}NAP$  computation in coastal areas. In any case, the coastal pixels do not significantly contribute to the distribution, since our spatial resolution is low (100 km). This is also confirmed by the frequency distribution of  $b_{bp}NAP$  (see Figure 2a). The pixels referred to open ocean represented the main domain (>70%).

### 3.2. The Spatial Distribution of $b_{bp}NAP$

$b_{bp}NAP$  (Figure 2c; here defined as the fraction of  $b_{bp}NAP$  with respect to the total  $b_{bp}$ ; in percentage) follows the inverse of the biomass spatial variability as a consequence of the higher relative variability in  $b_{bp}$  versus  $b_{bp}NAP$ . Indeed, in the North Atlantic Ocean, characterized by high biomass,  $b_{bp}NAP$  is lower than 30% of total  $b_{bp}$ , while it reaches values over 60% in the area influenced by the Gulf Stream current (at the border of the North Atlantic subtropical gyre). This pattern is consistent with expectations if  $b_{bp}$  is dominated by organic matter: In oligotrophic regions, perennial nutrient limitation drives low phytoplankton biomass, which is rapidly recycled in the surface layer, in turn supporting relatively high bacterial, small heterotrophic, and detrital biomass (Barbieux et al., 2018, and references therein). Similarly, in the productive North Atlantic,  $b_{bp}NAP$  is consistently low with the high biomass values observed during the spring bloom (Alkire et al., 2014, and references therein).

At the borders of the gyres,  $b_{bp}NAP$  exceeds 80% of the total  $b_{bp}$ . Here however, Chl- $b_{bp}$  correlation values are lower than 0.5, suggesting that the theoretical thresholds that we applied ( $r > 0, S > 95\%$ ) should be more stringent in excluding or including pixels from the analysis. High  $b_{bp}NAP$  could be due to high year-round NAP. Low  $b_{bp}NAP$  could be either due to low NAP or because NAPs are strongly correlated with Chl.

In the North Atlantic Ocean,  $b_{bp}$  appears to be dominated more by particles that covary with phytoplankton cells, as opposed to the Southern Ocean, in which  $b_{bp}$  seems to be dominated more by particles that do not covary with total phytoplankton biomass. Indeed,  $b_{bp}NAP$  shows hot spots in the Southern Ocean with values >70% (e.g., Patagonia shelf and along the Antarctic Circumpolar Current). In that respect, the  $b_{bp}NAP$  measurements, and its order of magnitude, are consistent with the results found by Balch et al. (2016, their Figure 2:  $b_{bp}'$  transect of in situ data) along the entire Southern Ocean. Balch et al. (2016) found that the  $b_{bp}$  associated with particulate inorganic carbon (e.g., coccoliths) ranges between 0 and  $1.0 \cdot 10^{-3} \text{ m}^{-1}$ . Here  $b_{bp}NAP$  in the same area ranges between  $5 \cdot 10^{-4}$  and  $1.5 \cdot 10^{-3} \text{ m}^{-1}$ , and  $b_{bp}NAP$  is around 80%. This suggests coccoliths being the driving signal of  $b_{bp}NAP$  in the Southern Ocean. Indeed, coccoliths covary with  $b_{bp}$  because they scatter light as all other particles have a  $b_{bp}$  signal. Thus, the  $b_{bp}NAP$  is reasonably related to the coccolithophorid seasonality (i.e., skeleton compounds of no longer living cells;  $b_{bp}NAP$  is the  $b_{bp}$  when Chl is zero). On the other hand, in the North Atlantic Ocean, where  $b_{bp}NAP$  is less than 30%,  $b_{bp}$  is dominated by the particles that covary with phytoplankton cells (see equation (1)), thus being more determined by phytoplankton dynamics.

### 3.3. Implications for Phytoplankton Carbon Biomass From Satellite

Our analysis shows that  $b_{bp}NAP$  accounts for between 20 and 80% of the  $b_{bp}$  signal (e.g., from North Atlantic to Southern Oceans). Thus, we recommend taking into account the variability of this term when estimating phytoplankton carbon from  $b_{bp}$ . To estimate the impact of varying  $b_{bp}NAP$  on the satellite-derived carbon estimation, we computed the global map of phytoplankton carbon using the  $b_{bp}NAP$  estimated here (Figures 2a and 3a). The spatial pattern of phytoplankton carbon (Figure 3a) generally agrees with the Chl geographical distribution (Figure 1b) with high values in the most productive regions such as the polar regions, the coastal upwelling, and along the equatorial belts of the Atlantic and Pacific oceans. Low values are located in correspondence of midlatitude areas such as the boundaries of the gyres (Figure 3a). However, variable  $b_{bp}NAP$  estimates have a strong impact on quantitative phytoplankton biomass estimates, yielding a median value of  $8.6 \text{ mg C m}^{-3}$  when considering all the pixels (both open and coastal waters) and  $8.07 \text{ mg C m}^{-3}$  considering only pixels in open ocean. When single value estimated by Behrenfeld et al. (2005) is used instead, we obtain much higher median estimates of 16.6 and  $16.19 \text{ mg C m}^{-3}$ , respectively (Figure 3a). The use of spatially varying  $b_{bp}NAP$  instead of the single coefficient dramatically impacts the

