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Water column stratification governs picophytoplankton community structure in the oligotrophic eastern Indian ocean

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ABSTRACT

Under the background of global warming, the area extent of the oligotrophic tropical oceans has growing due to increased water-column stratification over the past decades. Picophytoplankton is usually the most dominant phytoplankton group in oligotrophic tropical oceans and substantially contribute to carbon biomass and primary production three. Understanding how vertical stratification governs the community structure of picophytoplankton communities in oligotrophic tropical oceans is important for comprehensively understanding the plankton ecology and biogeochemical cycle in these areas. In this study, the distribution of the picophytoplankton communities in the eastern Indian Ocean (EIO) was investigated during a period of thermal stratification in the spring of 2021. *Prochlorococcus* contributed most (54.9%) to picophytoplankton carbon biomass, followed by picoeukaryotes (38.5%) and *Synechococcus* (6.6%). Vertically, the three picophytoplankton groups showed quite different distribution pattern: the abundance of *Synechococcus* was highest in the surface layer, while *Prochlorococcus* and picoeukaryotes were usually located between 50 m and 100 m. The relationship between the abundance of picophytoplankton and environmental factors was analyzed, and the results revealed that picophytoplankton distribution was strongly correlated with the degree of vertical stratification of the water column. The density of *Synechococcus* was higher in strongly stratified waters, while *Prochlorococcus* was more abundant in regions of weaker stratification. This is mainly attributed to variation of physicochemical parameters such as nutrient structures and temperature resulted from water column stratification. Understanding the distribution patterns of these organisms and their relationship with stratification in the oligotrophic EIO is essential for comprehensive understanding on oligotrophic tropical ecosystem with increasing stratification in future.

1. Introduction

The ecology of picophytoplankton (2 or 3 μm in diameter) has been a major area of oceanographic research since the discovery of small phytoplankter during the late 1970s (Waterbury et al., 1979; Chisholm et al., 1988; Takahashi and Hori, 1984). Picophytoplankton represent the smallest class of phytoplankton and comprise both prokaryotes and eukaryotes. Prokaryotic picophytoplankton belong to the phylum cyanobacteria and are subdivided into the *Prochlorococcus* and *Synechococcus* genera (Waterbury et al., 1979; Chisholm et al., 1988). The eukaryotic picophytoplankton represent a taxonomically diverse group with a large phylogenetic diversity and several novel lineages (Epstein and López-García, 2008; Massana, 2011). These groups are ubiquitous and represent the most abundant phytoplankton component on this planet (Fuhrman and Campbell, 1998; Partensky et al., 1999), and studies have confirmed their presence in all oceanic environments (Raven, 1998; Buitenhuis et al., 2012). *Prochlorococcus*, *Synechococcus*, and picoeukaryotic phytoplankton dominate oligotrophic oceans, contributing to at least 10% of the global primary productivity, and are central to global biogeochemical cycles (Visintini et al., 2021). Their high surface-to-volume ratio makes them the best competitors in low nutrient conditions (Raven, 1998). Marine picophytoplankton play a crucial role in the material circulation and energy flow of marine ecosystems. The total global biomass of picophytoplankton is estimated to

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be 0.53–1.32 Pg C (17–39% *Prochlorococcus*, 12–15% *Synechococcus*, and 49–69% picoeukaryotes), with an intermediate/best estimate of 0.74 Pg C (Buitenhuis et al., 2012). It has been reported that picophytoplankton contribute to up to 80% of the fixed carbon content of several oligotrophic regions, such as the oligotrophic Pacific Ocean and Atlantic Ocean (Campbell et al., 1997; Grob et al., 2011; Liang et al., 2017).

The oliogtrophic tropical oceans constitute an important part of the global ocean, and they contribute a significant fraction to the total primary production of the ocean owing to their large size (Christian et al., 2008). According to surface chlorophyll data collected by satellites, the area extent of the oligotrophic tropical ocean has been expanding during recent decades (Irwin and Oliver, 2009). Column stratification has been expected to enhance in the oligotrophic ocean due to global warming (Sarmiento et al., 2004). Determing the impact of column stratification on the community structure of picophytoplankton is important for understanding plankton ecology and biogeochemical cycle in oligotrophic tropical oceans.

The eastern Indian Ocean (EIO) is a typical oligotrophic tropical ocean (Shankar et al., 2002). The surface temperature of this region is relatively high, and the annual average temperature exceeds 28 °C (Shenoi et al., 2002). Both N and P in the surface layer of the EIO are usually below the detectable limits, and chlorophyll (Chl) *a* concentrations are always below 0.1 mg m^{-3} (Yuan et al., 2021). The environmental characteristics of the EIO are complex. The northern EIO is greatly affected by runoffs from the land, resulting in low salinity and high concentrations of nutrients there (Howden and Murtugudde, 2001). The southern EIO is affected by the equatorial counter current, with temperature being higher and nutrients level being lower there (Schott et al., 2009; Lin et al., 2014). The information on picophytoplankton community in the EIO is quite limited when compared with other oceanic regions (Yuan et al., 2021). It has been reported that picophytoplankton contribute to 35–92% of the phytoplanktonic Chl *a* in the EIO (Latasa and Bidigare, 1998; Brown et al., 1999), and *Prochlorococcus* is numerically dominant in the picophytoplankton community (Yuan et al., 2021). However, how physical processes such as column stratification regulate the picophytoplankotn community structure in the EIO is still unclear.

Stratification is defined as the amount of energy required for mixing the water throughout the water column (Simpson and Bowers, 1981). A strongly stratified water column requires more energy for mixing compared to a less stratified column. The stratification of water columns determines the availability of nutrients that are utilized for phytoplankton growth. The characteristically low levels of surface nutrients limit phytoplankton growth in the tropics and mid-latitudes where vertical mixing is limited owing to stabilization of the water column by thermal stratification (Karl-Erich et al., 1998). Climate warming further inhibits mixing, which reduces upward nutrient supply and lowers productivity, thereby worsening the situation in oligotrophic oceans. Considering the increasing importance of picophytoplankton and the accelerated water column stratification in the oligotrophic ocean in future, how stratification governs and affects the distribution of picophytoplankton in the oligotrophic tropical oceans becomes an interesting question. In this study, we used the EIO as an case study area to identify the mechanisms driving the composition of picophytoplankton communities in relation to vertical stratification in the area, and hope to provide comprehensive information regarding the dynamics of the picophytoplankton community in the oligotrophic EIO.

2. Materials and methods

2.1. Field surveys

A comprehensive investigation was conducted during the winter of 2021 (21st April 21–15th June) in the equatorial EIO (15° N~10° S, 80° E~95° E) on the R/V Shiyan III. Data were collected from 24 stations as depicted in Fig. 1. Based on the geographical location, we have categorized the sampling stations into four distinct groups: Group I (north of the equator), Group II (south of the equator), Group III (west of 87° E), and Group IV (east of 87° E). Samples of seawater were collected from different depths, within the upper 200 m of the water column (5, 25, 50, 75, 100, 150, 200 m), using 12-L Niskin bottles equipped with a Sea-Bird CTD rosette sampler (SBE 19 Plus) for measuring conductivity, temperature, and depth. For nutrient analysis, the samples of sea water were filtered through 0.45 μm cellulose acetate membrane filters for removing the particulate matter, and subsequently refrigerated at −20 °C for further analysis. Nutrients, mainly including DIN (Dissolved Inorganic Nitrogen, DIN: $NO_2^- + NO_3^- + NH_4^+$), phosphate and silicate, were determined using a Technicon AA3 Auto- Analyzer (Bran + Luebbe). For determining phosphorus (PO_4–P) with phosphor molybdenum blue spectrophotometry, the detection limit was set at 0.01 μmol/L; Determination of dissolved silicate (SiO_3–Si) using the silicon molybdenum blue spectrophotometry involved a detection limit was 0.01 μmol/L. Determination of nitrate (NO_3–N) using cadmium-copper column reduction involved a detection limit of 0.02 μmol/L. Determination of nitrite (NO_2–N) by the naphthylethylenediamine photometric method involved a detection limit of 0.01 μmol/L, while determination of ammonia (NH_4–N) with sodium salicylic acid used a detection limit of 0.01 μmol/L (Wei et al., 2022). For flow cytometry analyses, the samples were fixed with paraformaldehyde (1% final concentration) and subsequently incubated in the dark at room temperature for 10–15 min. The

