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Vertical Variability of Total and Size-Partitioned Phytoplankton Carbon in the South China Sea

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Abstract: The standing stock of phytoplankton carbon is a basic and essential property for understanding oceanic ecosystems, biogeochemical cycles, and regional climates. However, current related algorithms mainly focus on remote-sensed application, which cannot describe the vertical profile of phytoplankton carbon throughout the whole euphotic zone. In this study, we modified a previous absorption-based bio-optical algorithm to acquire vertical variabilities of the total and size-partitioned phytoplankton carbon based on field data from the South China Sea (SCS). The mean absolute errors and the biases between estimated and field picophytoplankton carbon were <2.14 and 0.6–2.0, respectively. The results showed that the vertical profile of total phytoplankton carbon displayed a Gaussian distribution in the stratified SCS basin. The picophytoplankton carbon was always the fundamental component of the total phytoplankton carbon within the whole euphotic zone. The dominant picophytoplankton species changed from *Synechococcus*-like cyanobacteria at the sea surface to pico-sized haptophytes at the phytoplankton carbon maximum layer. The strong covariation between total phytoplankton carbon and chlorophyll-a concentration suggested that they can be converted into each other through an accurate carbon-to-chlorophyll ratio in the open SCS. These results provide essential information that can be used to decipher the three-dimensional structure of total and size-partitioned phytoplankton carbon in the open SCS.

Keywords: phytoplankton carbon; size-partitioned phytoplankton carbon; carbon-to-chlorophyll ratio; phytoplankton absorption; non-water absorption; the South China Sea

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1. Introduction

Marine phytoplankton is a key component of global carbon cycling, accounting for about half (~50 Gt C) of global annual primary production through oxygenic photosynthesis [1,2]. Knowledge of the standing stock and dynamics of marine phytoplankton is crucial for understanding the global carbon cycle and climate. In recent decades, the most commonly used indicator of phytoplankton biomass has been the total chlorophyll-a concentration (*Chla*, in mg m^{-3}) [3,4]. However, in the “photoacclimation regime” [5], the first order changes in *Chla* are due to intracellular pigment variation resulting from light and nutrient variations [6], thus *Chla* cannot provide a full description of the state of the ecosystem under such a regime [7]. Instead of *Chla*, total phytoplankton carbon biomass (*C*, in mg m^{-3}) is the parameter more directly related to the carbon cycle, biogeochemical cycles, and climate [7,8]. Accurate estimation of *C* provides a means to observe the standing stocks of phytoplankton and their response to environmental variability [9].

However, direct measurement of C remains challenging due to the inability to isolate C from the other particulate forms of carbon in seawater (e.g., zooplankton, detritus, and bacteria) [9]. Consequently, estimating C from other easier to measure proxies, such as optical parameters, maybe an easier approach.

With the development of observed technology, many bio-optical models have been built to derive *Chla* as well as chlorophyll-a concentrations in three size classes (e.g., [10–12]). In terms of C, several bio-optical models for C estimation have been proposed recently as well [6,7,13–15]. C is an important component of particulate organic carbon (POC, in mg m^{-3}) in the vast oceans. Sathyendranath et al. [14] developed a simple conceptual model to calculate C from *Chla* based on the assumption that at any given *Chla*, the lowest POC observed represents the C associated with that *Chla*. C can also be computed through *Chla* or POC by assuming a C-to-*Chla* (χ) or C-to-POC ratio. Based on the assumption that the particles contributing to particulate backscattering coefficients ($b_{\text{bp}}(\lambda)$, in m^{-1}) are composed of a stable non-algal “background” component and a second component including phytoplankton and other particles that co-vary with phytoplankton, Behrenfeld et al. [6] subtracted the non-algal particulate backscattering coefficients ($b_{\text{nap}}(\lambda)$, in m^{-1}) based on the relationship between $b_{\text{bp}}(\lambda)$ and *Chla* and then calculated C through the remaining $b_{\text{bp}}(\lambda)$ based on a simple scaling factor. The simple scaling factor was derived such that the resulting C was ~25 to 40% of POC and the average χ value was within the range observed in laboratory studies [16]. However, $b_{\text{nap}}(\lambda)$ varies in different oceanic regions (e.g., [17,18]). Bellacicco et al. [17] reported that using a constant $b_{\text{nap}}(\lambda)$ to estimate C will lead to a 50% overestimation in satellite-based global C estimates with respect to the results based on varied $b_{\text{nap}}(\lambda)$ in different regions. Meanwhile, based on Biogeochemical-Argo data, Bellacicco et al. [18] also reported that $b_{\text{nap}}(\lambda)$ in the surface layer increased from Southern to Northern Hemisphere, and $b_{\text{nap}}(\lambda)$ was the main contributor to $b_{\text{bp}}(\lambda)$ in the surface oligotrophic waters while the contribution of $b_{\text{nap}}(\lambda)$ decreased in the surface layer of most productive areas. Besides, variabilities in particle size distributions also lead to differences in backscattering per unit carbon biomass due to different scattering efficiencies [7,19]. Accordingly, Kostadinov et al. [19] built a $b_{\text{bp}}(\lambda)$ model to estimate particle size distributions (power-law distribution), and later Kostadinov et al. [7] combined the allometric relationships to compute C and size-partitioned phytoplankton carbon biomass based on the assumption that the value of C-to-POC ratio was 30%. However, the uncertainty in C estimation due to contribution of other types of non-algal particles to $b_{\text{bp}}(\lambda)$ still exists. To avoid this problem, Roy et al. [15] developed a semi-analytical algorithm (R17) to calculate C and size-partitioned phytoplankton carbon that is based on the specific absorption coefficient of phytoplankton (which is defined as the ratio of the absorption coefficient of phytoplankton to *Chla*, $a_{\text{ph}}^*(\lambda)$, in $\text{m}^2 \text{mg}^{-1}$), which is directly related to phytoplankton. These advances in C estimation algorithms provide effective means to estimate C from in situ to remote platforms.

The South China Sea (SCS) is the largest trophic marginal sea in the northwestern Pacific Ocean, and it plays important roles in regulating the regional carbon cycle and climate due to its vast area and volume [20,21]. Macronutrient concentrations in the central basin of SCS are below the detection limit, which suggest the SCS basin is oligotrophic [20,22,23]. Because it is oligotrophic, the open SCS is dominated by picophytoplankton, namely *Prochlorococcus*, *Synechococcus*, and picoeukaryotes [20]. Previous studies of the phytoplankton biomass variation in the SCS have been based mostly on *Chla*. However, photoacclimation is an important factor controlling variability of the *Chla* in the open SCS [21], and this process limits our understanding of the real distribution and variation of the phytoplankton pool as well as the biological carbon pump in the SCS. Therefore, in this study we estimated the vertical standing stocks of phytoplankton from the perspective of carbon mass rather than *Chla*. It provides another perspective for studying the distribution and variation of phytoplankton biomass in the SCS.

To avoid using preset values of C:POC and effects of the non-algal particles, we chose the absorption-based carbon algorithm to estimate the phytoplankton carbon concentration

in the SCS. First, we modified the algorithm described by Roy et al. [15] using the in situ absorption coefficient of phytoplankton [$a_{ph}(\lambda)$, in m^{-1}] and *Chla* dataset, and then we applied it to the non-watery beam absorption [$a_{pg}(\lambda)$, in m^{-1}] that was measured by an absorption-and-attenuation-meter (AC-S, WET Lab Inc., Philomath, OR, USA). The algorithm-derived picophytoplankton carbon values were validated by in situ measurements of picophytoplankton carbon. We then analyzed the characteristics of the vertical profiles of total and size-partitioned phytoplankton carbon in the open SCS basin. To ease the conversion between *C* and *Chla*, we analyzed the regional relationships between *C* and *Chla* as well. Table 1 shows the main abbreviations used in this study. This study provides important information for studying phytoplankton dynamics and the regional carbon cycle and climate in the SCS.

