

Article

Response of Size-Fractionated Chlorophyll *a* to Upwelling and Kuroshio in Northeastern South China Sea

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Abstract: The variability of size-fractionated chlorophyll *a* (Chl *a*) biomass and related environmental variables was investigated in a survey conducted in the northeastern South China Sea (NESCO), to assess their responses to upwelling, Kuroshio, and nutrients in the summer of 2017. The depth-weighted total Chl *a* concentration varied from 0.057 to 0.496 µg/L. The contribution of size-fractionated Chl *a* to total Chl *a* biomass was determined, with the contributions of pico-Chl *a* (0.2–2 µm), nano-Chl *a* (2–20 µm), and micro-Chl *a* (>20 µm) found to be 52.87%, 38.54%, and 8.59%, respectively. We found that nano-Chl *a* contributes more to total-Chl *a* than pico-Chl *a* in areas affected by upwelling. In addition, the results indicated an upward shift in the deep chlorophyll maximum (DCM) content in the upwelling area and the Kuroshio intrusion area. The Chl *a* biomass was increased in the physical process. Overall, correlation analysis showed that environmental variables (temperature, salinity, phosphate, silicate, nitrate, nitrite, ammonium) significantly influenced the phytoplankton biomass. However, physical processes determined the changes in environmental variables, with upwelling and Kuroshio being the main factors regulating the distribution of Chl *a*.

Keywords: chlorophyll *a*; phytoplankton; northeastern South China Sea; Kuroshio current; upwelling



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1. Introduction

The chlorophyll *a* (Chl *a*) concentration is an important indicator of the biomass of phytoplankton and other marine photosynthetic autotrophs [1]. The concentration of Chl *a* is a basic parameter that directly reflects the growth, reproduction, and metabolism of phytoplankton, and profoundly affects the biogeochemical process of biogenic elements, so it is the basis for marine chemistry and marine biological investigations [2]. Phytoplankton is, at the basis of most trophic networks, thereby influencing a lot of carbon flows, and it is one of the most important parts of the carbon cycle in the ocean [3]. Although they only account for 1 to 2% of the biomass of primary producers in the Earth's biosphere, they provide nearly 50% of the primary production due to their high turnover rate [4]. Affected by physical, chemical, and biological processes at different scales, the spatial distribution of phytoplankton is different.

Phytoplankton size structure can be quantified by partitioning total Chl *a* into three typical size classes, that is, pico- (<2 µm), nano- (2–20 µm), and micro- phytoplankton (>20 µm) [5]. The abundance and distribution of phytoplankton play an important role in the community structure and trophic relationship of marine ecosystems, and their roles vary

with cell particle size. Generally speaking, there are obvious differences in the composition of plankton in different sea areas, which are closely related to the marine environmental conditions of the sea areas. In previous studies, many environmental variables were associated with the regulation of phytoplankton or Chl *a* [6]. The nutrients provided can adjust the phytoplankton community structure to a certain extent, and change the size ratio of phytoplankton [7], but physical factors also regulate the size and structure of phytoplankton. For example, in a hypereutrophic urban tropical estuarine system in Northeast Brazil, the >20 μm fraction contributed the most to total Chl *a* and biomass in the study area [8]. In comparison, in the oligotrophic Western Pacific Ocean, picophytoplankton abundance was nearly three to five orders of magnitude more abundant than micro/nanophytoplankton, indicating that picophytoplankton contributed a large proportion of the phytoplankton communities [9]. However, in a wind-driven upwelling zone in the eastern tropical Pacific, it was shown that picoplankton dominated phytoplankton biomass [10]. In this context, it is important to study the size distribution of phytoplankton to understand the ecosystems functioning, especially in upwelling regions subject to the number of environmental variations at spatial and temporal scales. However, in some of these ecosystems, the size distribution of phytoplankton remains unknown, like in the northeastern South China Sea, though significantly affected by environmental variability.

The South China Sea (SCS) is the largest semi-enclosed deep sea, with an area of 3,500,000 km^2 [11]. The northeastern South China Sea (NESCS) is located on the west side of the Luzon Strait where the waters of the SCS and the Northwest Pacific are frequently exchanged [12]. The NESCS is significantly affected by the Kuroshio intrusion, which is located northwest of the Luzon Strait [13]. Nutrients are usually the main factor limiting the growth of phytoplankton. In the oligotrophic NESCS, the structure of the seawater layer is stable, and the biomass of phytoplankton is very low in summer, due to water stratification [14,15]. In previous studies, phytoplankton or Chl *a* was involved in the regulation of biochemical and physical processes [10]. For example, the Chl *a* biomass in the waters of the northern South China Sea (NSCS) is regulated by hydrological conditions, such as summer monsoon, Kuroshio, and Pearl River plume [16]. Currently, there have been studies on size-fractionated Chl *a* in other regions of SCS. Liu et al. believe that nano- and pico- are the main contributors to the total phytoplankton biomass in the NSCS [16]. Micro-Chl *a* does not contribute as much to total Chl *a* biomass as pico-Chl *a* or nano-Chl *a* [7]. Due to the influence of coastal upwelling, the deep chlorophyll maximum (DCM) occurs at a depth of 30–50 m [17,18]. However, the size-fractionated Chl *a* in NESCS has not been studied. In the same scientific expedition of this study, there have been studies on the effects of the typhoons “Roke” and “Begonia” on microphytoplankton communities and the other study on picophytoplankton. It was shown that the influence of KC on microphytoplankton in NESCS mainly manifested that there was no obvious change in the abundance of dinophyta cells, and lightly decreased Bacillariophyta along the intrusion passage of KC [19]. Prochlorococcus (Pro) were the most abundant picophytoplankton in NESCS, and the abnormal presence of Pro near the coast of the South China Sea was associated with the invasion of the Kuroshio. Notably, there has been very little research on size-fractionated Chl *a* in NESCS, as well as nano-Chl *a*. In further marine scientific research, there is an urgent need to understand the regulation of phytoplankton biomass according to hydrological conditions.

In this study, we determined the distribution of size-fractionated Chl *a* and nutrients. The overall aims of this study are to (1) investigate the response of size-fractionated Chl *a* to environment variables, and (2) to integrate changes in size-fractionated Chl *a* with Upwelling and Kuroshio in NESCS.

2. Materials and Methods

2.1. Study Area and Sampling Stations

The Kuroshio originates from the North Equatorial Current. When the North Equatorial Current that flows westward meets the western boundary of the Pacific Ocean, it

is divided into a Mindoro Current to the south and a Kuroshio to the north. When the Kuroshio flows northward through the Luzon Strait along the east coast of the Philippines, the western part of the Kuroshio turns northwestward, flows through the Balintang Channel on the northern side of Luzon Island, and enters the NESCS [13]. The NESCS is affected by the strong northeast wind prevailing in winter and the southwest monsoon prevailing in summer [20].