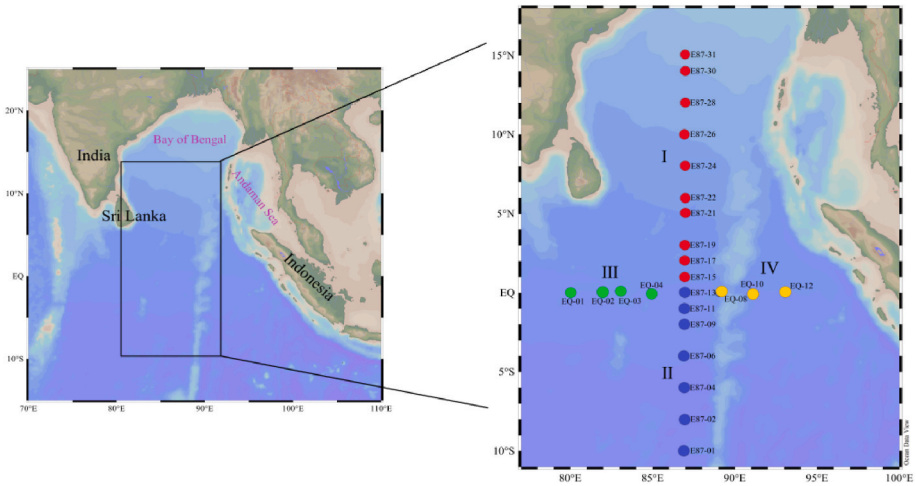

Fig. 1. Study area and sampling stations (the four groups covering the entire EIO have been highlighted in the panel on the right).

incubated samples were then deep frozen in liquid nitrogen and stored at −80 °C (Zhang et al., 2008).

2.2. Flow cytometry analysis

Three picophytoplankton groups, namely *Prochlorococcus*, *Synechococcus* and picoeukaryotes, were distinguished by flow cytometry (CytoFlex, Beckman), equipped with blue (488 nm) and red (638 nm) lasers. The photosynthetic pigments (chlorophyll, phycoerythrin, and other pigments) of the picophytoplankton have spontaneous fluorescence characteristics, and could show different fluorescence characteristics under different excitation wavelengths, and this strategy is used for distinguishing among these three groups (Phinney and Cucci, 1989).

The flow rate was calibrated on a daily basis after starting up the instrument. The frozen samples were thawed in water at room temperature before analysis. The concentration of cells was determined by spiking the samples with a known volume and concentration of 1 μm fluorescent yellow-green beads (Polysciences), and the unstained samples were subsequently analyzed at a high flow rate of 60 μL/min for 3 min. The discrimination of different groups of picophytoplankton populations were achieved by a comprehensive analysis of a two-parameter distribution map with multiple combinations of signals reflecting cell characteristics obtained from the measurement of light scattering (Forward scatter, FSC; Side scatter, SSC; characterizing cell size) and fluorescence parameters (chlorophyll, FL3; phycoerythrin, FL2; characterizing the type and content of photosynthetic pigments contained in cells) of each cell. For example, *Synechococcus* contains phycoerythrin, *Prochlorococcus* and picoeukaryotes do not contain phycoerythrin (FL2 height difference); cell size: picoeukaryotes » *Synechococcus* > *Prochlorococcus* (SSC height difference); chlorophyll content: picoeukaryotes » *Synechococcus* > *Prochlorococcus* (FL3 height difference). The carbon biomass of the three picophytoplankton groups was estimated from their cell abundance using conversion factors of 250, 53, and 2100 fg C cell^{-1} for *Synechococcus*, *Prochlorococcus*, and picoeukaryotes, respectively (Campbell et al., 1997).

2.3. Data analyses and statistical methods

The abundance of picophytoplankton cells in the water column was calculated using the trapezoidal integral method:

$$A = \left[\sum_{n}^{n+1} \frac{\left(\overset{i}{A} + A \right)}{2} \times \left(D - \overset{i}{D} \right) \right] \Big/ \left(D^{\mathrm{MSL}} - \overset{S}{D} \right)$$

where A represents the average abundance of picophytoplankton in the water column, A_i represents the abundance value of picophytoplankton in layer i, D_{MSL} represents the maximum sampling depth, D_S represents the surface layer, D_i represents the depth of layer i, and *n* represents the sampling level.

In order to quantify the stratification strength of the upper ocean, the vertical stratification index (VSI: high value indicates the large density difference and strong stratification) was calculated using the following formula for measuring the degree of vertical stratification of the water column:

$$VSI = \sum [\delta\sigma(m+1) - \delta\sigma(m)]$$

where δ_σ represents the potential density anomaly, and m represents the depth from 5 to 200 m (Mena et al., 2019).

The distribution of temperature, salinity, nutrients, and picophytoplankton groups was visualised using the Ocean Data View software, version 4. In order to determine the carbon biomass in the water column, we first calculated the integrated values using the trapezoidal rule and then divided the integrated values by the depth of the water column. The relationship between the environmental parameters and abundance of each of the three picophytoplankton groups was determined from the cellular abundance by redundancy analysis (RDA) using the CANOCO software, version 5. The length and orientation of the arrows indicate their relative importance and approximate correlations to the axes, respectively (Lepš and Šmilauer, 2003; Bemal et al., 2018). The abundance of the picophytoplankton groups was transformed to the respective log values before analyses.

3. Results

3.1. Environmental parameters

The surface temperature and salinity had different spatial distribution characteristics in the study area (Fig. 2). The temperature varied from 28.0 °C to 31.65 °C, with an average temperature of 30.21 ± 0.94 °C. Generally, the temperature was higher in the Bay of Bengal and decreased southwards (Fig. 2a). The surface salinity varied from 31.83 to 34.61, with an average value of 33.96 ± 0.84. The distribution pattern of surface salinity was opposite to that of the surface temperature. The surface salinity was lowest in the Bay of Bengal, which was attributed to the runoffs from the Bay of Bengal (Fig. 2b). The surface salinity was particularly high between 80° E and 90° E around the equator.

The latitudinal distribution of the VSI is depicted in Fig. 2c. The VSI tended to increase at increasing latitudes from the southern to the northern hemisphere. The minimum value of VSI (4.85) was observed in station E87-02 located at 8° S, and the maximum value of 8.06 was observed in station E87-31 located at 15 °N, and the average value of VSI was 6.08 ± 0.93. Interestingly, the values of VSI varied significantly across the latitudinal regions, being higher from 5° N to 15° N than from 10° S to the equator.

