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RESEARCH

Distribution of Size-Fractionated Chlorophyll *a* and Picocyanobacteria in Coastal Waters of Northwest and Southeast Peninsular Malaysia

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Abstract
Sampling was at two coastal sites in Peninsular Malaysia; Yan (along Straits of Malacca during Northeast and inter-monsoon) and Kuala Rompin (KR, facing the South China Sea during Southwest monsoon). Despite temporal offsets in sampling, distinct spatial patterns of nutrients and picocyanobacteria were observed. Nutrient variability at Yan was influenced by freshwater discharge, and there was a predominance of NH_4 (51 ± 25% of dissolved inorganic nitrogen). At KR, conditions were more stable and less eutrophic, and $NO_2 + NO_3$ predominated (53 ± 25% of dissolved inorganic nitrogen). Although the > 20 µm Chl *a* fraction was predominant, only *Prochlorococcus* (from 70 to 1.2×10^4 cells mL^{-1}) correlated with the < 2 µm Chl *a* fraction at Yan ($R^2 = 0.221$, $p < 0.01$) whereas at KR, only *Synechococcus* (from 100 to 8.5×10^4 cells mL^{-1}) correlated with the < 2 µm Chl *a* fraction ($R^2 = 0.135$, $p < 0.05$). Redundancy Analysis (RDA) revealed that *Synechococcus* was associated with higher salinity and lower temperature, DO, PO_4 and NO_2+NO_3 while *Prochlorococcus* occupied a distinct niche along a separate RDA axis. This baseline study is a novel investigation into picocyanobacterial dynamics for Malaysia, and reveals their niche differentiation in tropical coastal systems.

Keywords Phytoplankton · Chlorophyll *a* · Size fractionation · Synechococcus · Prochlorococcus · Tropical coastal waters

Introduction

Phytoplankton form the foundation of nearly all aquatic food webs and play a crucial role in sustaining marine life, supporting growth, and maintaining overall ecosystem productivity (Koeller et al. 2009; Platt et al. 2009). Photosynthesis by phytoplankton is also one of the most important biological processes responsible for the drawdown of carbon dioxide from the atmosphere into the ocean (Passow and Carlson 2012). Therefore, it is important to understand the distribution of phytoplankton, and the environmental factors affecting their distribution.

Chlorophyll *a* (Chl *a*) is the main pigment responsible for photosynthesis in primary producers and is commonly used as a proxy for phytoplankton biomass (Roesler and Barnard 2013). Among the different size classes of phytoplankton, the picophytoplankton fraction (< 2 µm) contributes approximately 15% – 45% of marine primary productivity, accounting for about 24% of the global net primary productivity (Uitz et al. 2010). This fraction mainly consists of picocyanobacteria such as *Synechococcus* and *Prochlorococcus*.

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Both *Synechococcus* and *Prochlorococcus* tend to dominate in warm oligotrophic waters (Partensky et al. 1999; Scanlan and West 2002; Flombaum et al. 2013), and they occupy different habitats due to their different niches. Their distribution is regulated by light, temperature and nutrients (Crosbie and Furnas 2001; Agawin et al. 2002; Scanlan and West 2002; Morán et al. 2010; Kent et al. 2016).

Although Malaysian waters have one of the most diverse marine ecosystems (Morton and Blackmore 2001; Mazlan et al. 2005; Vo et al. 2013; Pauly and Liang 2020), little is known about their picocyanobacterial distribution. In waters surrounding Peninsular Malaysia, there are only a few studies on *Synechococcus* (e.g. Lee et al. 2013; Heng et al. 2017) and only one previous report on *Prochlorococcus* (Amin et al. 2021). Studies by Lee et al. (2013) and Heng et al. (2017) were restricted to nearshore waters, whereas the absence of concurrent nutrient measurements in Amin et al. (2021) limited our understanding of picocyanobacterial distribution.

Therefore in this study, we investigated the distribution of picocyanobacteria (*Synechococcus* and *Prochlorococcus*) via flow cytometry at both Southeast and Northwest of Peninsular Malaysia. Southeast of Peninsular Malaysia lies the shallow (average depth of 60 m, Chu et al. 1999) continental Sunda Shelf and faces the South China Sea, which is one of the largest semi-enclosed marginal seas (Wyrtki 1961). In contrast, Northwest of Peninsular Malaysia faces the Straits of Malacca which connects the Andaman Sea and the South China Sea, and is one of the most important international waterways. The Straits of Malacca are impacted by the rapid population and economic growth along the coastal areas of the surrounding countries e.g. Indonesia and Malaysia (Chua et al. 2000).