From 12 July to 11 August 2017, research was carried out from 15–22° N and 114–120° E in the NESCS onboard R/V “Dongfanghong 2”. We investigated 26 stations and collected 528 samples in total (Figure 1). In order to study the size-fractionated change in Chl *a* as a function of the Kuroshio Current of the study site, a section KC was isolated corresponding to the highest current of the area (including stations A15, A16, A17, A13, A14, C2, C3, B2, B3, A6, A1, and A2; Figure 1c). Likewise, in order to study the size-fractionated change in Chl *a* as a function of the Upwelling of the study site, sections B and C were isolated, corresponding to the highest currents in the region (including upwelling affecting stations B1, B2, B3, B4, C1, C2, C3, and C4; Figure 1b). Other stations were normal stations.

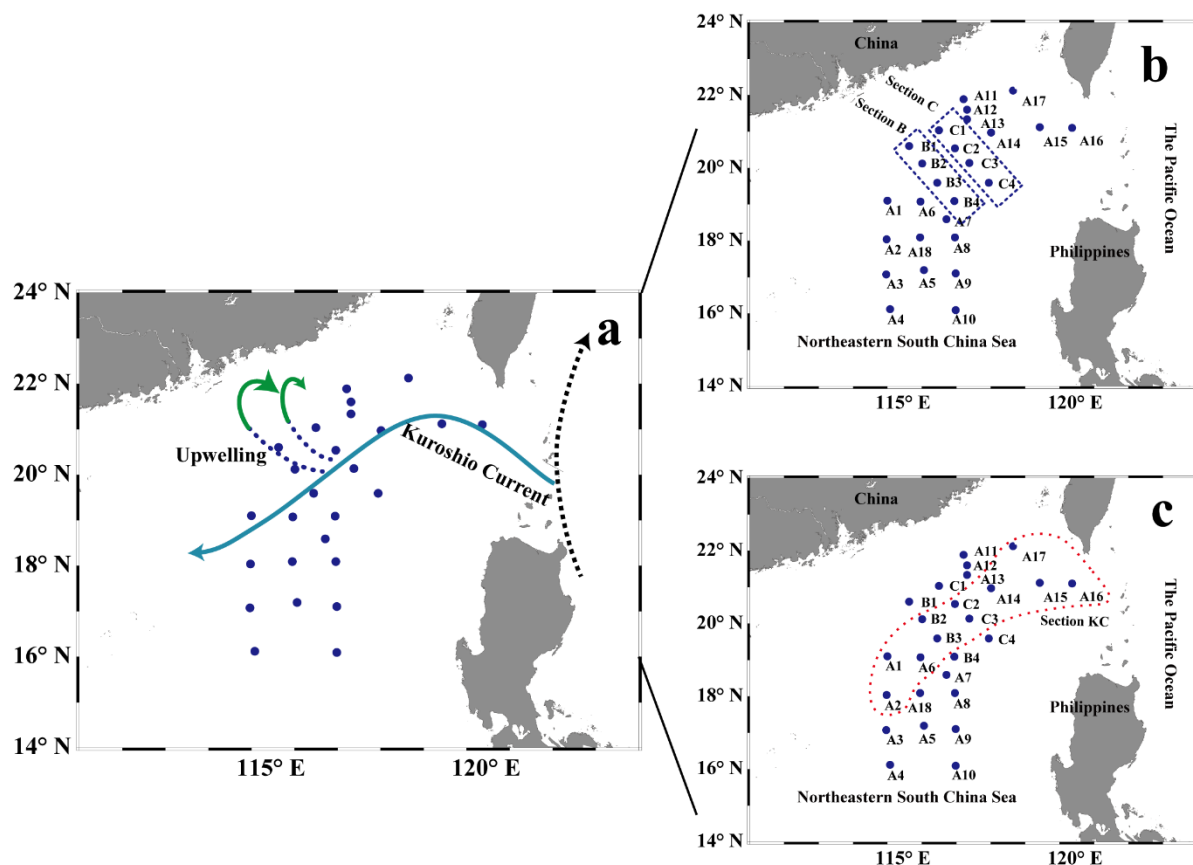


Figure 1. Stations sampled in northeastern South China Sea (NESCS). ((a): the appropriate locations of the different currents are described according to Shu et al. [21]; (b): The blue dotted lines show sampling sections defined as Section B, Section C; (c): The red dotted lines show sampling sections defined as Section KC.).

2.2. Sample Collection and Analysis

Temperature and salinity were measured using a SeaBird conductivity/temperature/depth (CTD) meter (SBE 917 Plus, Sea-bird Scientific, Bellevue, WA, USA). Seawater samples were collected using Niskin bottles from seven depths (surface (5 m), 25 m, 50 m, 75 m, 100 m, 150 m, and 200 m) at all stations without preliminary filtration. Directly on-site, Chl *a* and nutrients samples were sampled from those seawater samples on all the considered stations in this study. For each depth, the Chl *a* sample was obtained after successive

filtrations described below from 1 L of each seawater sample, while nutrient samples were collected after the filtration of 120–300 mL from each seawater sample through a 0.45 µm cellulose acetate membrane filter to remove large particles.

The mass concentration of Chl *a* in particle size fractionation was determined using the extraction fluorescence method [22]. Seawater samples were filtered serially through silk net (20 µm porosity), nylon membrane (2 µm porosity), and Whatman GF/F filters (0.7 µm porosity). Size-fractionated Chl *a* filtration was carried out using a diaphragm vacuum pump under a vacuum of less than 100 mmHg. Following filtration, these Chl *a* filters were folded in quarters and stored in liquid nitrogen at −80 °C until processing. The filter was placed into a 10 mL brown glass tube, and then 5 mL of acetone with a volume fraction of 90% was added to the glass tube and stored in the dark at 4 °C for 24 h. The Chl *a* biomass was measured using a Turner fluorometer (model 10-AU, TurnerBioSystems, Sunnyvale, CA, USA). The Chl *a* fluorescence was measured in the non-acidified mode and calculated according to the formula of Parsons [23]. The total Chl *a* biomass was calculated by summing each size-fractionated Chl *a* biomass.

The polyethylene (PE) bottles containing the nutrient sample were wrapped with Parafilm to avoid the contamination of the sample, then quickly frozen at −20 °C and analyzed as soon as possible. Nutrients, including nitrate (NO₃-N), nitrite (NO₂-N), ammonia (N-NH₄), phosphate (PO₄-P), and silicate (SiO₃-Si), were identified using the Technicon AA3 automatic analyzer (Bran + Luebbe) following the method reported by Brzezinski and Karl [24,25]. We set a minimum nutrient concentration of 0.01 µmol/L to avoid detection limit issues.