The temperature, salinity, and VSI of the four groups are depicted in Fig. 3. Groups I (average 23.29 ± 1.59 °C) and IV (average 25.06 ± 0.55 °C) had high temperatures, while the salinity of groups I (average 34.36 ± 0.39 °C) and IV (average 34.73 ± 0.34 °C) were low. The temperature of groups II (average 21.98 ± 1.86 °C) and III (average 23.97 ± 0.26 °C) were low, while the salinity of groups II (average 34.77 ± 0.22) and III (average 34.97 ± 0.07) were high (Fig. 3a). A distinct variation can be observed in the T-S in Fig. 3. The VSI of the four groups were also calculated (Fig. 3b), and the results revealed that the values of VSI were markedly higher in group I (average 6.81 ± 1.01) than in groups II (average 5.42 ± 0.44), III (average 5.76 ± 0.11), and IV (average 5.62 ± 0.13), indicating that the stratification of group I was more pronounced. We observed that the VSI was related to the temperature (Fig. 3a) and salinity (Fig. 3b). The temperature was positively correlated with the VSI ($P < 0.01$), while the VSI of all the groups was negatively correlated with salinity ($P < 0.01$) (Table 1). The changes in temperature and salinity were most pronounced in the vertical direction. Group I had a high value of VSI, and the variations in temperature and salinity were large within the group. However, groups III and IV had low values of VSI, and the changes in temperature and salinity were inconspicuous in these groups.

The spatial and vertical distributions of the nutrient concentrations are depicted in Fig. 4. The concentration ranges of DIN, DIP and DSi were 0~31.70, 0~2.32, and 0~35.01 μmol/L, respectively, and the average surface values were 0.14 ± 0.07, 0.06 ± 0.03, and 1.81 ± 0.83 μmol/L, respectively. The nutrient concentrations of several of the surface samples could not be detected as the nutrient contents were below the limit of detection. There were distinct differences in the surface distribution patterns of nutrients. The nutrient concentrations of groups I and II were significantly higher than those of groups III and IV (Fig. 4). The concentration of DIN was maximum at station EQ-08 (0.32 μmol/L), while the concentration of DIP was higher in the northern and southern sides and lower near the equator. The concentration of DSi was highest at 10° N. The environmental factors of group I were significantly different from those of groups II, III, and IV. Additionally, the nutrient

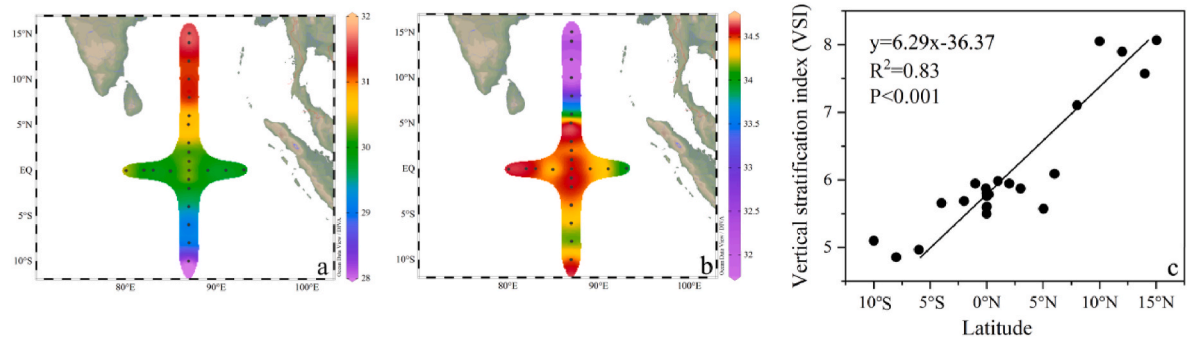

Fig. 2. Surface distribution of (a) water temperature (°C) and (b) salinity. (c) Linear fit of the VSI with the latitude in the EIO. The black dots represent the VSI of each station.

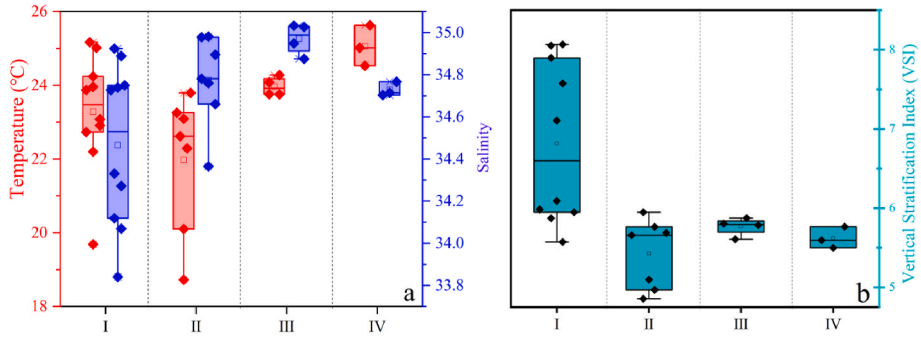

Fig. 3. Depth-weighted average values of (a) temperature (°C) and (b) salinity, and (c) VSI of the four areas.

Table 1
Pearson's rank correlation coefficients between environmental factors and VSI. *p < 0.05 (2-tailed); **p < 0.01 (2-tailed).

	Salinity	Temperature	DIP	DSi	DIN	N/P	Si/N	Si/P
VSI	−0.920**	0.848**	−0.246	−0.033	−0.501*	−0.477*	−0.021	−0.192

concentration of group I was significantly higher than that of the other groups. The nutrient concentrations were relatively low in the upper 75 m of the EIO, but increased rapidly from 75 to 200 m. The nutrients were generally depleted in the upper 100 m, with a deep nutricline at ~100 m, owing to the pronounced stratification in the EIO.

We compared the N: P, Si: P, and Si: N ratios in the upper, middle and bottom layers (Fig. 5). The nutrient structures were altered in the middle layer, where nitrogen, phosphorus, and silicon were no longer the abiotic limiting factors. With the depth increasing, the ratio of nutrients remained within a stable range. At the bottom layer, the nutrient ratio approached the Redfield ratio.

3.2. Cellular abundance and distribution of picophytoplankton

The spatial and vertical distributions of the three picophytoplankton area are depicted in Fig. 6. The findings revealed that the distribution pattern of *Synechococcus*, *Prochlorococcus*, and picoeukaryotes were different both horizontally and vertically. *Prochlorococcus* accounted for the majority of the picophytoplankton community and had an overwhelming dominance, followed by *Synechococcus*. The abundance of picoeukaryotes was the lowest.

The abundance of *Synechococcus* ranged from 6.17×10^2 to 2.02×10^4 cells/mL, with a mean value of $5.60 \pm 5.18 \times 10^3$ cells/mL in the surface layer. *Synechococcus* abundance was greatest in the surface water, and its surface distribution was similar to the distribution trend of surface temperature. The abundance gradually increased from the equator to the north, while the abundance was generally low in the southern hemisphere (Fig. 6). Analysis of the vertical distribution of *Synechococcus* revealed that the surface layer was most suitable for the survival of *Synechococcus*, followed by the 25–50 m layer, and their abundance gradually decreased from the 50 m layer to bottom layer. The abundance of *Prochlorococcus* ranged from 3.98×10^4 to 2.54×10^5 cells/mL, with a mean value of $1.28 \pm 0.48 \times 10^5$ cells/mL in the surface layer. The distribution of *Prochlorococcus* was quite different from that of *Synechococcus*. The cellular abundance of *Prochlorococcus* was significantly higher in the southern hemisphere than in the northern hemisphere. The abundance of *Prochlorococcus* increased from the surface to deeper layers and was highest at 50 m. The abundance of picoeukaryotes ranged from 5.22×10^2 to 2.63×10^3 cells/mL, with a mean value of $1.01 \pm 0.54 \times 10^3$ cells/mL in the surface layer. The picoeukaryotes were not uniformly distributed in the upper ocean. They were frequently absent in several regions of the open ocean, and the abundance of picoeukaryotes was lower than those of *Synechococcus* and *Prochlorococcus*. However, the cellular abundance of picoeukaryotes was high at stations EQ-08 and E87-01. The picoeukaryotes were concentrated at 75 m, but is lower in shallower and deeper layers, and the abundance decreased significantly with increasing depth from 75 m downwards.