Due to logistical constraints and to avoid challenging sea conditions, sampling along the northwest coast was conducted between March and May, coinciding with the late Northeast Monsoon and the inter-monsoon transition. This period is typically marked by heavier rainfall (Chua et al. 2000; Hastenrath 2015). Subsequently, the southeast coast was surveyed between June and September, corresponding to the drier Southwest Monsoon. Although this sampling design introduced a temporal offset between the northwest and southeast sites, it allowed for an assessment of regionally and seasonally representative conditions of the picoplankton community in Malaysian coastal waters that remain poorly studied.

Other than picocyanobacteria, we also measured total Chl *a*, its different size fractions and concurrent physico-chemical variables including inorganic nutrient concentrations. In this study, we reported picocyanobacterial abundance in waters off Peninsular Malaysia, and identified possible environmental drivers for *Synechococcus* and *Prochlorococcus*. This study also provided novel baseline information on picocyanobacterial ecology in Malaysian coastal waters that remain poorly characterized.

Materials and Methods

Sampling

Sampling was carried out along transects at two coastal regions of Peninsular Malaysia: the Southeast coast off Kuala Rompin (2°49’ N, 103°31’ E to 2°49’ N, 103°42’ E) and the Northwest coast off Yan (5°49’ N, 100°13’ E to 5°49’ N, 100°08’ E) (Fig. 1). Sampling was carried out over three years (2015–2017). The Yan transect was sampled between March and May, and the Kuala Rompin transect between June and September, corresponding to the late Northeast/early inter-monsoon and the Southwest Monsoon periods, respectively (Syafrina et al. 2015). Each transect comprised five stations located approximately 5, 10, 15, 20 and 25 km from the shoreline (Table 1). In 2017, the Kuala Rompin transect was extended to include an additional offshore station at 30 km. Hereafter, Yan transects will be referred to as Yan whereas Kuala Rompin transects will be referred to as KR.

Environmental Variables

In situ seawater temperature and salinity were obtained via YSI-Pro30 conductivity meter (YSI, USA), while seawater samples were collected at different depths (i.e. surface, 5, 10, 15 and 20 m) with a 10-liter Niskin sampler. For dissolved oxygen (DO) concentration, sample was siphoned carefully into triplicate 60 mL dissolved oxygen (DO) bottles before fixing with manganese (II) chloride (3 M) and alkaline–iodide solution (60% w/v KI and 30% w/v KOH). DO determination was conducted via the Winkler titration method (Grasshoff et al. 1999). Samples for flow cytometry analysis were preserved with 1% final concentration of glutaraldehyde, and then frozen in liquid nitrogen, before transferring to a −80 °C ultra-low freezer (ESCO Lexicon-ULT, Singapore) (Vaulot et al. 1989). The remaining seawater samples were kept cold until processing.

The seawater sample was filtered through pre-combusted (500 °C for 3 h) glass fiber filters (GF/F). The filters were kept for chlorophyll *a* (Chl *a*) and total suspended solid (TSS) measurements whereas the filtrate was kept frozen (–20 °C) until dissolved inorganic nutrient analysis. TSS was determined as dry weight increase of the GF/F filter whereas for dissolved inorganic nutrients, the colorimetric method was used (Parsons et al. 1984). Ammonium (NH_4), nitrite + nitrate ($NO_2 + NO_3$) and silicate (SiO_4) analyses