2.3. Statistical Analysis

As better suited for our distributional patterns than discrete sample data, Chl *a* concentration on each site was calculated over the entire water column by depth-weighted averages, which involve a series of abundance variations with depth. This is done by following the equation from Crosbie and Furnas [26]:

$$P = \left\{ \sum_{i=1}^{n-1} \frac{P_{i+1} + P_i}{2} (D_{i+1} - D_i) \right\} / (D_{MSL} - D_S) \quad (1)$$

where *P* was the average Chl *a* concentration in the water column, *P_i* was the Chl *a* concentration of the layer, *D_i* was the depth of layer *i*, and *i* was the number of sampling layers. The above is called the depth weighted value calculation, which assumes that the uniformity within the water column is different from the depth integral value (water column pressure). *D_{MSL}* and *D_S* are the depth of the maximum sampling layer (m) and the surface sampling depth (5 m), respectively.

All mean data were given ±SD. A pie chart was generated using ArcGis10.7 (Environmental Systems Research Institute (Esri), Redlands, CA, USA) and graphs were generated using Origin 2021 (Origin Lab, Northampton, MA, USA) and Ocean Data View 4.7.6 (Alfred-Wegener-Institut (AWI), Bremerhaven, Germany). Boxplot was generated by Origin 2021 (Origin Lab, Northampton, MA, USA). According to the results of Detrended correspondence analysis (DCA), the gradient length was <3, so Redundancy analysis (RDA) was selected. RDA analysis was performed using CANOCO 5.0 for Windows (Microcomputer Power, Ithaca, New York, NY, USA) to identify the structuring effects of environmental conditions on the distribution of size-fractionated Chl *a*. The Kolmogorov–Smirnov test (K-S test) was validated using SPSS 25.0 (IBM) and showed that the data for Chl *a*, which was log10-transformed, conformed to a normal distribution, and therefore, we have chosen Pearson's rank correlation coefficient. The influence of environmental variables on the phytoplankton community structure in NESCS was assessed using Pearson's correlation [27]. The relationship between Chl *a* and environmental variables could be explained by Pearson's ranking chart. Pearson's correlation analysis was achieved using SPSS 25.0

(International Business Machines Corporation (IBM), Armonk, NY, USA). In all tests, the statistical significance was $p < 0.05$.

3. Results

3.1. Hydrography and Nutrients

The surface distribution of environmental variables is shown in Figure 2. The average surface temperature and salinity were 29.39 ± 0.76 °C and 33.76 ± 0.26 , respectively. Seawater with high temperature and high salinity appeared near the Luzon Strait. However, low-temperature, high-salinity seawater was found near shelf slopes. The vertical distribution of environmental variables is shown in Figure 3. The water column temperature and salinity recorded from July to August 2017 ranged from 19.87 to 25.06 °C and from 34.29 to 34.65, respectively. Results showed that temperature values decreased with depth while salinity values increased (Figure 3). In section B (Figure 3), from B1 to B4, the temperature at same water depths gradually increased, but the salinity gradually decreased. The same is true for section C. The results show that, at section KC, the temperature and salinity gradually decreased from A15 to A2.

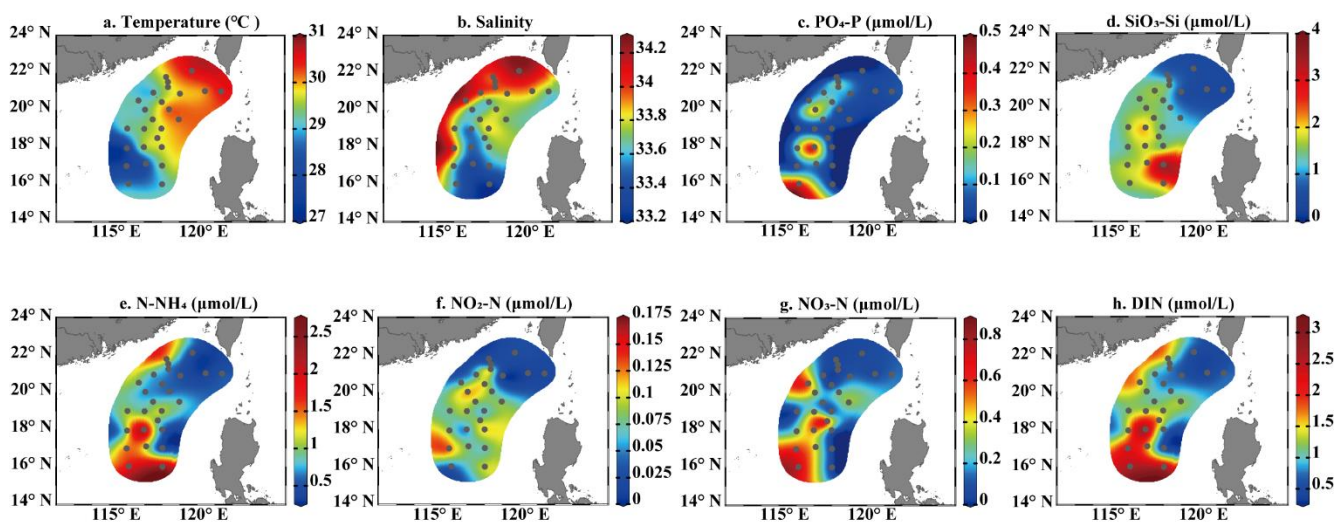


Figure 2. Surface distribution of environmental variables in NESCS.

Within the study area, the surface distribution of nutrients showed a trend of low concentration in the north and high concentration in the south (Figure 2). The $\text{PO}_4\text{-P}$ concentrations ranged from 0.01 to $2.04 \mu\text{mol/L}$. The $\text{SiO}_3\text{-Si}$ concentrations ranged from 0.33 to $18.14 \mu\text{mol/L}$, and the overall concentration was low, but high values appeared near the Philippines, with the highest at station A9. The N-NH_4 concentrations ranged from 0.01 to $16.95 \mu\text{mol/L}$. The $\text{NO}_2\text{-N}$ concentrations ranged from 0.01 to $1.34 \mu\text{mol/L}$. The $\text{NO}_3\text{-N}$ concentrations ranged from 0.01 to $14.56 \mu\text{mol/L}$. The concentrations of ammonium and nitrate were higher far from the shelf and slope. Overall, the concentration of nitrite was the lowest compared to other nutrients, while its distribution was relatively uniform (Figure 2).

Range and mean $\pm$ SD of environmental variables in three contrasting sections are showed in Table 1 and Figure 3. We conducted a more detailed analysis of the distribution of nutrients on sections perpendicular to the continental slope and shelf (sections B and C) and a section along the direction of the Kuroshio (section KC, Figure 3). Nutrients were generally higher at the sea bottom, showing a gradual decreasing trend from the bottom to the surface. But the concentrations of nutrients in these special sections changed in the vertical distribution. It can be seen in sections B and C that the distribution of N-NH_4 tended to mix up and down. At the same time, the distribution of $\text{NO}_2\text{-N}$ showed an upward shift in the highest value at section B, and the phenomenon that the high value area at section C widened in depth. The upper seawater had mixed, and the entire section was not clearly stratified in section KC.