In order to understand the specific differences in picophytoplankton distribution, we compared their cellular abundance among the four groups (Fig. 7). It is evident from Fig. 7 that the abundance of picoeukaryotes were higher in group I ($1.24 \pm 0.31 \times 10^3$) and II ($1.23 \pm 0.49 \times 10^3$), while the abundance of *Prochlorococcus* was lower in area II ($6.15 \pm 1.50 \times 10^4$), and the density of *Synechococcus* was high in group

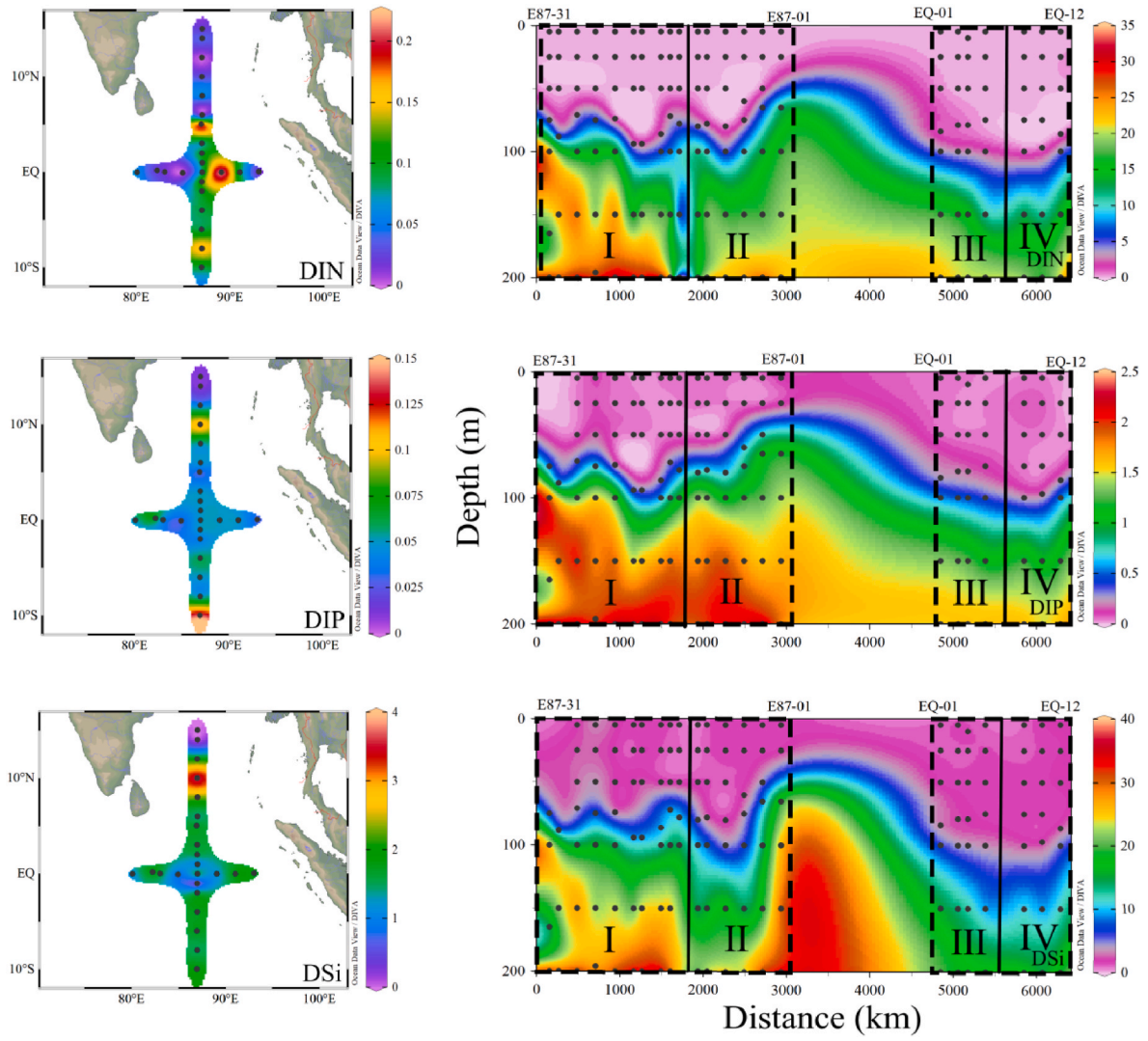

Fig. 4. Surface (left) and vertical (right) distribution of nutrients (μmol/L) in the EIO.

I ($2.06 \pm 0.95 \times 10^3$).

3.3. Contribution of picophytoplankton to community biomass

The biomass of *Prochlorococcus* and picoeukaryotes was significantly higher than that of *Synechococcus* at all stations. The biomass of picoeukaryotes were remarkably high at three stations, including E87-31, E87-26, and E87-04, while the other stations were characterized by extremely high biomass of *Prochlorococcus* but a very low biomass of *Synechococcus* (Fig. 8). The biomass of *Synechococcus* ranged from 0.14 to 0.91 μg C/L, which contributed to 6.6% of the total biomass. The biomass of picoeukaryotes ranged from 1.29 to 4.24 μg C/L, which contributed to 38.5% of the total biomass. Although *Synechococcus* was numerically more abundant than picoeukaryotes, the latter contributed more significantly to the photosynthetic carbon biomass. The biomass of *Prochlorococcus* ranged from 2.04 to 6 μg C/L, which contributed to 54.9% of the total biomass. Comparison of the mean carbon biomass of the subregions and percentage of each species revealed that the mean cellular abundance was lower while the percentage of *Prochlorococcus* was higher in group I than in the other three groups (Fig. 8b).

3.4. Variability in picophytoplankton structure across vertical stratification gradients

As depicted in Fig. 9a–c, the picophytoplankton community and environmental variables underwent significant vertical changes with increasing depth. The vertical variation in nutrient concentration and the abundance of picophytoplankton communities have been previously described in sections 3.1 and 3.2. Water temperature varied significantly from 100 to 150 m (Fig. 9b). The surface nutrients (DIN, DIP, and DSi) were usually depleted owing to the pronounced stratification, as the thermocline prevented nutrient replenishment. Therefore, the average nutrient concentrations followed a depth gradient with relatively higher nutrient concentrations at the bottom and relatively lower concentrations in the upper layer of the vertical patterns. The variations in the picophytoplankton communities were generally determined by the environmental conditions in the study area. We first used the Pearson's correlation analysis to test which environmental factors were significantly affected by VSI, and finally concluded that only temperature, salinity, DIN and N/P were significantly affected by VSI (Table 1). On the basis of this result, redundancy analysis (RDA) analysis was used to elucidate the correlation between picophytoplankton community abundance and temperature, salinity, DIN and N/P (Fig. 10). The key environmental variables that described the biogeographic variations in the picophytoplankton communities in the upper, middle, and bottom