Table 1. The main abbreviations used in this study.

Abbreviations	Definition	Unit
$a_{ph}(\lambda)$	The absorption coefficient of phytoplankton	m^{-1}
$a_{ph}^*(\lambda)$	The ratio of the absorption coefficient of phytoplankton to chlorophyll-a concentration (the specific-absorption coefficient of phytoplankton)	$m^2 mg^{-1}$
$a_{pg}(\lambda)$	The non-watery beam absorption	m^{-1}
$a_{LH}(676)$	The absorption line height at 676 nm	m^{-1}
$a_{LH}^*(676)$	The specific-absorption coefficient of phytoplankton at 676 nm derived from $a_{pg}(\lambda)$	$m^2 mg^{-1}$
a^m	The maximum $a_{ph}^*(676)$ or $a_{LH}^*(676)$ determined from in situ measurements	$m^2 mg^{-1}$
$a_{Chla}^*(676)$	The observed specific absorption coefficient of chlorophyll-a at 676 nm derived from $a_{ph}^*(676)$ or $a_{LH}^*(676)$	$m^2 mg^{-1}$
$a_{Chla}^*(676, D)$	The theoretical specific absorption coefficient of chlorophyll-a at 676 nm	$m^2 mg^{-1}$
<i>Chla</i>	Total chlorophyll-a concentration	$mg m^{-3}$
<i>Chla</i> _{LH}	The value of <i>Chla</i> derived from $a_{pg}(\lambda)$ based on the absorption line height method	$mg m^{-3}$
ξ	The exponent of the phytoplankton size spectra	Dimensionless
<i>C</i>	Total phytoplankton carbon biomass	$mg m^{-3}$
<i>C_p</i>	The picophytoplankton carbon biomass	$mg m^{-3}$
<i>C_n</i>	The nanophytoplankton carbon biomass	$mg m^{-3}$
<i>C_m</i>	The microphytoplankton carbon biomass	$mg m^{-3}$
<i>F_p</i>	The fractions of carbon biomass associated with picophytoplankton	Dimensionless
<i>F_n</i>	The fractions of carbon biomass associated with nanophytoplankton	Dimensionless
<i>F_m</i>	The fractions of carbon biomass associated with microphytoplankton	Dimensionless
χ_p	The ratio of <i>C_p</i> to the chlorophyll-a concentration associated with picophytoplankton	Dimensionless
χ_n	The ratio of <i>C_n</i> to the chlorophyll-a concentration associated with nanophytoplankton	Dimensionless
χ_m	The ratio of <i>C_m</i> to the chlorophyll-a concentration associated with microphytoplankton	Dimensionless
χ	The ratio of <i>C</i> to <i>Chla</i> (<i>C:Chla</i>)	Dimensionless
<i>POC</i>	Particulate organic carbon concentration	$mg m^{-3}$
<i>MLD</i>	The mixed layer depth	m
<i>Z_{eu}</i>	The depth of the euphotic zone	m
<i>Z_{T22}</i>	The depth of 22 °C	m
<i>CML</i>	The C maximum layer	none

2. Materials and Methods

2.1. Study Area and Field Sampling

The SCS extends from 3° S to 23° N and from 99° E to 121° E, and it includes two wide shallow shelves in the northern and southern parts and a large deep basin in between [24]. The upper ocean layer of the SCS is mainly affected by eastern Asian monsoons [25], periodic typhoons, Kuroshio intrusions, and fresh water inflow [26]. The circulation of the SCS is cyclonic in winter but anticyclonic in summer [24]. The open SCS is generally stratified, warm, and oligotrophic, with low phytoplankton biomass [20,21]. The vertical *Chla* is generally characterized by a pronounced deep maximum at 60–100 m in the open SCS [21,27–29].

Three cruises were carried out in the SCS to collect bio-optical parameters: 27 June to 17 July 2015 (cruise 2015), 3–23 September 2016 (cruise 2016), and 1–22 October 2017 (cruise 2017). The bio-optical parameters (absorption coefficient of phytoplankton [$a_{ph}(\lambda)$, in m^{-1}], *Chla*, picophytoplankton carbon biomass, and *POC*) were obtained at four depths (0 or 5, 25, 50, and 75 m). *POC* data were only collected during cruises 2015 and 2017. Additionally, an AC-S instrument was used to measure the vertical profiles of $a_{pg}(\lambda)$ during cruises 2015 and 2016. A simultaneously seabird conductivity-temperature-depth (*CTD*) was used to obtain the profiles of temperature and salinity. The AC-S and *CTD* were assembled in a cage to measure the optical and hydrographic parameters from surface to about 120 m. Figure 1 shows the locations of the sampling stations.

Figure 1. Locations of stations in the SCS. The black hollow circles represent the stations for the $a_{ph}^*(676)$ dataset. The red squares represent the stations for the $a_{pg}(\lambda)$ dataset. The green stars represent the warm and oligotrophic stations (>1000 m) with strong stratification in the SCS basin.

2.2. Field in Situ Data

2.2.1. Measurement of $a_{ph}(\lambda)$ and Calculation of $a_{ph}^*(676)$

To obtain $a_{ph}(\lambda)$ from 350 to 750 nm, 0.5–3.0 L of seawater, depending on the station, were filtered through a 25 mm glass fiber filter (Whatman, GF/F, Maidstone, UK) under low vacuum conditions. Because our laboratory bought a new spectrophotometer in 2016, the measurements of $a_{ph}(\lambda)$ for cruise 2015 were made using a Shimadzu UV-2550 spectrophotometer (Kyoto, Japan), and those for cruises 2016 and 2017 were made using a PerkinElmer Lambda 650S spectrophotometer (Waltham, MA, USA) based on the quantitative filtered technique (QFT). The reference blank was a clear filter that was presoaked in pure water. First, the absorption coefficient of total particles [$a_p(\lambda)$, in m^{-1}] was measured. Then the absorption coefficient of non-algal particles [$a_{nap}(\lambda)$, in m^{-1}] was measured after soaking the filters in methanol for 90–180 min to remove phytoplankton pigments. All measurements were corrected for the background signals by subtracting the absorption values at 750 nm over the whole wavelength [30]. Corrections for pathlength amplification were made according to Stramski et al. [31]. Finally, $a_{ph}(\lambda)$ was calculated as the difference between $a_p(\lambda)$ and $a_{nap}(\lambda)$. The values of $a_{ph}^*(676)$ were calculated by dividing $a_{ph}(676)$ by the corresponding field in situ *Chla*.

2.2.2. Measurement of $a_{pg}(\lambda)$

The vertical profiles of $a_{pg}(\lambda)$ were measured using a 25 cm pathlength AC-S with 82 wavebands from 401.6 to 744.1 nm. Pure water was used to calibrate the drift of the AC-S instrument and as the reference blank before cruises. To avoid the influence of bubble, the AC-S was lowered below the water's surface for ~5 min to warm up, and after the warm up period, the AC-S was steadily lowered through the water column to collect data. Before data correction, the software "WET Labs Archive File Processing" (WAP) was used to merge the AC-S and CTD data. The corrections for temperature and salinity effects were made using contemporaneously recorded CTD data [32]. All measurements were corrected for scattering by setting the absorption values as zero around the infrared wavelengths [33].