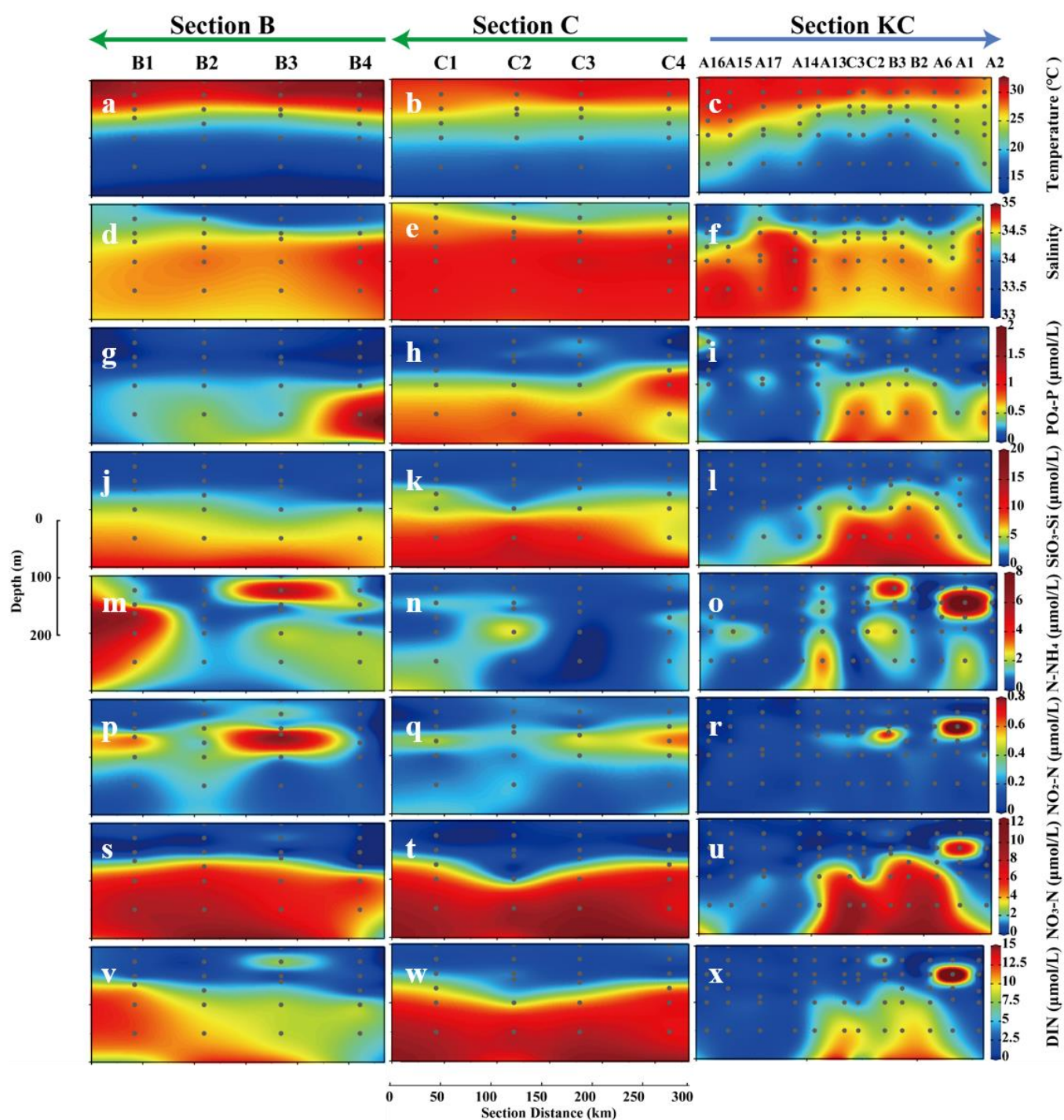


Figure 3. Vertical distribution of environmental variables (temperature (a–c), salinity (d–f), $\text{PO}_4\text{-P}$ (g–i), $\text{SiO}_3\text{-Si}$ (j–l), N-NH_4 (m–o), $\text{NO}_2\text{-N}$ (p–r), $\text{NO}_3\text{-N}$ (s–u), DIN (v–x)) in section B, C, and KC. The green arrow represents the direction of the upwelling, and the blue arrow represents the direction of the Kuroshio current.

Table 1. Range and mean $\pm$ SD of environmental variables in three contrasting sections.

	Section B		Section C		Section KC	
	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD
Temperature ($^{\circ}$ C)	13.72–29.70	22.04 $\pm$ 5.86	13.70–30.18	22.58 $\pm$ 5.45	13.70–30.54	23.71 $\pm$ 5.13
Salinity	33.60–34.81	34.39 $\pm$ 0.33	33.58–34.71	34.37 $\pm$ 0.33	33.44–34.93	34.39 $\pm$ 0.37
PO ₄ -P (μ mol/L)	0.01–1.95	0.37 $\pm$ 0.43	0.01–1.15	0.38 $\pm$ 0.34	0.01–1.15	0.26 $\pm$ 0.26
SiO ₃ -Si (μ mol/L)	1.09–18.14	5.95 $\pm$ 5.31	1.02–14.41	4.87 $\pm$ 4.38	0.33–18.14	3.49 $\pm$ 3.96
N-NH ₄ (μ mol/L)	0.54–6.39	1.77 $\pm$ 1.57	0.01–2.49	0.75 $\pm$ 0.53	0.01–16.95	1.19 $\pm$ 1.99
NO ₂ -N (μ mol/L)	0.05–0.77	0.14 $\pm$ 0.14	0.02–0.34	0.12 $\pm$ 0.07	0.01–1.34	0.12 $\pm$ 0.17
NO ₃ -N (μ mol/L)	0.01–11.51	3.48 $\pm$ 3.62	0.01–12.69	3.54 $\pm$ 4.18	0.01–12.69	2.25 $\pm$ 3.32
DIN (μ mol/L)	0.72–12.34	5.40 $\pm$ 3.94	0.50–13.20	4.42 $\pm$ 4.15	0.39–28.10	3.55 $\pm$ 4.33

3.2. Total Chl *a* and Size-Fractionated Chl *a*

The depth-weighted total Chl *a* concentration ranged from 0.057 to 0.496 μ g/L, with the highest Chl *a* concentration at station D4. The Chl *a* concentration in the area near the Luzon Strait was much higher than that in the other area. The size-fractionated Chl *a* had different contributions at different stations (Figure 4, Table 2). The contribution of micro-Chl *a* to the depth-weighted total Chl *a* was 8.59% (0.02 ± 0.014 μ g/L), nano-Chl *a* was 38.54% (0.09 ± 0.07 μ g/L), and pico-Chl *a* was 52.87% (0.123 ± 0.108 μ g/L). The size-fractionated Chl *a* had different contribution as a function of the station's localization. In section B, nano-Chl *a* had the highest contribution to total Chl *a*, followed by pico-Chl *a* and finally micro-Chl *a* (Figure 4). However, in section C, pico-Chl *a* had the highest contribution to the total Chl *a*. Interestingly, different changes took place at station B4 though, where pico dominated, not nano.