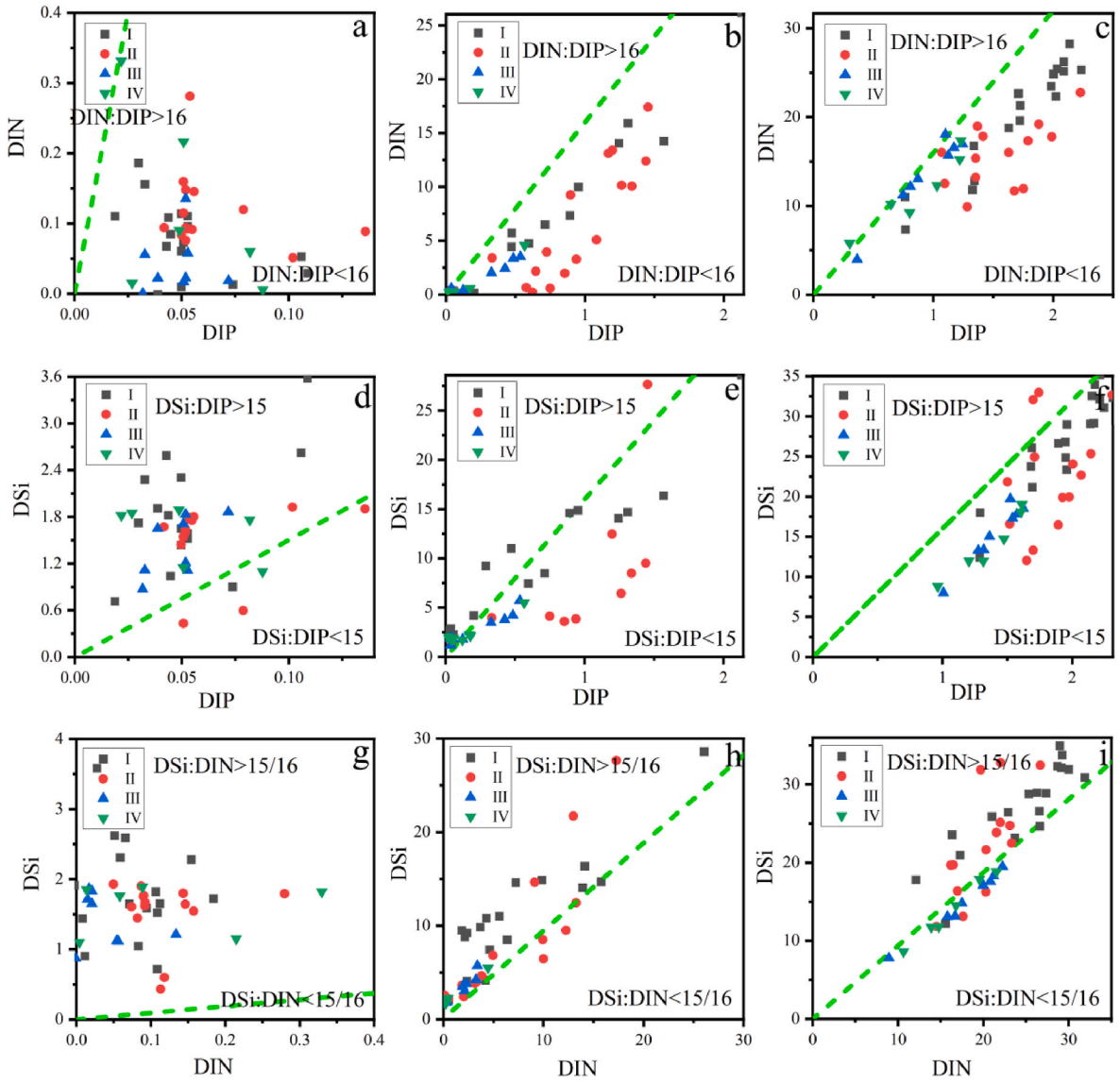

Fig. 5. Variation in nutrient structure with seawater depth. The N:P ratio in the (a) upper waters (5–25 m), (b) middle (50–100 m), and (c) bottom (150–200 m). The Si:P ratio in the (d) upper (5–25 m), (e) middle (50–100 m), and (f) bottom (150–200 m). The Si:N ratio in the (g) upper (5–25 m), (h) middle (50–100 m), and (i) bottom (150–200 m). The dashed lines indicate the Redfield ratio of N:P = 16:1, Si:P = 15:1, and Si:N = 15:16.

layer were different (Fig. 10a–c). In the surface layer, *Synechococcus* was negatively correlated with DIN and N/P, and positively correlated with temperature, while *Prochlorococcus* was positively correlated with salinity, DIN and N/P, and negatively correlated with higher seawater temperature. There was a positive correlation between DIN and picoeukaryotes. In the middle and the bottom layer, the concentration of DIN gradually increased with depth, N/P also gradually approached Redfield ratio, and the negative correlation with picophytoplankton gradually increased, while temperature decreased with depth, and the positive correlation with picophytoplankton gradually increased. Combined with the VSI, we performed a comprehensive analysis of the photic zone water column. Certainly, we observed that VSI significantly influenced the distribution of picophytoplankton populations along the cruise track (Fig. 9d–e & 10d). Fig. 10d showed that *Synechococcus* was positively correlated with DIN, N/P and VSI (Figs. 9d & 10d), it was negatively with temperature and salinity; the results of *Prochlorococcus* and *Synechococcus* were opposite. There was a significant negative correlation between *Prochlorococcus* and VSI (Figs. 9e & 10d). Unfortunately, the direct effect of water column stratification on picoeukaryotes was not found in this study (Figs. 9f & 10d).

4. Discussion

4.1. Abundance of picophytoplankton in the EIO and comparison with existing literature

We compared the results in this study with other studies on picophytoplankton communities in the Indian Ocean (Table 2). Mitbavkar et al. (2020) reported that the *Synechococcus* group is dominant throughout most of the year in the Bay of Bengal, with respect to both abundance and biomass. The abundance and carbon biomass of *Synechococcus* are higher in the nutrient-rich coastal regions. Although the distribution pattern of picoeukaryotes is similar to that of *Synechococcus*, the numbers and biomass of picoeukaryotes are relatively lower. The abundance and biomass of *Prochlorococcus* are higher in the open ocean regions of the central Bay of Bengal. Not et al. (2008) and Bemal et al. (2018) summarized that *Prochlorococcus* is dominant species in both the Arabian Sea and the Indian Ocean (from South Africa to Australia). Not et al. (2008) reported that *Prochlorococcus* is dominant in oligotrophic areas, while picoeukaryotes and *Synechococcus* usually co-vary and have a higher abundance at the more "coastal" nutrient-rich stations. This

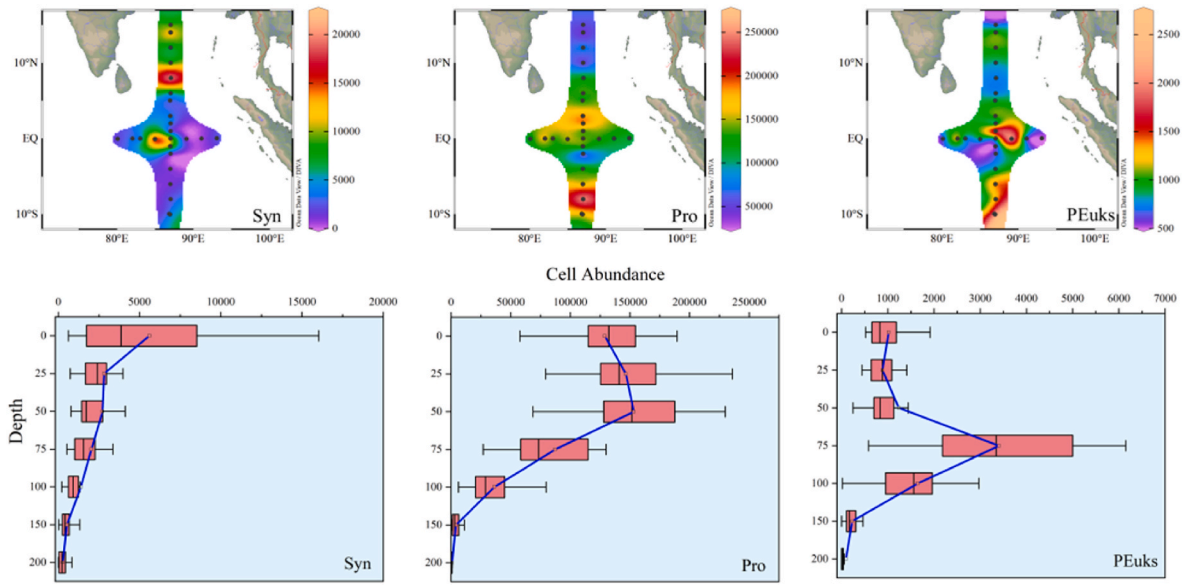

Fig. 6. Surface and vertical distribution of the abundance (cells/mL) of *Prochlorococcus* (*Pro*), *Synechococcus* (*Syn*), and picoeukaryotes (PEuks).