2.2.3. Pigment Concentration Measurement and Determination of Dominant Phytoplankton Species

The values of *Chla* were measured in two ways: fluorescence method and high-performance liquid chromatography (HPLC). For the fluorescence method, 0.5–1.0 L of seawater were filtered through a 25 mm Whatman GF/F filter with 0.7 μm pore size to obtain *Chla*. In the laboratory, filters were soaked in acetone in the dark for 24 h to extract the chlorophyll *a*. Then, *Chla* was measured using a Turner Design 10 fluorometer (Sunnyvale, CA, USA) [34]. For HPLC, 2.5–10 L of seawater were filtered through 25 mm or 47 mm Whatman GF/F filters with 0.7 μm pore size and stored in liquid nitrogen until analysis in the laboratory. For surface samples (0 or 5 m), 8–10 L of seawater were filtered on the 47 mm Whatman GF/F filters. As for the samples at 25, 50 and 75 m, 2.5–5 L of seawater were filtered on the 25 mm Whatman GF/F filters. The collection of HPLC samples was generally according to the Joint Global Ocean Flux Study (JGOFS) protocols [35]. See Vidussi et al. [36] for analysis details. The HPLC data were also used to calculate the size-partitioned *Chla* according to the method in Brewin et al. [10].

Determination of dominant phytoplankton species was made according to the criteria in Table 4 from Alvain et al. [37] and this method was based on the relative concentrations of main biomarkers of the *Prochlorococcus*, *Synechococcus*-like cyanobacteria, haptophytes, dinoflagellates and diatoms of the water samples to determine the dominate phytoplankton species.

2.2.4. Picophytoplankton Carbon Biomass and POC Measurements

To measure picophytoplankton carbon biomass, seawater samples were filtered through a 20 μm sieve and preserved with formaldehyde (2% final concentration) for picophytoplankton cell (*Prochlorococcus*, *Synechococcus* and autotrophic picoeukaryotes) counting. The samples were freeze-trapped in liquid nitrogen after 15 min of standing in the dark. Measurements of picophytoplankton cell abundances were made using a BD FACSCanto II flow cytometer (Franklin Lakes, NJ, USA). Before measurement, velocity correction was carried out according to Marie et al. [38]. According to the scatterplots of different fluorescence or side scattering, cell abundances of the three picophytoplankton categories were determined. Carbon contents of the three picophytoplankton categories were estimated from cell abundances by assuming conversion factors of 17.6 fg C cell^{−1} for *Prochlorococcus*, 74.55 fg C cell^{−1} for *Synechococcus*, and 779.9 fg C cell^{−1} for picoeukaryotes respectively [summer-winter averaged values in Chen et al. [20]]. The sum of the carbon contents of the three picophytoplankton types is defined as the field picophytoplankton carbon biomass.

For POC measurement, 0.5–4.0 L seawater was filtered onto a pre-combusted (450 °C for 5 h) 25 mm Whatman GF/F fiberglass filter and then stored in a −20 °C fridge. The method of POC measurements was generally consistent with the Joint Global Ocean Flux Study (JGOFS) protocols [35,39]. In the laboratory, the POC samples were dried at 60 °C for 8 h and then acidified by hydrochloric acid fumigation to remove the inorganic carbon. Finally, the filters were dried again and the POC concentrations were measured using a Vario UNICUBE elemental analyzer (Elementar Analysensysteme GmbH, Langenselbold, Germany).

2.3. Derived Data

2.3.1. Physical and Biogeochemical Layer Depths (Layers) of the Water Column

The mixed layer depth (*MLD*, in m) was estimated based on a threshold potential density difference (0.03 kg m^{-3}) from a near-surface value (at 10 m) [21]. The depth of the euphotic zone (Z_{eu} , in m) was estimated based on average *Chla* within 10 m ($Chla_{surf}$, in mg m^{-3}) as $Z_{eu} = 35 Chla_{surf}^{-0.35}$ (from Cao et al. (2002) [40]). The depth of 22°C isotherm (Z_{T22} , in m) was used as the proxy for the nutricline [24]. The C maximum layer (*CML*) was defined as the layer where a pronounced C maximum appeared in the vertical profile.

2.3.2. Definition of Trophic Categories

The trophic category (for stratified waters) of each station was defined by the value of *Chla* at 0 or 5 m according to the threshold in Table 3 from Uitz et al. [41]. The trophic level increased sequentially from S1 (the most oligotrophic) to S9 (the most nutritious) in the stratified waters.

2.3.3. Algorithm Performance Metrics

The mean absolute error (*MAE*), the root mean square (*RMSE*), and *bias* between algorithm estimations and field observations were calculated to evaluate the performance of the algorithm [42]:

$$MAE = 10 \left(\frac{\sum_{i=1}^n |\log(C_{derived}) - \log(C_{field})|}{n} \right), \quad (1)$$

$$RMSE = \sqrt{\frac{1}{n} \sum [C_{derived} - C_{field}]^2}, \quad (2)$$

$$Bias = 10 \left(\frac{\sum_{i=1}^n \log(C_{derived}) - \log(C_{field})}{n} \right), \quad (3)$$

where n , $C_{derived}$, and C_{field} represent the number of samples, the estimated products, and field measurements, respectively.

2.4. Phytoplankton Carbon Estimation

Figure 2 shows the flow chart of the phytoplankton carbon estimation. The $a_{ph}(\lambda)$ was first used to validate the phytoplankton carbon model, and then we applied the model to the $a_{pg}(\lambda)$ data to obtain high-resolution vertical distribution profiles of total and size-partitioned phytoplankton carbon in the SCS.

Figure 2. Flow chart of the regional phytoplankton carbon algorithm reparameterization and application into field data.

2.4.1. Phytoplankton Carbon Estimation Algorithm

The phytoplankton carbon estimation algorithm, *R17*, uses the $a_{ph}(676)$ and *Chla* as inputs and combines the allometric relationship between phytoplankton cell size and carbon content to calculate total and size-partitioned phytoplankton carbon. A main

assumption of *R17* is that the phytoplankton size spectrum follows a power-law distribution. In preparation for estimation of *C*, the exponent of the phytoplankton size spectra (ζ) is first computed from $a_{ph}^*(676)$ using the method described in Roy et al. [12]. The ζ can be computed following Equation (4) in MATLAB using a single-variable bound non-linear-function minimization method based on golden section search and parabolic interpolation [12]:

$$a_{Chla}^*(676) = \frac{4 - \zeta - m}{D_{max}^{4-\zeta-m} - D_{min}^{4-\zeta-m}} \int_{D_{min}}^{D_{max}} [D^{3-\zeta-m} \times a_{Chla}^*(676, D)] dD, \quad (4)$$

where $a_{Chla}^*(676)$ on the left-hand side is the observed specific absorption coefficient of chlorophyll-a at 676 nm [43]; $a_{Chla}^*(676, D)$ on the right-hand side is the theoretical value of specific absorption coefficient of chlorophyll-a at 676 nm, which is expressed as a function of the equivalent spherical diameter *D* of phytoplankton [43]; *m* is the exponent of the relationship between intracellular *Chla* ($Chla_{cell}$, $mg\ m^{-3}$) and *D* ($Chla_{cell} = c_0 D^{-m}$), here set as *m* = 0.06 (dimensionless) and $c_0 = 3.9 \times 10^6$ ($mg\ Chla\ m^{-2.94}$) [43]; minimum diameter $D_{min} = 0.2\ \mu m$; and maximum diameter $D_{max} = 50\ \mu m$ [15].