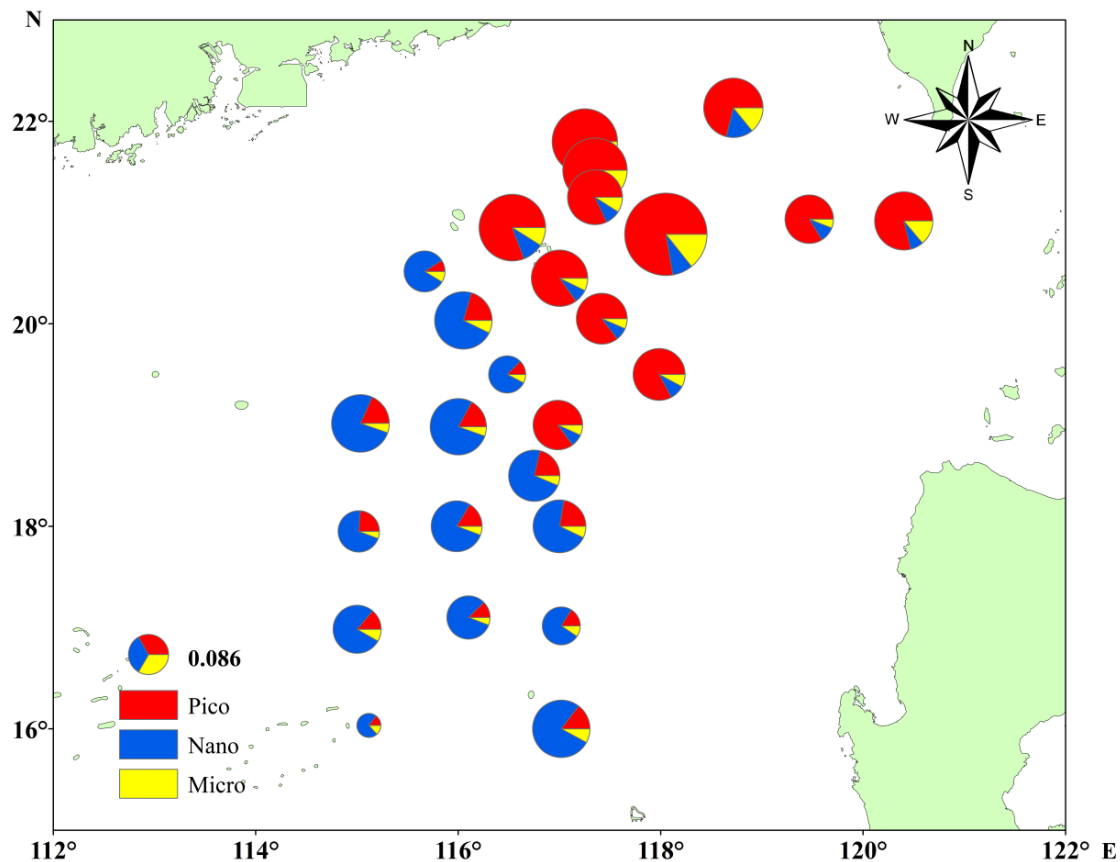
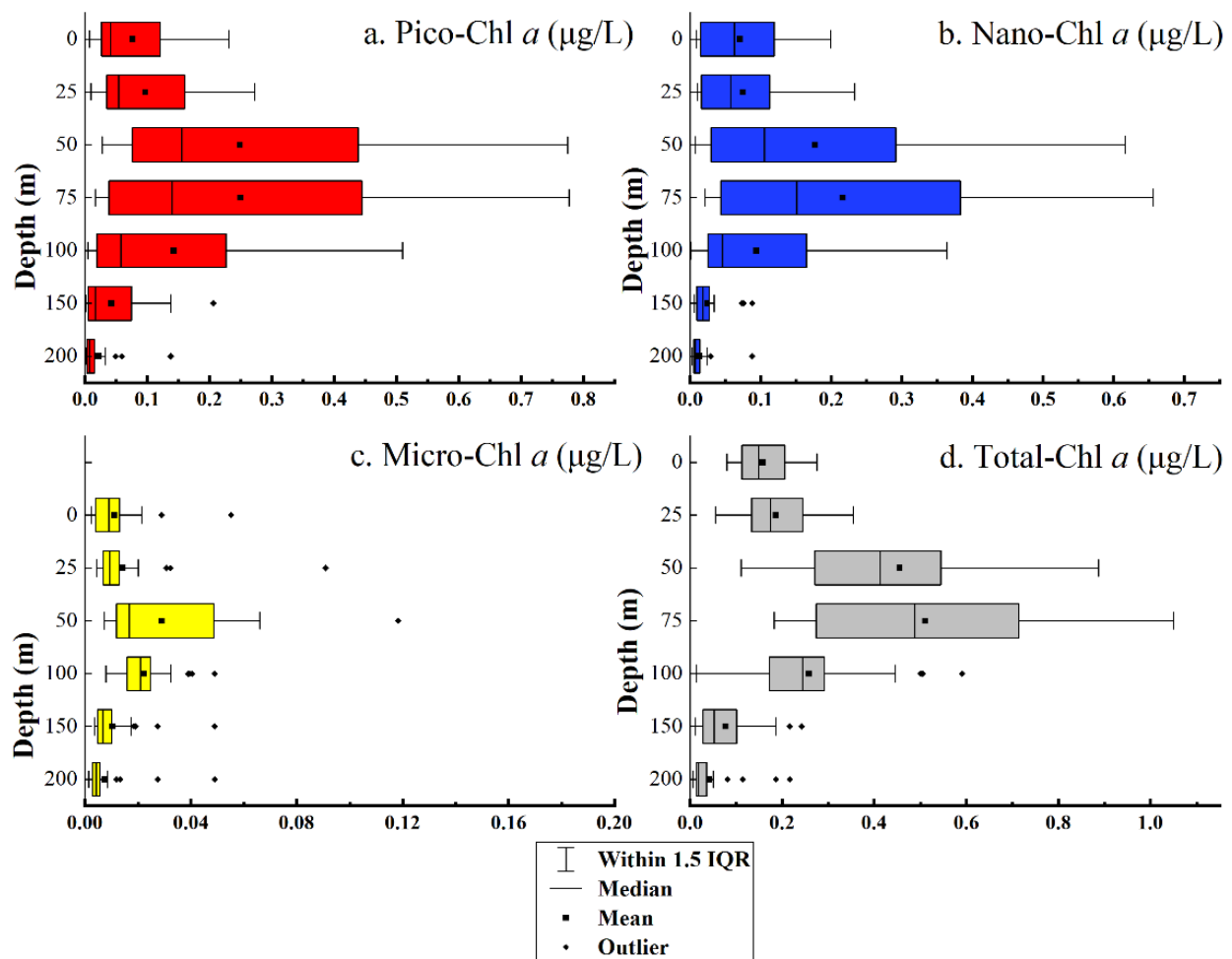
**Figure 4.** Pie chart of size-fractionated Chl *a* bases on water column integration. The size of the pie chart is related to the phytoplankton biomass.