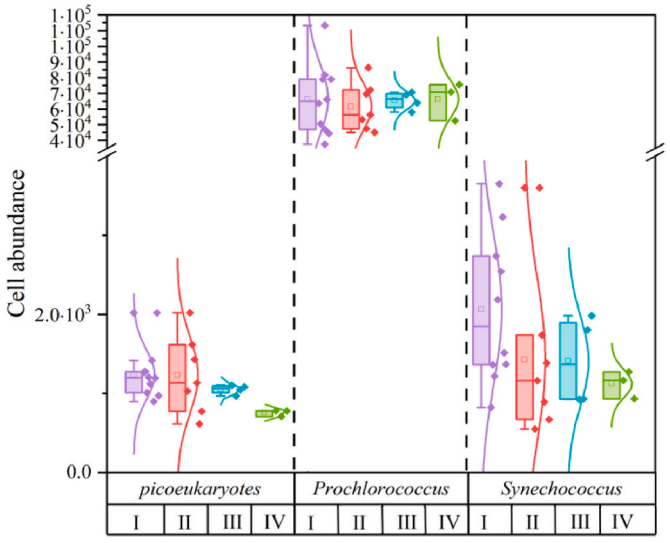

Fig. 7. Cellular abundance (cells/mL) of picophytoplankton (depth-weight averages) in the four groups.

was quite similar with the distribution pattern of *Synechococcus*, *Prochlorococcus* and picoeukaryotes in this study (Fig. 6).

The result of this study was also compared with data reported in other oceans adjacent to the EIO, such as the Pacific Ocean (Blanchot and Rodier, 1996), the South China Sea (Pan et al., 2006), and the Peninsular Malaysia (Amin et al., 2021) (Table 2). Blanchot and Rodier (1996) reported that *Prochlorococcus* numerically dominates the entire vertical column, irrespective of depth, in the western tropical Pacific Ocean during the El Niño in 1992. The authors further observed that the distribution of *Synechococcus* is light-dependent and their abundance increased remarkably when the conditions of light and nitrate concentrations are favorable. However, their abundance declined sharply when the level of light is around 1%. Picoeukaryotes and *Prochlorococcus* are less light-dependent than *Synechococcus* and can thrive in poorly lit layers (Llabrés, M., & Agustí, 2006). Paradoxically, the highest abundance of *Prochlorococcus* is observed in the nitrate-depleted layer, suggesting that the population of *Prochlorococcus* is weakly sensitive to nitrate depletion. Pan et al. (2006) determined the abundance of picophytoplankton groups in South China Sea and proved that the dynamic characteristics of picophytoplankton groups are markedly different between nearshore eutrophic regions and offshore oligotrophic waters. They observed that *Prochlorococcus* is more abundant in waters with relatively high temperatures and salinity than in nearshore areas. It was reported that the temperature is of great importance to the growth of *Synechococcus* and *Prochlorococcus*. Picoeukaryotes are less sensitive to alterations in hydrographic conditions and have greater adaptability

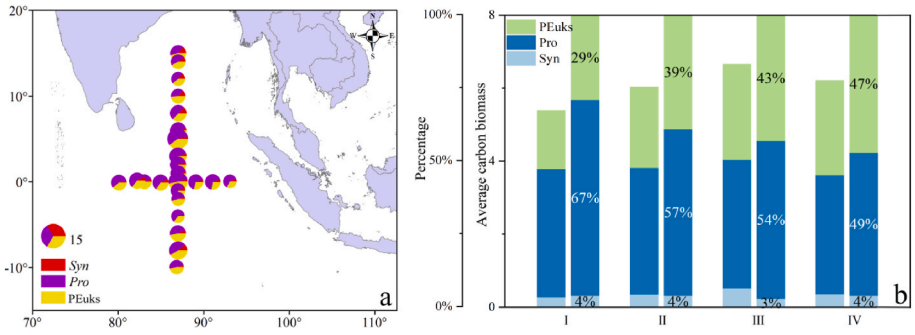

Fig. 8. (a) Distribution of the depth-weighted average carbon biomass (μg C/L) of picophytoplankton. (b) Average carbon biomass (μg C/L) and percentage of different groups. *Prochlorococcus* (*Pro*), *Synechococcus* (*Syn*), and picoeukaryotes (PEuks).

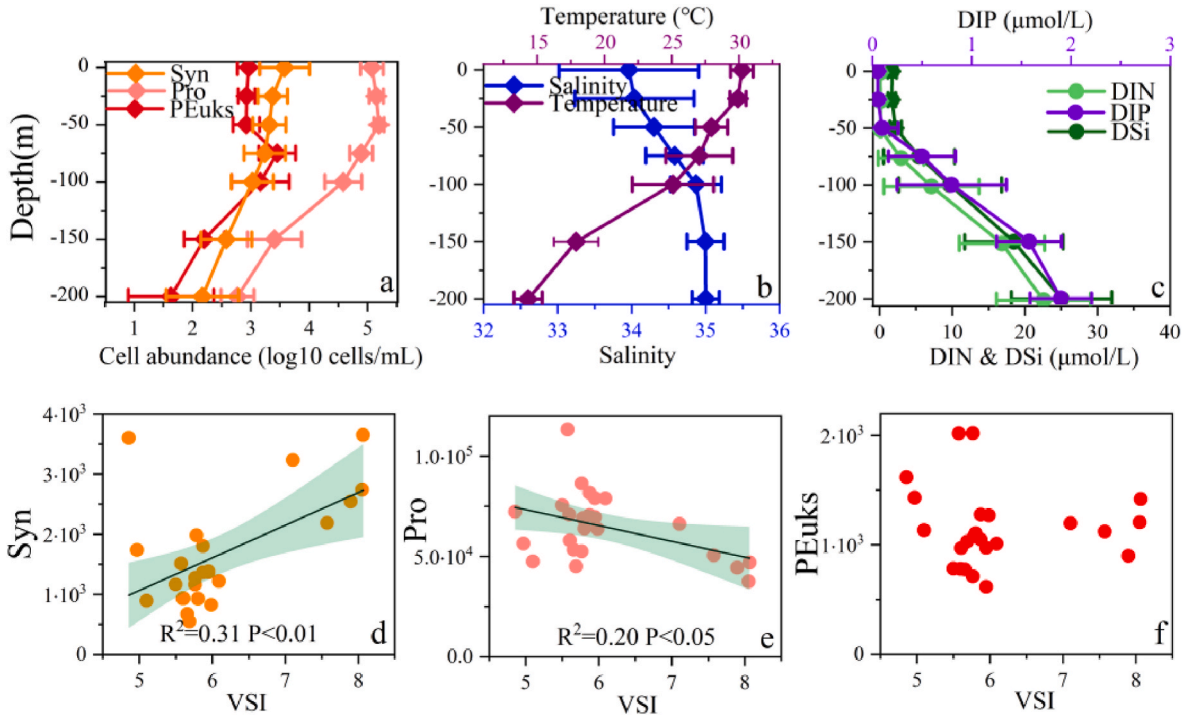

Fig. 9. (a–c) Average and standard error of the vertical distribution of picophytoplankton communities (log_{10} cells/mL) and environmental variables across 0–200 m. (d–f) Correlation between VSI and picophytoplankton abundance (cells/mL).