The allometric relationship between the cellular content of phytoplankton carbon (C_{cell}) and cell volume (V_{cell}) for phytoplankton communities was then used to calculate *C* [44]:

$$C_{cell} = a V_{cell}^b, \quad (5)$$

where V_{cell} is the volume of a phytoplankton cell expressed in μm^3 , C_{cell} is expressed in $pg\ C\ cell^{-1}$, and *a* = 0.54 and *b* = 0.85 are constants [15]. *C* within a diameter range [D_{min} , D_{max}] can then be expressed as:

$$C = \chi_{Chla} = \frac{10^{-9} a \left(\frac{10^{18} \pi}{6} \right)^b}{\left(\frac{\pi}{6} \right) c_0} \left(\frac{D_{max}^{3b-\zeta+1} - D_{min}^{3b-\zeta+1}}{D_{max}^{4-\zeta-m} - D_{min}^{4-\zeta-m}} \right) \left(\frac{4 - \zeta - m}{3b - \zeta + 1} \right) Chla. \quad (6)$$

It should be noted that 10^{-9} and 10^{18} are the conversions of units from pg to mg and from m^3 to μm^3 , respectively. The diameter ranges of pico-, nano-, and micro-sizes were set at 0.2–2.0, 2–20, and 20–50 μm , respectively [15]. The carbon biomass of pico- (C_p , in $mg\ m^{-3}$), nano- (C_n , in $mg\ m^{-3}$), and microphytoplankton (C_m , in $mg\ m^{-3}$) was calculated through the product of χ_i and $Chla_i$, where *i* represents pico-, nano-, or microphytoplankton. χ_i is expressed as a function of ζ , *m*, and the upper and lower bounds of diameter of the three size classes. The $Chla_i$ was estimated using the *Chla* and chlorophyll-a fractions of the three size classes (see Roy et al. [12] for details). Finally, the fractions of carbon associated with pico- (F_p), nano- (F_n), and microphytoplankton (F_m) were calculated through C_i and *C*.

2.4.2. Modification of the Algorithm

The $a_{ph}^*(676)$ is not necessarily equal to $a_{Chla}^*(676)$, especially in low-*Chla* conditions [43]. Therefore, $a_{ph}^*(676)$ values were converted to the corresponding $a_{Chla}^*(676)$ values using an ad-hoc non-linear function [43]:

$$a_{Chla}^*(676) = \frac{a_{ph}^*(676)}{1 + \sigma a_{ph}^*(676)}, \quad (7)$$

where $\sigma = \frac{1}{a_{ci}^*} - \frac{1}{a^m}$, and $a_{ci}^* = 0.028\ m^2\ (mg\ Chla)^{-1}$ was the maximum numerical value of $a_{Chla}^*(676)$ reported for laboratory cultures, and a^m was the maximum $a_{ph}^*(676)$ determined from in situ measurements. To estimate ζ over a realistic range of measured $a_{ph}^*(676)$, a^m was set to $0.0226\ m^2\ mg^{-1}$ for the $a_{ph}^*(676)$ dataset; for the $a_{pg}(\lambda)$ dataset, a^m was set to $0.0128\ m^2\ mg^{-1}$. In addition, the upper bounds for $a_{ph}^*(676)$ were the a^m values in different datasets, respectively, and the lower bound for $a_{ph}^*(676)$ was set to $0.007\ m^2\ mg^{-1}$.

2.4.3. Application of the Algorithm to $a_{pg}(\lambda)$

It is not enough to apply *R17* to remote sensing data (which only observes the surface distribution) and $QFT-a_{ph}^*(676)$ data (which only observes the variations at several discrete depths) to obtain a three-dimensional distribution of C , C_p , C_n , and C_m . Thus, we tried to apply the *R17* algorithm to $a_{pg}(\lambda)$ data to obtain the high-spatial-resolution vertical profiles of total and size-partitioned phytoplankton carbon. To do this, the values of $Chla$ were first derived using the absorption line height method ($Chla_{LH}$, in $mg\ m^{-3}$) [45]. The absorption line height at 676 nm [$a_{LH}(676)$, in m^{-1}] was calculated from $a_{pg}(\lambda)$ as follows:

$$a_{LH}(676) = a_{pg}(676) - [0.52 \times [a_{pg}(700) - a_{pg}(650)] + a_{pg}(650)]. \quad (8)$$

The $Chla_{LH}$ was then calculated using $a_{LH}(676)$ based on a regional empirical power-law relationship between field $Chla$ and $a_{LH}(676)$ in the SCS:

$$Chla_{LH} = 65.57 \times a_{LH}(676)^{0.96}. \quad (9)$$

The correlation coefficient (R), $RMSE$, $bias$, and MAE between field $Chla$ and $Chla_{LH}$ were 0.88, 0.11 $mg\ m^{-3}$, 1.03, and 1.45, respectively (Figure 3). The specific-absorption coefficient of phytoplankton from $a_{pg}(\lambda)$ (a_{LH}^* , in $m^2\ mg^{-1}$) was defined as: $a_{LH}^*(676) = a_{LH}(676)/Chla_{LH}$. Finally, the $Chla_{LH}$ and $a_{LH}^*(676)$ were used to estimate the total and size-partitioned phytoplankton carbon.

Figure 3. Relationship between field $Chla$ and $Chla_{LH}$. The black line is the 1:1 line. The *Num* is the number of sample.

3. Results

3.1. Algorithm Validation

To evaluate the applicability of *R17*, validation of *R17* was carried out using field data (both $QFT-a_{ph}^*(676)$ and $AC-S-a_{pg}(676)$ data) from the SCS. Because field C , C_n , and C_m are difficult to obtain, validations were limited to C_p . The field observed C_p for algorithm validation was the product of flow-cytometry-measured picophytoplankton cell abundance and the corresponding carbon conversion coefficient. The field observed C_p was independent of the algorithm-derived C_p . The details of the field observed C_p measurement were in Section 2.2.4.

3.1.1. Validation of Estimations from $a_{ph}^*(676)$

Figure 4a shows validation results for estimations from $a_{ph}^*(676)$. The value of R between field C_p and estimated C_p based on *R17* was 0.58 ($p < 0.001$), and the values of MAE and $bias$ between field C_p and the $a_{ph}^*(676)$ -derived estimations were 2.14 and 0.62. The scatter points were distributed near the 1:1 line (black line in Figure 4a). Uncertainties in the carbon conversion factors would lead to 2- to 3-fold overestimation of field C_p [46].

The median value of the estimated C_p was lower than that of the default field estimations but higher than those of a 2- or 3-fold overestimations of the field observations (Figure 4b). In addition, the field χ_p was calculated as the ratio of field C_p and picophytoplankton chlorophyll-a concentration derived from HPLC measured pigments [10]. In Figure 5, the median value of algorithm-estimated χ_p (82.26) was between the median value of field χ_p (120.44) and the median value of 2-fold-error field χ_p (60.22). These results suggested that the $a_{ph}^*(676)$ -derived C_p compared well with the corresponding field C_p .

Figure 4. (a) Comparison plot for the observed C_p and $R17$ -derived C_p using the $a_{ph}^*(676)$ dataset. (b) Box plots of the observed and derived C_p corresponding to the default in situ values and in situ values with possibilities of 2- and 3-fold overestimations.