Table 2. Mean $\pm$ SD of Chl *a* ($\mu\text{g/L}$) in three contrasting sections.

Size-Fractionated		Section B	Section C	Section KC
Pico	Mean	0.07 ± 0.13	0.23 ± 0.18	0.15 ± 0.16
	Percentage	33	86	60
Nano	Mean	0.13 ± 0.15	0.02 ± 0.01	0.09 ± 0.13
	Percentage	62	7	26
Micro	Mean	0.01 ± 0.01	0.02 ± 0.02	0.02 ± 0.03
	Percentage	5	7	4
Total		0.21 ± 0.21	0.27 ± 0.21	0.25 ± 0.21

The vertical distribution of size-fractionated Chl *a* was shown in Figure 5. The concentration range of the pico-size fraction was $0.001\text{--}0.777\text{ }\mu\text{g/L}$ ($0.132 \pm 0.173\text{ }\mu\text{g/L}$), mainly concentrated at the depth of 50–100 m. The concentration range of the nano-Chl *a* was $0.003\text{--}0.656\text{ }\mu\text{g/L}$ ($0.099 \pm 0.137\text{ }\mu\text{g/L}$), mainly concentrated at 75 m, and the concentration range of the micro-Chl *a* was $0.001\text{--}0.210\text{ }\mu\text{g/L}$ ($0.204 \pm 0.243\text{ }\mu\text{g/L}$), mainly distributed at 50–75 m. Figure 6 showed that the DCM of the stations near the shore in Section B is shallower than those farther from the shore. Section C was also like this in Figure 6. However, the depth of the DCM in section KC was getting deeper and deeper along the direction of Kuroshio in Figure 6.

**Figure 5.** Vertical distribution of size-fractionated Chl *a*.

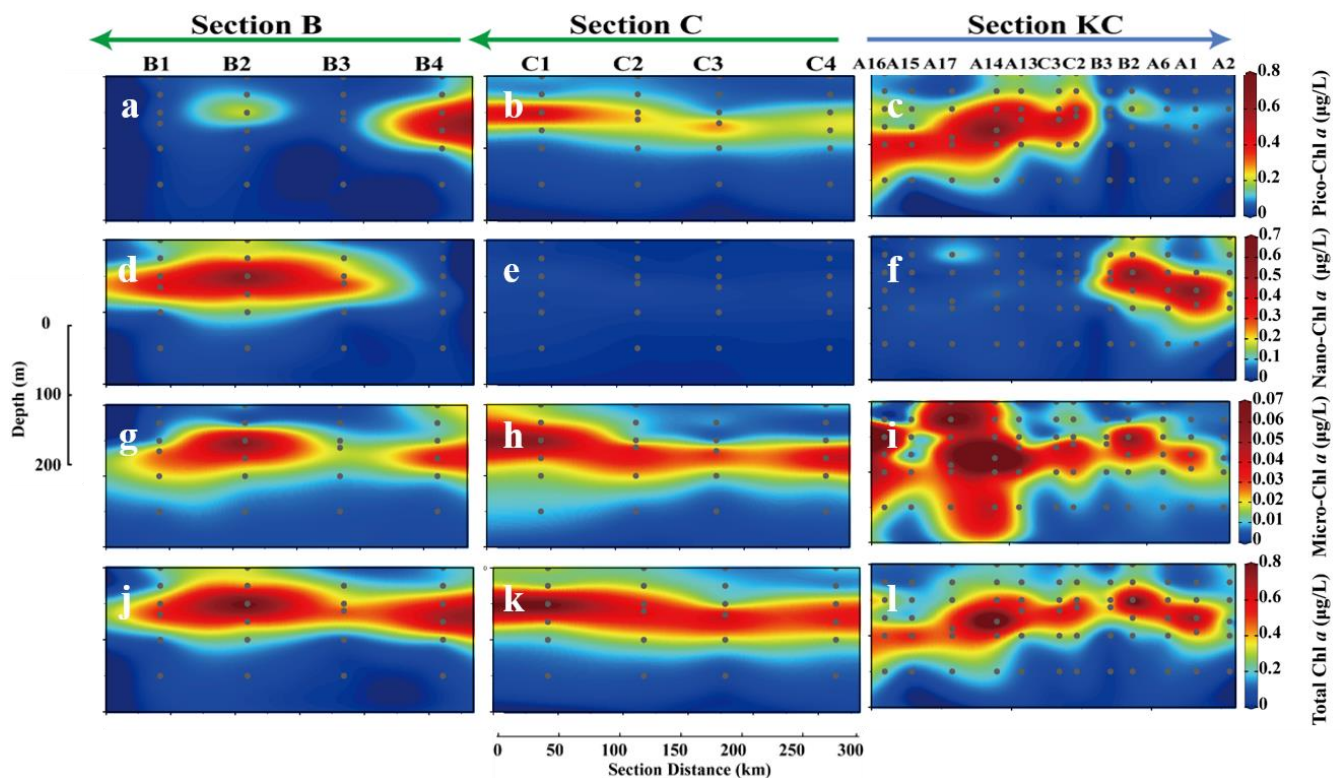


Figure 6. Vertical distribution of Chl *a* in section B, C, and KC. (pico-Chl *a* (a–c), nano-Chl *a* (d–f), micro-Chl *a* (g–i), and total-Chl *a* (j–l)).

3.3. Correlation Analysis

RDA and Pearson's correlation analysis was used to identify which key environmental variables explained the biogeographic variations of picophytoplankton in the 3 contrasted sections (Figure 7, Table 3). Within our study, the *p*-value for the significance test of all canonical axes was 0.002.

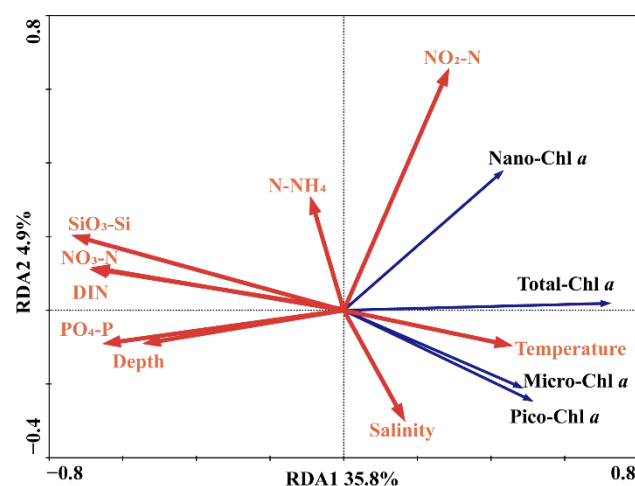


Figure 7. Redundancy analysis (RDA) plot for the relationship between size-fractionated Chl *a* groups and environmental variables in NESCS. The blue vectors correspond to size-fractionated Chl *a*. The red vectors show the direction and strength of the environmental variables relative to the overall distribution. The concentrations of size-fractionated Chl *a* were log-transformed prior to analysis.