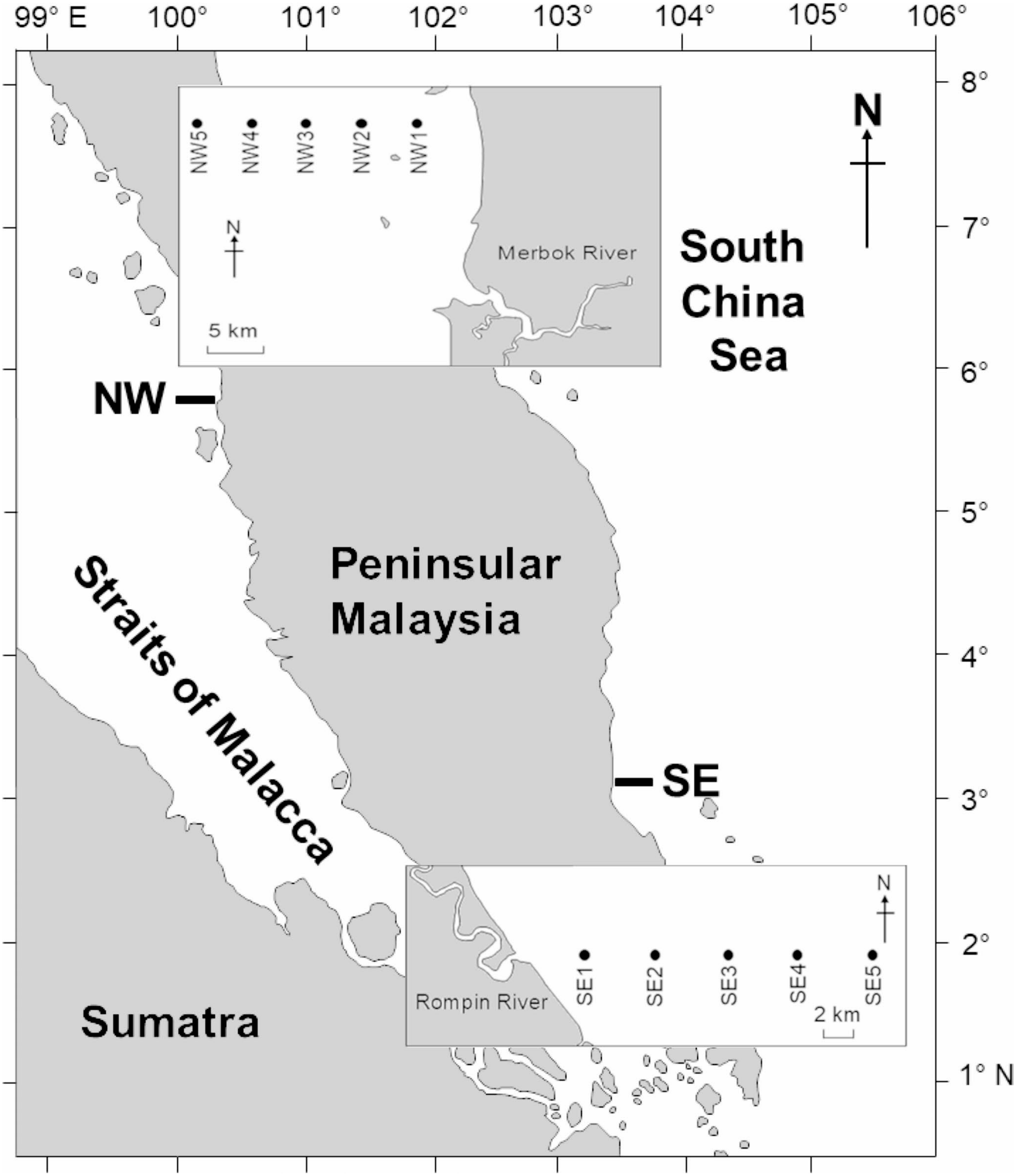

Fig. 1 Yan transect located northwest (NW) and KR transect located southeast of Peninsular Malaysia. Insets showing the location of Merbok River and Rompin River are also shown

were measured via a spectrophotometer (Hitachi U-1900, Japan) with a 50 mm optical path length glass cuvette while phosphate (PO_4) concentration was determined using the MAGIC method (Karl and Tien 1992).

Table 1 Geographic coordinates of sampling stations along the Yan and KR transects

Yan transect	5 km	10 km	15 km	20 km	25 km	
Coordinates	5°49’ N, 100°19’ E	5°49’ N, 100°16’ E	5°49’ N, 100°13’ E	5°49’ N, 100°11’ E	5°49’ N, 100°08’ E	
KR transect	**5 km**	**10 km**	**15 km**	**20 km**	**25 km**	**30 km**
Coordinates	2°49’ N, 103°31’ E	2°49’ N, 103°34’ E	2°49’ N, 103°37’ E	2°49’ N, 103°39’ E	2°49’ N, 103°42’ E	2°49’ N, 103°45’ E

Chlorophyll a Measurement

Chl *a* pigment retained on GF/F filter (nominal pore size of 0.7 µm) was extracted with 90% ice-cold acetone for about 16 h before measuring via a spectrofluorometer (Perkin Elmer LS-55, USA) at 440 nm excitation and 680 nm emission wavelengths (Parsons et al. 1984). Chl *a* measurement was calibrated using a commercial Chl *a* standard (Sigma-Aldrich, USA) (Lohrenz et al. 2003). In 2016 and 2017, Chl *a* size fractionation was also carried out on surface samples to obtain additional > 20 µm, 2–20 µm and < 2 µm fractions (Lim et al. 2021). The < 2 µm fraction was obtained by filtering seawater sample through 2 µm polycarbonate filter and then trapping Chl *a* pigment on a pre-combusted GF/F filter. Similarly, the < 20 µm fraction was obtained with a 20 µm polycarbonate filter before trapping on a GF/F filter. The difference between < 20 µm and < 2 µm were denoted as the 2–20 µm fraction whereas the difference between total Chl *a* and < 20 µm fraction were denoted as the > 20 µm fraction.