Figure 5. Box plots of the observed χ_p corresponding to the default in situ values and in situ values with the possibility of 2-fold overestimation and algorithm-derived χ_p .

3.1.2. Validation of Estimations from $a_{LH}^*(676)$

Figure 6 shows the validation results for $a_{LH}^*(676)$ estimations. The MAE and bias between $a_{LH}^*(676)$ -estimated and field C_p were 1.9 and 1.39, respectively. The scatter points fell around the 1:1 line. The median value of the estimated C_p was similar to but slightly higher than that of the default field estimates (Figure 6b), which may result from the uncertainty of a^m and $Chla_{LH}$ (see Section 4.1 for detailed discussion). The median value of the derived χ_p was 91.17, which was lower than the median value of field χ_p (120.44) but higher than the median value of 2-fold-error field χ_p (60.22) shown in Figure 5. Figure 7 shows the performances of $R17$ when using different input data. The values of R , $RMSE$, and MAE between $a_{LH}^*(676)$ -derived and field C_p were similar to those between $a_{ph}^*(676)$ -derived and field C_p . This result suggested that the performance of $R17$ applied to the $a_{LH}^*(676)$ was similar to that of $R17$ applied to the $a_{ph}^*(676)$. Accordingly, the $a_{LH}^*(676)$ can be used to estimate the phytoplankton carbon in the SCS.

Figure 6. (a) Comparison plot for the observed C_p and $R17$ -derived C_p using the $a_{pg}(\lambda)$. (b) Box plots of the observed and derived C_p corresponding to the default in situ values and in situ values with possibilities of 2- and 3-fold overestimations.

Figure 7. Comparison plot for the observed C_p and $R17$ -derived C_p . Note that the field C_p matched both $a_{ph}^*(676)$ - and $a_{pg}(\lambda)$ -derived C_p .

3.2. Vertical Variation of Phytoplankton Carbon and Related Bio-Parameters

3.2.1. Statistical Results from $a_{ph}^*(676)$

We analyzed the variations of total and size-partitioned phytoplankton carbon and related bio-parameters based on the results derived from $a_{ph}^*(676)$ data within the euphotic layer covering the coastal region to the deep basin in the SCS. As shown in Table 2, the C varied from 2.38 to 62.02 mg m⁻³, with an average value of 16.53 mg m⁻³. The ranges of C_p , C_n , and C_m were 0.62–47.21, 0.21–25.70, and 0.0056–13.45 mg m⁻³, respectively. The average values of C_p , C_n , and C_m were 11.91, 3.69, and 0.93 mg m⁻³. Figure 8 shows the boxplot of F_p , F_n , and F_m . The median of F_p (0.67) was higher than the median of F_n (0.27), and the median of F_m (0.06) was lowest. Moreover, 87.44% of F_p were higher than the corresponding F_n and F_m . These results suggested that the picophytoplankton was the major contributor to C in the SCS, which is consistent with previous studies reporting that the open SCS is oligotrophic and that the picophytoplankton constitutes an essential component of the phytoplankton community [20,29,47]. The values of χ varied from 25.85 to 91.44, with an average value of 53.77. The value ranges of χ_p , χ_n , and χ_m were 72.15–96.36, 29.39–39.26, and 17.04–17.91, respectively. The value of C:POC is an important input in other phytoplankton carbon estimation models, and it is usually set to 30% [6,7]. However, the value of C:POC is not a constant, and it varies from 14% to 85% in different oceanic regions [13,48–51]. In our study, the C:POC value in the SCS ranged from 5.54% to 95.32%, and the average value was $41.27 \pm 25.8\%$ (Table 2). This variability of C:POC is consistent with the results reported in previous studies across a variety of oceanic regions [13,48–51].

Table 2. Variations of C , size-partitioned phytoplankton carbon, POC , $C:POC$, χ , and the ratios of size-partitioned phytoplankton carbon to size-partitioned phytoplankton carbon based on the a_{ph}^* (676) dataset in the SCS.

Parameters	Units	Mean	Max	Min	SD	Num
C	$mg\ m^{-3}$	16.53	62.02	2.38	12.57	215
C_p	$mg\ m^{-3}$	11.91	47.21	0.62	10.47	215
C_n	$mg\ m^{-3}$	3.69	25.70	0.21	3.46	215
C_m	$mg\ m^{-3}$	0.93	13.45	0.0056	1.36	215
χ	None	53.77	91.44	25.85	17.55	215
χ_p	None	83.09	96.36	72.15	5.96	215
χ_n	None	33.85	39.26	29.39	2.43	215
χ_m	None	17.44	17.91	17.04	0.21	215
POC	$mg\ m^{-3}$	60.84	185.48	27.23	32.59	83
$C:POC$	%	41.27	95.32	5.54	25.80	83

Notes: Mean, Max, Min, SD, and Num represent the average value, maximum, minimum, standard deviation, and number of samples, respectively.

Figure 8. Box plot of F_p , F_n , and F_m values derived from $R17$ based on a_{ph}^* (676) data.

3.2.2. Vertical Profiles in the SCS Basin

To understand the basic vertical profile of total and size-partitioned phytoplankton carbon as well as χ in the open SCS, we plotted the results from the stations > 1000 m with strong stratification in the oligotrophic SCS basin. Figure 9 shows the values of C , size-partitioned phytoplankton carbon, and χ at four depths (0 or 5, 25, 50, and 75 m) derived from a_{ph}^* (676). Figure 10 shows the continuous high spatial resolution vertical profiles of these parameters derived from a_{LH}^* (676).

Figure 9. Variabilities of (a) C , (b) C_p , (c) C_n , (d) C_m , (e) F_p , (f) F_n , (g) F_m , and (h) χ derived from $a_{ph}^*(676)$ data at four depths (the filled circles from top to bottom represent values of the parameters at: 0 or 5, 25, 50, and 75 m in each bin, and the bins are divided by black dotted lines). The asterisks represent the $Chla$ maximum among four depths at each station.

Figure 10. The vertical profiles of (a) C , (b) $Chla_{LH}$, (c) χ , (d) C_p , (e) C_n , (f) C_m , (g) F_p , (h) F_n , and (i) F_m derived from $a_{LH}^*(676)$ data in the open SCS (green stars in the Figure 1). White solid lines represent the MLD, and white dotted lines represent the depth of the C maximum, and black solid lines represent the Z_{T22} , and black dotted lines represent the Z_{eu} .

Vertical Profiles at Four Discrete Depths

According to the trophic categories, 92% of stations shown in Figure 9 were in the most oligotrophic environment (trophic categories were within S2–S4). The subsurface

C maximums usually appeared at 50 or 75 m and were accompanied by the subsurface *Chla* maximums. The vertical profiles of C_p were similar to those of C at all stations. The values of C_p were the highest among C_p , C_n , and C_m at the depths of the subsurface C maximum. While 67% of vertical profiles of C_n were similar to those of C , 80% of vertical profiles of C_m were different from those of C , whereby the C_m maximums did not appear at the depths of the subsurface C maximum. Additionally, 88% of vertical profiles of F_p were similar to those of C . At the depth of the subsurface C maximum, the maximum values of F_p (generally > 0.5) were also observed at all stations. Most of vertical distributions of F_n and F_m showed the opposite trend as those of F_p , and the vertical maximum of F_p always coincided with the minimums of F_n and F_m and the highest χ value. This result indicated that at the depths of subsurface C maximum, the picophytoplankton was increasing, either in terms of total carbon biomass or fraction, which is consistent with the results reported in Uitz et al. [41] for S2–S4 waters and the results reported in Sauzède et al. [11] at the Bermuda Atlantic Times Series Study site from June to October. In most areas of the SCS basin, strong density stratification results in oligotrophic waters [52], thus the pico- and nanophytoplankton are dominant at the CML, and the contribution of C_m is low [41].