phytoplankton carbon estimates from space. Indeed, in the North Atlantic Ocean,  $b_{bp}NAP$  does not significantly deviate from the constant coefficient found by Behrenfeld et al. (2005, Figure 3b; RPD lower than 10%). On the other hand, in regions dominated by  $b_{bp}NAP$  of inorganic nature not covarying with Chl, such as the Southern Ocean, the computation of phytoplankton carbon via  $b_{bp}$  exhibits large differences: RPD values greater than 100% (Figure 3b). The order of magnitude of our phytoplankton carbon biomass is consistent with the recent estimates of phytoplankton carbon by Arteaga et al. (2016) computed with a biogeochemical model able to resolve the Chl:C ratio and accounting for the optical acclimation of phytoplankton to nutrient, light, and temperature. A future challenge concerns to take into account the change of the scaling factor relating  $b_{bp}$  to C, as reported in Kostadinov et al. (2009, 2010, 2016), coupled with the  $b_{bp}NAP$  spatial variability as found in this work. Kostadinov et al. (2016) developed a carbon-based phytoplankton size class approach from satellite data considering the variation of the particle size distribution that influences the scaling factor. In this way, the phytoplankton carbon from space should consider both the changes in the particle size distribution that impact on backscattering per unit C biomass due to different scattering efficiencies and the  $b_{bp}NAP$  coefficient. It should increase the efficiency of phytoplankton carbon biomass retrieval from ocean color remote sensing data. To date, the impact of the Chl:C ratio, and thus of the SF term, on phytoplankton carbon computation is still not known. Future studies should be aimed at evaluating whether the variability induced by the SF term piles up or reduces the one induced by  $b_{bp}NAP$  in the computation of phytoplankton carbon biomass (Arteaga et al., 2016).

#### 4. Conclusions

Pixel-scale estimations showed marked  $b_{bp}NAP$  geographical variability. In productive regions, such as the North Atlantic Ocean,  $b_{bp}NAP$  and biomass are anticorrelated. This is presumably because nearly all NAP is strongly correlated with Chl, while in less productive regions with shallower winter mixed layers, there is a more constant population of noncovarying bacteria and detritus. In regions containing NAP of inorganic origin, including some coastal regions and the calcite belt of the Southern Ocean, we find high  $b_{bp}NAP$  values. Within the subtropical gyres,  $b_{bp}NAP$  could not be estimated, due to lack of positive correlation between satellite  $b_{bp}$  and Chl estimates, likely driven by photoacclimation. Throughout most of the ocean, our spatially resolved  $b_{bp}NAP$  estimates were higher than the single estimate calculated by Behrenfeld et al. (2005). These higher  $b_{bp}NAP$  estimates had a large impact on estimates of phytoplankton biomass from satellite  $b_{bp}$ . Our median phytoplankton C estimate in the pixels considered ( $8.6 \text{ mg C m}^{-3}$ ) was roughly half of the median estimate obtained using a single  $b_{bp}NAP$  estimate ( $16.6 \text{ mg C m}^{-3}$ ). Although we currently lack sufficient in situ phytoplankton carbon estimates to validate either estimate at global scale, our results strongly suggest that spatial variability in  $b_{bp}NAP$  should not be ignored.

Future work in this research pathway should (1) focus on comparing existing in situ inherent optical property data (i.e., BGC-Argo) to satellite products without leaving out the collection of in situ optical and plankton carbon data, (2) validate the impact of  $b_{bp}NAP$  variability on phytoplankton carbon estimation from space, and (3) give insight on the actual composition of  $b_{bp}NAP$  in various zones of the world ocean. Finally, inclusion of the reported relationships into phytoplankton carbon models will help improve their predictions.

#### Acknowledgments

M.B. started this work funded by the fellowship RITMARE at the Institute of Atmospheric Sciences and Climate (ISAC) of the Italian Research National Council (CNR). Now M.B. is at the Laboratoire d'Océanographie de Villefranche sur Mer (LOV) with a postdoctoral fellowship funded by the Centre Nationales d'Etudes Spatiales (CNES, Paris, France). N.B. collaborated at LOV, and now N.B. is on the National Oceanographic Center (NOC) of Southampton (UK). A special thanks to the ESA Ocean Color-Climate Change Initiative team for providing free access to the data time series (<http://www.esa-oceancolour-cci.org>). Special thanks to Francesco Bignami and Sorin Constantin for their criticism and suggestions.

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