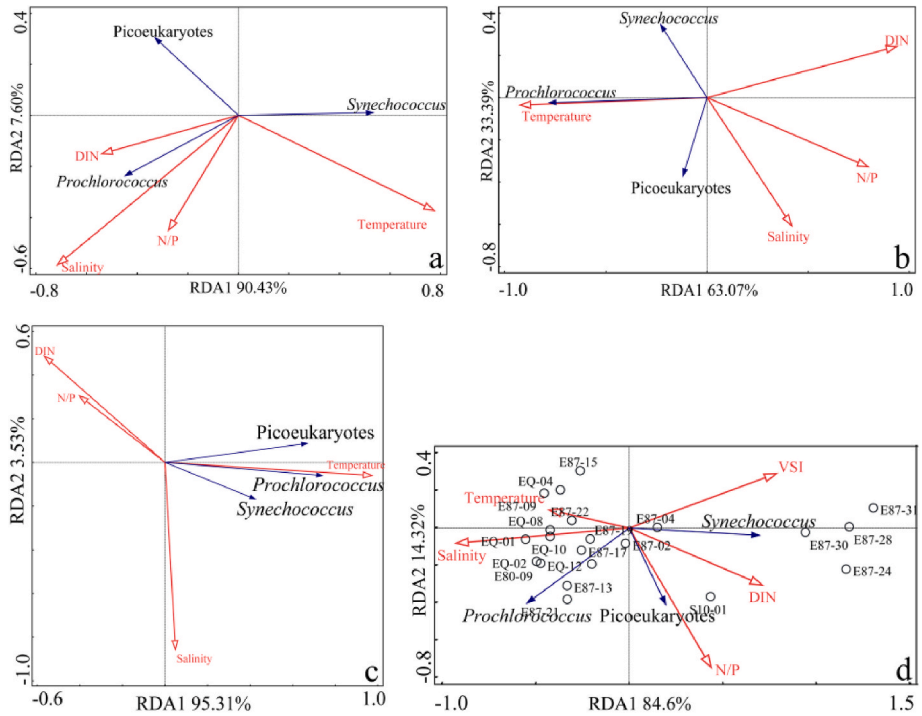

Fig. 10. Results obtained by RDA of picophytoplankton abundance and environmental factors in the (a) upper, (b) middle, and (c) bottom layer. (d) Stations and environmental parameters. The colored dots indicate the stations. The red vectors represent the environmental variables while the black vectors indicate the phytoplankton groups constrained in the RDA model. The length and direction of the vectors indicate the relative strength of the correlation with the RDA axe.

than *Synechococcus* and *Prochlorococcus*. Amin et al. (2021) investigated the distribution of picophytoplankton in the southeastern coast of Peninsular Malaysia. The results demonstrated that *Synechococcus* were predominant along the cruise track in the study area, comprising as much as 50% of the total picophytoplankton population. Analysis of the spatial distribution revealed that *Synechococcus* and picoeukaryotes are more dominant in coastal waters, while *Prochlorococcus* appeared to be more abundant in offshore waters.

From a comparative study of historical data, we concluded that the distribution pattern of our picophytoplankton communities were

Table 2
Statistical data pertaining to the abundance of *Synechococcus* (*Syn*), *Prochlorococcus* (*Pro*), and picoeukaryotes (PEuks) in the EIO and areas adjacent to the EIO ($\times 10^3$ cells/mL).

Study area	Picophytoplankton groups	Cell abundance	Average density	Reference
Bay of Bengal	*Syn*	Total	7.6	Mitbavkar et al., (2020)
	Pro	0.32–91.8	1.9	
	PEuks		1.2	
Arabian Sea	*Syn*	3.2–35.7	10.4	Bemal et al., (2018)
	Pro	10.3–38.5	18.9	
Indian Ocean	*Syn*	~47		Not et al., (2008)
	Pro	~250		
	PEuks	~12		
Pacific Ocean	*Syn*	~64		Blanchotet al. (1996)
	Pro	10~440		
	PEuks	~13		
South China Sea	*Syn*		16 ± 12.1	Pan et al., (2006)
	Pro		5.13 ± 2.18	
	PEuks		4.39 ± 1.45	
Peninsular Malaysia	*Syn*	2.13–13.65	7.36 ± 3.29	Amin et al., (2021)
	Pro	0.52–5.86	2.59 ± 1.42	
	PEuks	1.37–14.43	4.6 ± 3.33	
EIO	*Syn*	~20.2	2.21	Present study
	Pro	254.3	80.3	
	PEuks	6.1	1.19	

consistent with previous findings, and this pattern was not specific to the Indian Ocean only, but was also observed in the oligotrophic waters of the Pacific Ocean and South China Sea. Based on these findings we proved that *Prochlorococcus* dominates in open oligotrophic seas. Analysis of the spatial distribution revealed that the structure of the picophytoplankton community altered significantly from the coastal regions to the offshore ocean: *Synechococcus* abundance decreased gradually, while *Prochlorococcus* increased continuously; picoeukaryotes were more adaptable to the changes in the hydrological environment owing to their advanced structure, and the range of variation in abundance was small.

4.2. Relationships between picophytoplankton communities and environmental factors

Low nutrient concentration was the main limiting factor in the surface layer. *Synechococcus* had the highest abundances in the surface layer, indicating that the growth of *Synechococcus* was not constrained by low nutrient levels. Seawater temperature in the surface layer was high (>28 °C), combined with the strong solar ultraviolet radiation, inhibited the distribution and abundance of *Prochlorococcus* and picoeukaryotes. *Synechococcus* was not inhibited by light and had a positive correlation with temperature. In the middle and the bottom layer, where nutrient concentrations gradually reached highest level, nutrients were not the main factors inhibiting picophytoplankton growth. Seawater temperature gradually decreased (<20 °C) in the bottom layer, and picophytoplankton showed a significant positive correlation with temperature, with *Prochlorococcus* being more significantly influenced by water temperature. As can be seen from Fig. 10a and c, the temperature threshold acceptable for *Synechococcus* was large. Fig. 10d showed that the VSI had high values near the Bay of Bengal (E87-31, E87-30, E87-28, E87-26, E87-24), this region was affected by the diluted water, and the salinity gradient varied greatly. While in the open ocean, the VSI value was low. The correlation between *Prochlorococcus*, *Synechococcus* and VSI indicating that the relative abundance of *Synechococcus* was higher near the shore, while *Prochlorococcus* was concentrated in the open ocean.

The water temperature has pronounced effects on the productivity and community structure of picophytoplankton in open-ocean ecosystems and regulates their photophysiological responses (Schmittner et al., 2005). We have shown that *Synechococcus* prefers to be distributed in the warmer surface layers, while *Prochlorococcus* and picoeukaryotes are concentrated in the slightly cooler 50 m and 75 m layers. This finding was consistent with the study by Kulk et al. (2012) who concluded that picophytoplankton area benefit from the altered photophysiology at elevated temperatures, and these changes in photophysiology may alter the depth distribution of picophytoplankton to a certain extent. A previous study also suggested that the production rates and relative contribution of *Synechococcus* to the total phytoplanktonic biomass in temperate waters are dependent on the temperature (Agawin et al., 1998). Low temperatures induce alterations in the light-harvesting complexes of picoeukaryotes (Davison, 1991). The constraints on photosynthesis gradually decrease as the temperature increases, which results in increased Chl *a* synthesis and enhanced light capture (Stramski et al., 2002). Salinity, which was highly correlated with VSI, had been less studied for its effects on *Prochlorococcus* and picoeukaryotes, and only a few studies had been carried out on the response of *Synechococcus* to salinity changes (Rosales et al., 2005; Ludwig and Bryant, 2012; Kim et al., 2018). Salinity affected the growth, photosynthetic parameters, and nitrogenase activity of *Synechococcus*. When *Synechococcus* was exposed to high saline conditions, the amount of phycobiliprotein eventually changed during acclimation (Kim et al., 2018). It is yet to be addressed whether the changes of *Prochlorococcus* and picoeukaryotes is related to salinity.