High Spatial Resolution Vertical Profile

Figure 10 shows seven higher spatial resolution vertical profiles of the phytoplankton carbon and bio-parameters, which were obtained from the $a_{LH}^*(676)$ in the SCS basin. The stations with strong stratification, where water depths were >1000 m and measuring depths were >100 m, were chosen as the display stations. These vertical profiles derived from $a_{LH}^*(676)$ show more detail about the variabilities of phytoplankton carbon and related bio-parameters within the whole euphotic zone. The $a_{LH}^*(676)$ -derived vertical profiles of C , size-partitioned phytoplankton carbon, and related bio-parameters were similar to those derived from the $a_{ph}^*(676)$ data. The CML was a universal feature at the seven stations, and the depths of the CML were all above the Z_{eu} and Z_{T22} . The subsurface C maximum ($>20 \text{ mg m}^{-3}$) appeared at 50–100 m with the subsurface *Chla* maximum layer and highest χ values. The values of C_p and C_n increased while the values of C_m decreased slightly at the CML. Figure 10g–i show that the F_p increased while F_n and F_m decreased at the CML. These results suggested that the contribution of picophytoplankton still increased while the contributions of nano- and microphytoplankton decreased at the CML.

4. Discussion

4.1. Sources of Uncertainty in the Algorithm

Two main sources of uncertainties in $R17$ are those associated with estimated values of ζ and those in the allometric parameterization [13]. Deriving a new allometric relationship for phytoplankton in the SCS was out of the scope of our study, thus, we mainly focused on the uncertainties associated with ζ . The value of ζ was estimated based on the observed $a_{ph}^*(676)$ or $a_{LH}^*(676)$ [12]. If the value of a_{ci}^* is reliable, the uncertainty of the ζ -estimated method in [12] is mainly due to the error in the value of a^m based on the field data. The value of a^m directly impacts the estimated values of ζ from $a_{ph}^*(676)$ or $a_{LH}^*(676)$. To evaluate the overall uncertainties in the estimations of C and size-partitioned phytoplankton carbon, we added 0 to 30% uncertainties in the a^m into the algorithm. Regardless of whether $a_{ph}^*(676)$ or $a_{LH}^*(676)$ was used, the overestimation of a^m resulted in underestimation of C and C_p and overestimation of C_n and C_m (Figure 11). For the C derived from $a_{ph}^*(676)$, when $a_{ph}^*(676)$ was $>0.025 \text{ m}^2 \text{ mg}^{-1}$, a small underestimation ($\sim 5\%$) was observed, even when $>20\%$ uncertainty of a^m was added into the algorithm. However, significant underestimation ($\sim 30\%$) was observed when $a_{ph}^*(676)$ was in the range of $0.020\text{--}0.025 \text{ m}^2 \text{ mg}^{-1}$ and $>20\%$ uncertainty of a^m was added into the algorithm. For other cases, the uncertainty of algorithm-derived C showed an increasing trend with increasing uncertainty in a^m , but underestimation was generally $<25\%$. For the C_p derived from the $a_{ph}^*(676)$, when $a_{ph}^*(676)$ was $>0.025 \text{ m}^2 \text{ mg}^{-1}$, a small underestimation ($\sim 5\%$) was observed even when $>20\%$

uncertainty of a^m was added into the algorithm. The underestimation increased up to 20–50% when $a_{ph}^*(676)$ was $<0.025 \text{ m}^2 \text{ mg}^{-1}$ and $>10\%$ uncertainty of a^m was added into the algorithm. As for C_n and C_m , when $a_{ph}^*(676)$ was in the range of $0.020\text{--}0.025 \text{ m}^2 \text{ mg}^{-1}$, a significant overestimation ($>100\%$ for C_n and $>1000\%$ for C_m) was observed even when only 5% uncertainty of a^m was added into the algorithm. For other cases, smaller overestimation ($\sim 10\%$ for C_n and $\sim 30\%$ for C_m) was observed. For $a_{LH}^*(676)$, the uncertainty of algorithm-derived C and C_p showed an increasing trend with increasing uncertainty in a^m when $a_{LH}^*(676)$ ranged from 0.011 to $0.013 \text{ m}^2 \text{ mg}^{-1}$. Approximately 20% underestimation of C and 35% underestimation of C_p occurred when 10% uncertainty of a^m was added into the algorithm. For C_n and C_m , when $a_{LH}^*(676)$ was $>0.012 \text{ m}^2 \text{ mg}^{-1}$, significant overestimations ($>60\%$ for C_n and $>110\%$ for C_m) were observed when $>5\%$ uncertainty of a^m was added into the algorithm.

Figure 11. Level of uncertainties in C and size-partitioned phytoplankton carbon computed by the $R17$ using the SCS field data. (a–d) Uncertainties in C , C_p , C_n , and C_m estimations due to possible errors in a^m for the uncertainty range 0–30% based on $a_{ph}^*(676)$. (e–h) Uncertainties in C , C_p , C_n , and C_m estimations due to possible errors in a^m for the uncertainty range 0–30% based on $a_{LH}^*(676)$.

On the whole, the effect of the uncertainty of a^m was relatively weak for underestimation of C [$<35\%$ for $a_{ph}^*(676)$ data and $<45\%$ for $a_{LH}^*(676)$] and C_p [$<40\%$ for $a_{ph}^*(676)$ data and $<60\%$ for $a_{LH}^*(676)$]. However, the effect of the uncertainty of a^m was significant for overestimation of C_n and C_m when $a_{ph}^*(676)$ ranged from 0.02 to $0.025 \text{ m}^2 \text{ mg}^{-1}$ or $a_{LH}^*(676)$ was $>0.012 \text{ m}^2 \text{ mg}^{-1}$. Overall, the impact of uncertainty of a^m on the $a_{LH}^*(676)$ data was greater than that on the $a_{ph}^*(676)$ data. In this study, 80% of $a_{ph}^*(676)$ values were in the range

of $0.012\text{--}0.021\text{ m}^2\text{ mg}^{-1}$, and 80% of $a_{\text{LH}}^*(676)$ values were within $0.0116\text{--}0.0125\text{ m}^2\text{ mg}^{-1}$, and different a^{m} values were chosen according to 95% quantile values for $a_{\text{ph}}^*(676)$ and $a_{\text{LH}}^*(676)$ data, respectively.