Table 3. Pearson’s rank correlation coefficients between environmental factors and concentrations of size-fractionated Chl *a*. The concentrations of size-fractionated Chl *a* were log transformed prior to analysis. * $p < 0.05$ (2-tailed); ** $p < 0.01$ (2-tailed).

	Pico	Nano	Micro	Total
Temperature	0.502 **	0.357 **	0.245 **	0.552 **
Salinity	−0.045	−0.158 *	0.224 **	−0.081
Depth	−0.509 **	−0.472 **	−0.298 **	−0.622 **
PO ₄ -P	−0.529 **	−0.459 **	−0.376 **	−0.625 **
SiO ₃ -Si	−0.678 **	−0.445 **	−0.477 **	−0.736 **
N-NH ₄	−0.136	0.091	−0.072	−0.048
NO ₂ -N	0.044	0.329 **	0.132	0.195 **
NO ₃ -N	−0.603 **	−0.402 **	−0.399 **	−0.653 **
DIN	−0.601 **	−0.400 **	−0.396 **	−0.651 **

Total and size-fractionated Chl *a* were affected by the studied environmental variables as follows: Three different phytoplankton sizes were positively correlated with water temperature ($r > 0.245$, $p < 0.01$). Meanwhile, three different phytoplankton sizes were negatively correlated with depth ($r < -0.298$, $p < 0.01$), with PO₄-P ($r < -0.376$, $p < 0.01$), with SiO₃-Si ($r < -0.445$, $p < 0.01$), and with NO₃-N ($r < -0.399$, $p < 0.01$). Furthermore, Nano-Chl *a* was negatively correlated with salinity ($r = -0.185$, $p < 0.05$). While micro-Chl *a* was positively correlated with salinity ($r = 0.224$, $p < 0.01$). This result indicated that the growth of three different phytoplankton sizes was not limited by low nutrient levels in NESCS. Therefore, water temperature and nutrient availability are important factors explaining the biogeographic variation of phytoplankton, while salinity explains relatively less.

4. Discussion

4.1. Comparison with Historical Data

As there were fewer investigations of this study area on size-fractionated Chl *a*, we compared a similar region of the SCS (Table 4). When compared with previously published reports, it is clear that pico predominates the total Chl *a* most of the time [28–30]. Liu et al. found that the nano-level concentration exceeds the pico-level concentration in studies of the continental slope area in NSCS [16], which is the same as our results. In this study, the phytoplankton biomass mainly had pico components in NESCS. This could be explained by the low nutrient concentrations recorded in relation to the size of the cells. Indeed, when the constant, specific surface area is small, the nutrient dissipation rate around the cell is faster, and when the extracellular nutrient concentration is low, the nutrient supply cannot continue to maintain the growth of the cells [31]. Thereby, Pico-class phytoplankton, with a small volume, large specific surface area, half-full nutrients, and small constant, are more suited to environments with low nutrient concentrations, so they have the advantage in oligotrophic waters [28].

In section KC, the results showed a nano dominance (Figure 4); this could be explained by the Kuroshio current. Indeed, when the Kuroshio invading the SCS flows through the Luzon Strait, due to the action of the continental shelf and slope, upwelling and mesoscale eddy currents arise. These factors work together to enhance the vertical mixing of water bodies in the Luzon Strait and adjacent waters, bringing nutrient-rich seawater from the lower layers to the upper layers, an environment that allows the nano-class to grow as nutrients are replenished. Our results thus highlight that there is a complex spatial variation pattern of Chl *a* at the surface of the SCS Regional upwelling driven by the monsoon and mesoscale eddies was the main reason for the complex pattern of Chl *a* at the sea surface.

Table 4. Historical data of the size-fractionated Chl *a* in the South China Sea.

Date	Research Area	Concentration (µg/L)				References
		Total	Pico	Nano	Micro	
July–August 2017	15–22° N, 114–120° E	0.232 ± 0.860	0.123 ± 0.108	0.090 ± 0.070	0.020 ± 0.014	This study
August–September 2014	18–22° N, 114–116° E	0.321 ± 0.250	0.093 ± 0.071	0.148 ± 0.192	0.023 ± 0.036	Liu et al. [15]
Spring and autumn 2014, summer 2015	21.5° N, 118° E	0.450 ± 0.072	0.320 ± 0.181	0.071 ± 0.028	0.037 ± 0.021	Jiang et al. [28]
June 2009	9–16° N, 110–118° E	0.10 ± 0.09	0.10 ± 0.07	0.02 ± 0.02	0.006 ± 0.009	Che et al. [17]
February 2009	18–23° N, 110–118° E	0.39 ± 0.09	0.24 ± 0.07	0.10 ± 0.05	0.05 ± 0.05	Zeng et al. [29]
August 1999	18.5–22° N, 110–117° E	2.51 ± 1.53	1.83 ± 1.22	0.47 ± 0.28	0.21 ± 0.15	Cai et al. [30]

4.2. Relationship between the Size-Fractionated Chl *a* and Environment Factors

The present study indicates that environmental variables have a significant impact on the total Chl *a* or size-fractionated Chl *a* (micro, nano, and pico). The contribution of micro-Chl *a* to the total Chl *a* was the least, and the biomass reached the highest level at a depth of 50–70 m (Figure 5). Nitrogen was an important limiting nutrient in subtropical areas of the South Pacific and SCS [32,33]. Temperature, nitrate, silicate and phosphate are the main controlling factors of micro-Chl *a* in NESCS [34,35]. This is consistent with the results of this study. The contribution of micro-Chl *a* was higher than nano-Chl *a* in the area near the Luzon Strait. The nutrient concentrations and temperature in the section KC were significantly lower than in the other areas. Nitrogen and phosphorus have a significant limiting effect on micro-Chl *a*. At the same time, the joint limiting effect of nitrogen and phosphorus on phytoplankton in the deep sea has also been recognized by some researchers [36–39].

The concentration of nano-Chl *a* was highest in the end region of the Kuroshio influx direction. Under warm and stratified conditions, smaller cell combinations have a higher photosynthetic efficiency, which impacts carbon fluxes in the ocean [40]. The concentration of nano-Chl *a* reached its maximum at 75 m. Nano-Chl *a* was limited by PO₄-P, SiO₃-Si, and NO₃-N, and at the same time, promoted by NO₂-N. The ability of nano-Chl *a* to regulate buoyancy enables it to stay close to the surface and maximize the absorption of light and nutrients in stratified waters, to promote its development [41]. Overall, nano-Chl *a* was less than pico-Chl *a*. Extremely low phosphate levels lead to phosphorus limitation for phytoplankton growth in the section KC. Some studies indicate that the availability of nitrogen to phytoplankton affects its ability to absorb phosphorus [20,42,43]. After phosphate enrichment, the proportion of nano-Chl *a* increased significantly [44,45].