Flow Cytometry Determination of Picocyanobacteria

Samples for flow cytometry were analyzed within 14 days according to Marie et al. (2014). Flow cytometry analysis was carried out with a MACSQuant analyzer (Miltenyi Biotec, Germany). Prior to analysis, seawater sample was thawed to room temperature and the analyzer calibrated with MACSQuant calibration solution. Based on 1 and 2 µm size beads, the forward and side scatter acquisition signals were gated into two different populations i.e. 0.5 to 0.8 µm and 0.8 to 1.5 µm in size. The smaller size fraction with red fluorescence (Per-CP: 655 to 730 nm bandpass filter) signal represented *Prochlorococcus* population whereas the bigger size fraction with orange fluorescence signal (Pe-A: 585 nm bandpass filter) represented *Synechococcus* population (Christaki et al. 1999; Van den Engh et al. 2017). All acquisition was performed at a medium flow rate of 50 µL min^{-1}.

Statistical Analyses

All values were reported as mean ± standard deviation (SD) unless stated otherwise. Abundance for *Synechococcus* and *Prochlorococcus* was log-transformed before statistical analysis was carried out. Analysis of variance (ANOVA) was used to evaluate for differences among the sites within a transect, among the different years and among the different Chl *a* size fractions. If ANOVA was significant, a post-hoc Tukey’s test was conducted for pair-wise comparisons among the different groups. Correlation analysis was used to show relationships between the parameters measured, whereas data outside the range of mean ± 2 × SD were determined as outliers. The ordination method of Redundancy Analysis (RDA) was used to investigate possible physico-chemical drivers for log-transformed *Synechococcus* and *Prochlorococcus* distribution. All statistical tests were conducted with the software PAST version 4.03 (Hammer et al. 2001).

Results

Environmental Variables

Tables 2 and 3 show the physico-chemical variables measured at both Yan and KR, respectively. Seawater temperature at Yan and KR ranged from 28.4 to 32.2 °C and 28.2 to 31.8 °C, respectively. Coefficient of variation (CV) for temperature was calculated for each water column, and ranged from 0 to 2.9% at Yan and 0–3% at KR. At Yan, only two water column profiles (total profiles = 43) exhibited CV > 2.0% (2.5% on 19 Mar 2015 at 5 km distance and 2.9% on 9 Mar 2016 at 10 km distance) whereas at KR, only one profile (total profiles = 59) exceeded 2.0% (i.e., 3% on 14 Jun 2015 at 5 km distance). The water columns exhibited minimal vertical temperature variation.

For salinity, it ranged 25.3 to 33.8 ppt at Yan and 27.0 to 34.0 ppt at KR. CV ranged from 0.2 to 3.8% at Yan where only six profiles exceeded 2.0%, half of which occurred at 5 km distance. At KR, CV ranged from 0 to 8.8%, of which six profiles > 2.0%, four of which were also at 5 km distance. This suggested episodic freshwater inflow that could affect water column homogeneity, but was not frequently observed. TSS exhibited no consistent spatial variation at both Yan and KR, while DO increased away from shore at Yan (two-way ANOVA; $F = 3.16$, $df = 119$, $p < 0.05$). Among the dissolved inorganic nutrients measured, $NO_2 + NO_3$ and PO_4 at Yan decreased away from shore (two-way ANOVA; $NO_2 + NO_3$: $F = 2.70$, $df = 140$, $p < 0.05$; PO_4: $F = 5.12$, $df = 119$, $p < 0.001$), but showed no spatial variation at KR.