When the *R17* algorithm was transplanted into the $a_{\text{pg}}(\lambda)$ data, $Chla_{\text{LH}}$, which was determined using the absorption line height method [45], also introduced uncertainties into the algorithm. Compared to the in situ *Chla*, the averaged relative error of $Chla_{\text{LH}}$ could reach 20%. We evaluated the uncertainties in the estimations of *C* and size-partitioned phytoplankton carbon when 0–20% uncertainties were added into $Chla_{\text{LH}}$ (Figure 12). The uncertainty of algorithm-derived *C* and size-partitioned phytoplankton carbon showed an increasing trend with increasing uncertainty in $Chla_{\text{LH}}$. A small uncertainty of *C* (around −20% to 10%) was observed when $a_{\text{LH}}^*(676)$ was $>0.0135\text{ m}^2\text{ mg}^{-1}$ and even when 20% uncertainty was added into $Chla_{\text{LH}}$. For other cases, the uncertainty of *C* slightly increased but was $<35\%$ underestimation even if 20% uncertainty was added into the $Chla_{\text{LH}}$. Similarly, a small uncertainty of C_{p} (around −25% to 10%) was observed when $a_{\text{LH}}^*(676)$ was $>0.013\text{ m}^2\text{ mg}^{-1}$ and 10% uncertainty was added into $Chla_{\text{LH}}$. The uncertainty of C_{p} (around −40% to −55%) increased when $a_{\text{LH}}^*(676)$ was $<0.0125\text{ m}^2\text{ mg}^{-1}$ and $>10\%$ uncertainty was added into the $Chla_{\text{LH}}$. As for C_{n} and C_{m} , a small overestimation ($<10\%$) was observed when $a_{\text{LH}}^*(676)$ was $>0.013\text{ m}^2\text{ mg}^{-1}$ and 5% uncertainty was added into $Chla_{\text{LH}}$. When $>10\%$ uncertainty was added into $Chla_{\text{LH}}$, significant overestimation of C_{n} and C_{m} ($>200\%$ for C_{n} and $>1000\%$ for C_{m}) was observed when $a_{\text{LH}}^*(676)$ ranged from 0.012 to $0.014\text{ m}^2\text{ mg}^{-1}$.

Figure 12. Uncertainties in (a) *C*, (b) C_{p} , (c) C_{n} , and (d) C_{m} estimations due to possible errors in $Chla_{\text{LH}}$ for the uncertainty range 0–20% based on $a_{\text{LH}}^*(676)$ data.

Overall, the effect of $Chla_{\text{LH}}$ uncertainty on *C* and C_{p} estimations (−35% to 10% for *C* and −55% to 10% for C_{p} when uncertainty of $Chla_{\text{LH}}$ was $<20\%$) was smaller than that on C_{n} and C_{m} estimations, which could reach $>100\%$ for C_{n} and $>1000\%$ for C_{m} when uncertainty of $Chla_{\text{LH}}$ was $>10\%$.

4.2. Relationship between *C* and *Chla*

The values of *C* and *Chla* are both used as proxies for the standing stock of phytoplankton biomass, and whether *C* or *Chla* is the appropriate proxy is controversial. The arguments for *Chla* are as follows: (i) chlorophyll-*a* is the transducer in the energy-ecosystem, and (ii) measurement of *Chla* is the simplest of all biological parameters [8]. For *C*, the argument is

that C is a more direct parameter in the study of the carbon cycle and other climate-relevant variables in the ocean [8]. However, C and $Chla$ can convert into each other through χ , and it is no longer necessary to make a choice between C and $Chla$ [8]. Considering that the demand is for C in biogeochemical research but that $Chla$ is the most commonly measured biological parameter, whether in situ or in remote sensing platform, we analyzed the relationship between C and $Chla$ to facilitate the conversion between the two parameters. Because the value of χ varies among different algae species, we also analyzed the variability in relationships between C and $Chla$ among different dominant phytoplankton species to provide more precise conversion parameters. As shown in Figure 13a, we detected significant covariation between C and $Chla$, which was consistent with the results reported in previous studies [8,53,54]. In previous studies, the form of $C = iChla^j$, where i and j are fitted parameters, was used to describe the relationship between C and $Chla$. The results from Buck et al. [54], Sathyendranath et al. [14], Marañón et al. [53], and Loisel et al. [55] are plotted in Figure 13a. The empirical relationships from Buck et al. [54] ($C = 83Chla^{0.69}$) and Sathyendranath et al. [14] ($C = 64Chla^{0.63}$) overestimated C when $Chla$ was $<0.3 \text{ mg m}^{-3}$. The empirical relationships from Marañón et al. [53] ($C = 62Chla^{0.89}$) and Loisel et al. [55] ($C = 73Chla^{0.91}$) performed better for our data, although they also overestimated C when $Chla$ was $<0.2 \text{ mg m}^{-3}$. The empirical relationship between C and $Chla$ in our study was $C = 46Chla^{0.8}$ (Table 3). The value of j could be used to describe how χ varied with $Chla$. The χ became constant when $j = 1$, which suggested that values of χ decreased as $Chla$ increased when j was <1 , whereas the values of χ increased as $Chla$ increased when j was >1 . All values of j in the five relationships were <1 . The value of j in our relationship was lower than those reported by Marañón et al. [53] and Loisel et al. [55] but higher than those reported by Buck et al. [54] and Sathyendranath et al. [14]. These results suggested that the values of χ decreased as $Chla$ increased and that the variability in χ with $Chla$ in our study was more significant than that found by Marañón et al. [53] and Loisel et al. [55] but more modest than that reported by Buck et al. [54] and Sathyendranath et al. [14].

In reality, changes in nutrients, irradiance, temperature, cell size (phytoplankton species) and $Chla$ are all intimately related to each other in the marine environment, thus, it would be difficult to rule out the possible effects of these factors on χ [8]. As shown in Figure 13a, the dominant phytoplankton species varied from *Prochlorococcus* at the lowest $Chla$ ($\sim 0.1 \text{ mg m}^{-3}$) to diatoms at the highest $Chla$ ($\sim 1 \text{ mg m}^{-3}$). Xing et al. (2019) [21] reported that variability of phytoplankton community dominated the values of $Chla:b_{\text{bp}}$ at subsurface chlorophyll maximum layer in the SCS based on Bio-Argo data. Accordingly, in the SCS basin, change in dominant phytoplankton species may be one of the main factors resulting in variability in χ . To study the influence of variability in χ among different dominant algae species on $Chla$ -to- C relationships, different empirical relationships between C and $Chla$ were established among different dominant phytoplankton species based on our dataset (Table 3). Since dominant phytoplankton species will vary in the different specific range of $Chla$, the values of i in the relationships can be used to describe the rough χ values of different phytoplankton species. The values of i in *Prochlorococcus* ($i = 78$), *Synechococcus*-like cyanobacteria ($i = 64$), haptophytes ($i = 53$), and diatoms ($i = 49$) decreased sequentially, which suggested that the values of χ gradually decreased from *Prochlorococcus* to diatom dominant waters. The relative error between different relationship-estimated and a_{ph}^* (676)-estimated C was calculated as $100\% \frac{C_{\text{relationship}} - C}{C}$, where $C_{\text{relationship}}$ was calculated using the empirical relationships in Table 3 for waters dominated by different phytoplankton species, and C was estimated based on a_{ph}^* (676). As shown in Figure 13b, the median relative error of the *Prochlorococcus* relationship ($\sim 4\%$) was around 0 when the dominant phytoplankton species was *Prochlorococcus*, whereas it increased to $\sim 47\%$ in diatom dominant waters. The median relative error of the *Synechococcus*-like cyanobacteria relationship was $\sim 11\%$ in *Synechococcus*-like cyanobacteria dominant waters, but the median relative errors of the *Synechococcus*-like cyanobacteria relationship had a greater deviation from 0% in *Prochlorococcus* ($\sim 24\%$), haptophyte ($\sim 11\%$), and diatom (30%) dominant waters. For the haptophyte and diatom relationships, the largest median

relative errors (both > 50%) were observed in *Prochlorococcus* dominant waters, and the median relative errors decreased as the cell size of the dominant algae increased. The smallest median relative errors of haptophytes (~4%) and diatoms (~9%) were observed in the haptophyte and diatom dominant waters, respectively. For the total relationship, the trend of median relative errors was similar to that of the diatoms relationship. The median relative errors of the total relationship decreased as the cell size of dominant algae increased. The largest median relative error of the total relationship was ~57% in the *Prochlorococcus* dominant waters, and in diatom dominant waters, the median relative error was ~3%. These results suggested that variability in values of χ due to changes in phytoplankton species can introduce apparent uncertainty to C converted from $Chla$ when using a constant value of χ . Therefore, it is better to identify the dominant phytoplankton species to derive an accurate χ before converting $Chla$ to C through χ .