Because strong stratification inhibits exchange between surface waters and those at depth, it limits introduction of nutrients from below, situated close to the mixed layer bottom, into the upper layers, intense forcing, such as that during cyclones, may be required to erode the stratification and inject nutrients into the euphotic zone to enhance biomass (Sarma et al., 2016). We found an N: P $< 16:1$ in the surface seawater indicated that the nitrogen content in the surface seawater was limited. Ocean warming has expanded the oligotrophic zones of the oceans, thereby worsening the situation (Roxy et al., 2016). For smaller phytoplankton, they have larger surface area-to-volume ratio, and could dominate in the oligotrophic regions (Marañon, 2014). The differences in response to nitrogen depletion and preferences for nitrate during growth of *Synechococcus* is the reason for its widespread distribution (Glibert et al., 1986; Collier et al., 1999). Interestingly, certain marine strains of *Synechococcus* are able to swim using a unique mechanism of motility (Waterbury et al., 1985). As an adaptive trait, motility may result in an enhanced ability to detect and take up nitrogen, and these motile strains are usually found in oligotrophic oceans where nitrogen levels are limited (Toledo and Palenik, 1999). *Prochlorococcus* is the smallest autotrophic photosynthetic phytoplankton (~0.6 μm), and the small size increase their advantage among other groups. *Prochlorococcus* is more successful in converting available nutrients into new cell biomass than coexisting eukaryotes, despite having equal access to nutrients. Friebele et al. (1978) observed that smaller cells have a faster uptake rates per cubic micrometre of biomass than larger cells, and inferred that small cells have a competitive advantage due to faster nutrient uptake rates. It is noteworthy that *Prochlorococcus* possesses a gene encoding a phosphate-binding protein that is expressed only under conditions of phosphate depletion, and may play a role in its adaptation to oligotrophy (Scanlan et al., 1997). These findings suggest that stratification significantly influences the input of nutrients to the euphotic layer, resulting in variations in picophytoplankton community structure.

4.3. Stratification and its impact on picophytoplankton community structure in the EIO

It has been reported that column stratification plays an important role in regulating the seasonal variation of phytoplankton community in

coastal waters (Cushing, 1989; Ruardij et al., 1997; Berger et al., 2010). According to the effect of physical environment on phytoplankton community structure, the classical Margalef's phytoplankton mandala separates various phytoplankton area based on the levels of turbulence and nutrient availability (Margalef, 1978). Although the conceptual model proposed by Margalef principally focuses on large phytoplankton, such as diatoms and dinoflagellates, several other studies have demonstrated that the water column stability could determine distribution patterns in the overall size structure of phytoplankton communities (Li, 2002; Bouman et al., 2003).

The values of VSI gradually increased with the increased of latitude, and were greatest near the Bay of Bengal (Fig. 2c). The Bay of Bengal was strongly density stratified due to large freshwater input from various rivers and heavy precipitation (Sarma et al., 2016). The data obtained here showed that the abundances of *Prochlorococcus* decreased with the VSI and were negatively correlated with the concentration of DIN. However, the abundances of *Synechococcus* showed the opposite trend, and the abundance of *Synechococcus* was higher under conditions of strong stratification. *Synechococcus* had a significant positive correlation with nutrient (Fig. 10d), so it had a higher abundance at the more "coastal" nutrient rich stations. While *Prochlorococcus* tended to dominate in nutrient-depleted regions. With the higher surface area to volume ratio than *Synechococcus* and picoeukaryotes, *Prochlorococcus* could better acquire nutrients compared with other picophytoplankton under nutrients limited conditions (Partensky and Garczarek, 2010), which could explain its prevalence in nutrient-depleted conditions.

The effect of water column stratification on the abundance of the picoeukaryotes group was not significant, indicating that picoeukaryotes are being better adapted to grow in physically dynamic environments than marine cyanobacteria. Moreover, picoeukaryotes exhibit high growth rates and account for a large fraction of primary production despite their lower abundance compared to prokaryotic picophytoplankton in oligotrophic oceans (Li, 1995; Worden et al., 2004; Jardillier et al., 2010; Mena et al., 2019). Fawcett et al. (2011) observed that picoeukaryotes have a large contribution to the downward export of biomass under stratified conditions during summer.

The EIO is an oligotrophic area with strong stratification, and the interannual variations of picophytoplankton abundance and Chl *a* concentration are not significant (Wei et al., 2019). Vertical stratification determines the distribution of environmental resources, including nutrients, resulting in the formation of contrasting environments, each with its own unique picophytoplankton community structures. The data obtained here showed that the numbers of *Prochlorococcus* decreased with the VSI and were negatively correlated with the concentration of DIN; however, the abundance of its sister taxon, *Synechococcus* showed the opposite trend (Fig. 10c). The results demonstrated that stratification and the vertical nutrient and temperature gradients are the main regulators of picophytoplankton community structure. Stratification causes sharp gradients in nutrient availability within the photic layer, above the thermocline. Below the thermocline, nutrient and light availability strongly modulate the composition of the picophytoplankton communities (Latasa et al., 2017). The components of the picophytoplankton community show differences in nutrient uptake efficiency and requirements (Agawin et al., 2004).

5. Conclusions

This study highlighted the vertical variability in the composition of picophytoplankton, which was caused by water column stratification in the EIO. The EIO is an oligotrophic ocean with a weak water exchange capacity owing to the thermocline and severe stratification in the water column. The picophytoplankton community structure mainly comprised of *Prochlorococcus* and *Synechococcus*, while the abundance of picoeukaryotes was low. The vertical distribution of picophytoplankton varied greatly, with the abundance of *Synechococcus* being high in the surface layer, but decreasing with increasing depth. *Prochlorococcus* and picoeukaryotes were concentrated in the middle layer. The potential influence of the physicochemical parameters on the abundance of picophytoplankton was analyzed by RDA, and how vertical stratification determined community structure of picophytoplankton via regulating nutrient structure in different layers was discussed. Overall, our results demonstrated that the community structure of picophytoplankton varied significantly in different depths in the EIO, which was primarily modulated by the vertical gradients in different environmental factors. The surface was characterized by high temperature and limited nutrient conditions, and supported the growth of *Synechococcus*. The middle layer was characterized by moderate temperature and nutrient concentration, and supported the growth of *Prochlorococcus* and picoeukaryotes. Below the thermocline, the picophytoplankton community was limited by low temperature. The results of this study confirmed that the relative importance of prokaryotic and eukaryotic picophytoplankton is intimately associated with the level of stratification of the upper ocean in the EIO. A deeper understanding of the ecological and physiological mechanisms underlying the shifts in the community structure of phytoplankton across gradients of vertical stability is fundamental for predicting the response of ocean systems to global climate change.

Author statement

Feng Wang: Formal analysis, Writing - Original Draft, Writing - Review & Editing. Shujin Guo: Writing - Original Draft, Writing - Review & Editing. Junhua Liang: Investigation. Xiaoxia Sun: Conceptualization, Writing - Review & Editing, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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