Pico-Chl *a* (52.87%) contributed the most to the phytoplankton biomass in this research. In the oligotrophic sea area, pico is more adaptable to the environment of low nutrient concentration than micro and nano [7,46]. Pico's growth is less restricted. The distribution of *Prochlorococcus* (Pro) may be affected by the Kuroshio. Temperature promotes the growth of Pro, *Synechococcus* (Syn), and picoeukaryotes (PEuks) in the NESCS [19,31]. Interestingly, negative correlation of pico-Chl *a* with nutrient indicate that pico-Chl *a* is more suitable for growth in oligotrophic waters.

4.3. Coupling of Physical and Biological Factors

The NESCS is located on the west side of the Luzon Strait. It is a sea area where the waters of the SCS and the Northwest Pacific are frequently exchanged. It is significantly affected by the Kuroshio intrusion. NESCS is also affected by upwelling due to the south-west monsoon in summer. Tropical oceans have plenty of light and heat; the nutrients in

the photosphere are usually low due to consumption by phytoplankton growth [38]. On the other hand, Thermocline restricts the entry of nutrients to the eutrophic layer [39].

In terms of the Kuroshio invasion, due to the influx of the Kuroshio, the high-temperature, high-salt, low-nutrient Kuroshio water enters NESCS through the Luzon Strait (Figure 3). At the same time, the Chl *a* was also mixing upward. But despite this, the concentration of Chl *a* on the surface of the Kuroshio area is still very low. The growth of pico-Chl *a* was stimulated by the high temperature, high salinity and, low nutrients brought by the Kuroshio invasion [40,47]. According to the depth-weighted Chl *a* distribution, the concentration of pico-Chl *a* was the highest near the Luzon Strait (Figure 4). It is interesting to note, in NESCS, although pico is dominant in general, it is not difficult to find that the dominant Chl *a* of different stations is different (Figure 4). Environmental factors in different geographical locations limit Chl *a*, to varying degrees. Our results show that the concentration of nano-Chl *a* was the highest near the SCS. This is because the effect of the Kuroshio on phytoplankton mainly shows that the micro-Chl *a* abundance changes insignificantly along the section KC invasion route [34]. However, with the mixing of the Kuroshio into the NESCS, the effect gradually abates. The environment of the SCS is more suited to the growth of nano-Chl *a*, which is stimulated by NO₂-N, and limits the growth of pico-Chl *a* (Figure 7). The invasion of the Kuroshio caused the fluctuation of the spatial distribution of micro in this study.

In terms of upwelling, the southwest monsoon prevails in the SCS in summer [41,42]. It is reported that during our investigation, there have been two typhoons in the NESCS, “Roke” and “HaiTang” [34]. When the Kuroshio invaded the SCS and passed through the Luzon Strait, the upwelling and mesoscale eddy were caused by the action of the coast and the ridge [43]. The upwelling and turbulence produced by the Kuroshio intruding through the Luzon Strait will disturb the sea water, which will break the pycnocline layer, supplement the nutrients in the upper layer of the sea area, and significantly increase the primary productivity [46,48]. The activity of the wind field promotes the appearance of upwelling in the continental shelf and slope area. In the Figure 3, the data shows that in sections B and C, due to the existence of upwelling, the surface seawater is moved by the wind, and the deeper seawater is replenished upward. The station on the land slope (station B1 and C1) has obviously lower temperature and higher salinity. This situation is very consistent with the existence of upwelling. The deep water is brought to the surface by this upwelling movement (within a certain minimum period and range) and carried out of the upwelling area by horizontal flow [46,48]. In research on the Chl *a* concentration and distribution characteristics of the background field, the Chl *a* concentration has been proven to be closely related to the temperature, wind field, and hydrological field [39,47]. As can be seen from the Chl *a* distribution in section B and C, the DCM rose from 75 to 50 m. In the coastal upwelling area, the Chl *a* concentration increases significantly and tends to be relatively uniform in the vertical direction [48,49]. The upward transport of nutrient-rich bottom water will eventually activate the growth of phytoplankton in the surface water, leading to the accumulation of large-scale biomass (Chl *a*) [50,51].

In addition, we compared other regions affected by upwelling globally (Table 5), including the Northwestern Pacific Ocean, Southern Ocean, and Sargasso Sea. We had found that upwelling is generally studied in summer. Most importantly, we found that pico-Chl *a* contributes the most to total Phytoplankton biomass in oligotrophic waters, including NESCS. On the surface area, upwelling is physically characterized by colder and higher salinity seawater than surrounding waters. During upwelling, deeper, cooler but nutrient-rich seawater is drawn to the surface [52]. Overall, phytoplankton biomass increased due to the log abundance of nutrients brought by upwelling [53]. Interestingly, we found that nano-Chl *a* contributes more to total-Chl *a* than pico-Chl *a* in section B in NESCS. This was due to the co-limitation of phytoplankton nitrogen and phosphorus in oligotrophic seas. However, the upwelling brings rich nutrients, which are more suitable for nano-Chl *a* with larger particle size. This was consistent with the findings in Sargasso Sea [54].

Table 5. Comparison with other areas affected by upwelling.

Research Area		Concentration (µg/L)				References
		Total	Pico	Nano	Micro	
Northeastern the South China Sea	15–22° N, 114–120° E	0.233	0.123	0.090	0.020	This study
Northwestern Pacific Ocean	8° N, 127–134° E	8.843	4.888	3.161	0.794	Chen et al. [53], 2014
Southern Ocean	50°7' S, 1–7° E	27.63	12.12	8.67	6.85	Froneman et al. [52], 2001
Sargasso Sea	29–32° N, 63–64° W	29	24	3	2	Rausch et al. [54], 2020

5. Conclusions

This study provides useful information for understanding the total and size-fractionated Chl *a* biomass distribution in the NESCS. In the study area, pico-Chl *a* and nano-Chl *a* were found to be the main components of the total Chl *a*. This study also separately studied the distribution of total Chl *a* and size-fractionated Chl *a* in the upwelling and Kuroshio, which has not been mentioned in other studies. We found that nano-Chl *a* contributes more to total-Chl *a* than pico-Chl *a* in areas affected by upwelling. The changes in temperature and nutrients caused by upwelling and Kuroshio promote the growth of nanophytoplankton and picophytoplankton, respectively. The information provided in this article helps us to better understand the spatial distribution of size-fractionated Chl *a* in the NESCS and its main environmental variables. This research also helps us to understand the phytoplankton biomass and environmental variables that regulate the distribution of different functional groups of phytoplankton in the NESCS.

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