Figure 13. (a) Relationship between C and $Chla$. The magenta, blue, red, and green dotted lines, respectively, represent the empirical relationships between C and $Chla$ from Buck et al. (1996) [54] (curve B 1996), Sathyendranath et al. (2009) [14] (curve S 2009), Maraño et al. (2014) [53] (curve M 2014), and Loisel et al. (2018) [55] (curve L 2018). The black, red, blue, magenta, and green solid lines, respectively, represent the empirical relationships between C and $Chla$ in our study for total data (curve T), *Prochlorococcus* (curve P), *Synechococcus*-like cyanobacteria (curve S), haptophytes (curve H), and diatom (curve D) dominated data. (b) Boxplots of relative errors of the total data, *Prochlorococcus*, *Synechococcus*-like cyanobacteria, haptophyte, and diatom $Chla$ -to- C relationships in different sample groups dominated by different phytoplankton species. The black line represents relative error = 0.

Table 3. Empirical power-law relationships between C and $Chla$ in samples containing different dominant phytoplankton species in previous studies and this study.

Empirical Relationship	Reference/Dominated Phytoplankton Species	Num	R	RMSE	Bias	MAE
$C = 83Chla^{0.69}$	Buck et al. (1996) [54]	215	0.90	19.96	2.53	2.53
$C = 64Chla^{0.63}$	Sathyendranath et al. (2009) [14]	215	0.90	13.29	2.13	2.13
$C = 62Chla^{0.89}$	Marañón et al. (2014) [53]	215	0.88	8.19	1.42	1.51
$C = 73Chla^{0.91}$	Loisel et al. (2018) [55]	215	0.88	11.50	1.63	1.66
$C = 46Chla^{0.80}$	This study/All data	215	0.89	5.85	1.20	1.40
$C = 78Chla^{1.28}$	This study/ <i>Prochlorococcus</i>	65	0.91	1.60	1.02	1.19
$C = 64Chla^{1.08}$	This study/ <i>Synechococcus</i> -like cyanobacteria	29	0.82	4.25	1.08	1.36
$C = 53Chla^{0.74}$	This study/Haptophytes	60	0.82	6.21	1.06	1.24
$C = 49Chla^{0.84}$	This study/Diatoms	7	0.84	9.97	1.09	1.29

4.3. General Vertical Profile of Phytoplankton Carbon in the SCS Basin

Figure 14a shows the general vertical distribution of C , size-partitioned phytoplankton carbon, and χ for oligotrophic stratified waters in the open SCS that is based on the profile shape shown in Figures 9 and 10. It should be noted that C_n and C_m are sensitive to the choice of a^m , thus, interpretation of their profile shape should be made with caution. Overall, in the open SCS, the vertical profile of C displayed a Gaussian distribution with a peak near the bottom of the euphotic zone and the top of the nutricline, which was similar to that of the vertical $Chla$ distribution [11,56]. C and $Chla$ exhibited significant covariation (Figures 10 and 13a), and it indicated that photoacclimation has little impact on the formation of the subsurface $Chla$ maximum layer, which was consistent with results of Xing et al. [21].

Figure 14. (a) Schematic representation of the vertical profiles of C , C_p , C_n , C_m , and χ ; (b) the frequency of dominant phytoplankton species at the sea surface and the CML and (c) the relationship between the $19'$ hexanoyloxy-fucoanthin concentrations and cell abundances of picoeukaryotes in the open stratified SCS.

The open SCS is an oligotrophic environment that is characterized by a “microbial loop” or “microbial food web” due to strong stratification [57]. Most (92%) of our survey stations were in the most oligotrophic condition. As shown in Figure 14a, the picophytoplankton dominated the phytoplankton biomass in the euphotic zone, and vertical distribution of C_p was similar to that of C (displayed a Gaussian distribution). This phenomenon was also reported by Uitz et al. [41], who found that the picophytoplankton biomass displayed a distinct deep maximum that was slightly sharper than that for nanophytoplankton biomass in S1–S4 trophic conditions. Meanwhile, the results in Sauzède et al. [11] at the Bermuda Atlantic Time Series Study site also showed that the picophytoplankton

dominated the whole euphotic zone from June to October, and the deep maximum of picophytoplankton biomass was also sharper than that of nanophytoplankton biomass. We used HPLC data to analyze the dominant phytoplankton species and found that the phytoplankton community varied from *Synechococcus*-like cyanobacteria dominating at the sea surface to haptophytes dominating at the CML (Figure 14b). However, haptophytes are always classified as nanophytoplankton in many oceanic regions, ranging from tropical to polar systems [58,59], which was contrary to our result that the picophytoplankton was dominant at the CML. Moon-van der Staay et al. [59] reported that prymnesiophytes (class Prymnesiophyceae, division Haptophyta) was dominant among picoeukaryotes in the Pacific Ocean based on molecular biological techniques. Similarly, Ho et al. [60] suggested that haptophytes were the major picoeukaryotic phytoplankton in the northern SCS based on the relationship between concentrations of 19'hexanoyloxy-fucoxanthin and cell abundances of picoeukaryotes. Figure 14c shows a strong covariation between 19'hexanoyloxy-fucoxanthin concentrations and cell abundances of picoeukaryotes based on our data. A reasonable explanation for this contradictory result (haptophytes dominated the CML but picophytoplankton also dominated the CML) is that haptophytes in the open SCS were mostly pico-size. Therefore, the increase of haptophytes was the main factor involved in the formation of the CML. Thus, it was not surprising that the values of F_p and χ increased at the CML (Figures 9 and 10) in the open stratified SCS.

5. Conclusions

We transplanted the remote sensing absorption-based phytoplankton carbon algorithm (R17) from Roy et al. [15] into field a_{ph}^* (676) and a_{LH}^* (676) to obtain vertical profiles of C and size-partitioned phytoplankton carbon in the SCS. The accuracy of a^m was an important factor affecting the accuracy of C and size-partitioned phytoplankton carbon estimations. Different values of a^m were chosen according to the 95% quantile values in the a_{ph}^* (676) and a_{LH}^* (676) datasets, respectively. For a_{ph}^* (676), the values of R, MAE, and bias between estimated and field C_p were 0.58, 2.14, and 0.62, respectively, and for a_{pg}^* (676) the values were 0.53, 1.9, and 1.39, respectively. The algorithm performed well for field data from the SCS. The vertical profiles of C and size-partitioned phytoplankton carbon in the SCS were then derived from field a_{ph}^* (676) and a_{LH}^* (676). The vertical profiles of C and C_p displayed Gaussian distributions, and the CML appeared at the bottom of the euphotic zone and the top of the nutricline in the stratified open SCS basin. Picophytoplankton was the dominant phytoplankton carbon contributor within the whole euphotic zone. The dominant picophytoplankton species varied from *Synechococcus*-like cyanobacteria at surface to pico-sized haptophytes at the CML. We detected strong covariation between C and *Chla*, and they can be converted to each other through an accurate value of χ . These results show the vertical profiles of phytoplankton biomass from the perspective of carbon mass and provide basic information for understanding primary production, the carbon cycle, and climate change in the SCS.

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