Table 2 Physico-chemical variables (mean ± SD) at Yan

Dates	Temperature (°C)	Salinity (ppt)	Dissolved oxygen (μM)	Total Suspended Solids (mg L^{-1})	NH_4 (μM)	NO_2+NO_3 (μM)	PO_4 (μM)	SiO_4 (μM)
19 Mar 2015 (n=18)	29.3 ± 0.6	25.5 ± 0.2	270 ± 20	108 ± 130	1.08 ± 1.12	0.39 ± 0.25	0.16 ± 0.06	0.49 ± 0.29
23 Apr 2015 (n=21)	31.1 ± 0.5	30.9 ± 0.8	260 ± 30	81 ± 9	0.69 ± 0.49	0.98 ± 1.15	0.22 ± 0.19	0.81 ± 0.51
20 May 2015 (n=24)	31.3 ± 0.4	30.9 ± 0.4	230 ± 20	89 ± 93	1.42 ± 0.83	0.47 ± 0.23	0.15 ± 0.10	0.96 ± 0.44
9 Mar 2016 (n=20)	29.7 ± 0.5	32.8 ± 0.5	240 ± 20	86 ± 7	3.85 ± 5.56	0.67 ± 0.48	0.38 ± 0.11	0.62 ± 0.23
20 Apr 2016 (n=24)	30.7 ± 0.6	33.4 ± 0.5	180 ± 30	76 ± 13	0.84 ± 1.11	1.07 ± 1.15	0.55 ± 0.30	0.55 ± 0.55
11 May 2016 (n=24)	31.4 ± 0.2	31.6 ± 0.3	230 ± 20	81 ± 43	3.12 ± 12.80	0.93 ± 0.37	0.29 ± 0.18	0.59 ± 0.57
8 Mar 2017 (n=23)	29.8 ± 0.2	29.7 ± 0.2	220 ± 20	49 ± 11	0.65 ± 0.49	0.74 ± 1.01	0.18 ± 0.17	0.63 ± 0.44
12 Apr 2017 (n=23)	29.7 ± 0.2	31.9 ± 0.4	230 ± 20	67 ± 11	0.73 ± 0.48	0.87 ± 0.74	0.21 ± 0.26	0.83 ± 0.49
24 May 2017 (n=23)	30.9 ± 0.3	30.8 ± 0.4	240 ± 20	57 ± 12	0.49 ± 0.68	0.95 ± 0.67	0.06 ± 0.06	0.88 ± 0.52

Table 3 Physico-chemical variables (mean ± SD) at KR

Dates	Temperature (°C)	Salinity (ppt)	Dissolved oxygen (μM)	Total Suspended Solids (mg L^{-1})	NH_4 (μM)	NO_2+NO_3 (μM)	PO_4 (μM)	SiO_4 (μM)
9 Jul 2015 (n=21)	29.2 ± 0.2	31.0 ± 0.7	200 ± 10	107 ± 129	0.40 ± 0.31	0.35 ± 0.34	0.12 ± 0.04	0.59 ± 0.35
13 Aug 2015 (n=23)	29.1 ± 0.2	33.4 ± 1.2	200 ± 10	94 ± 30	0.99 ± 0.63	0.82 ± 0.59	0.11 ± 0.03	0.94 ± 0.19
17 Sep 2015 (n=23)	28.9 ± 0.2	33.7 ± 0.2	210 ± 10	82 ± 15	1.15 ± 1.25	1.42 ± 0.67	0.07 ± 0.02	0.80 ± 0.25
7 Jun 2016 (n=25)	29.9 ± 0.4	32.2 ± 1.1	220 ± 10	100 ± 80	0.87 ± 0.37	0.56 ± 0.69	0.25 ± 0.22	0.40 ± 0.18
12 Jul 2016 (n=22)	30.2 ± 0.4	32.0 ± 0.1	240 ± 10	88 ± 15	0.96 ± 0.40	0.50 ± 0.18	0.13 ± 0.04	0.13 ± 0.08
10 Aug 2016 (n=22)	29.6 ± 0.3	31.8 ± 0.1	230 ± 10	79 ± 17	0.35 ± 0.30	0.67 ± 0.25	0.13 ± 0.03	0.20 ± 0.10
14 Sep 2016 (n=22)	29.2 ± 0.2	31.5 ± 0.3	220 ± 10	79 ± 9	1.69 ± 1.39	0.57 ± 0.15	0.13 ± 0.05	0.11 ± 0.06
14 Jun 2017 (n=23)	29.6 ± 0.6	32.3 ± 1.0	220 ± 20	61 ± 9	0.27 ± 0.28	0.59 ± 0.91	0.08 ± 0.03	0.83 ± 0.63
17 Jul 2017 (n=28)	29.3 ± 0.2	33.7 ± 0.6	220 ± 10	69 ± 16	0.28 ± 0.34	0.46 ± 0.33	0.04 ± 0.02	0.27 ± 0.22
15 Aug 2017 (n=25)	28.6 ± 0.2	30.9 ± 0.4	220 ± 20	88 ± 9	0.59 ± 0.44	0.25 ± 0.15	0.03 ± 0.02	0.45 ± 0.10
13 Sep 2017 (n=28)	29.7 ± 0.4	32.4 ± 0.3	210 ± 20	84 ± 10	0.20 ± 0.19	0.38 ± 0.13	0.05 ± 0.02	1.31 ± 0.39

Distribution of Chlorophyll a (Chl a)

Chl *a* concentration averaged 0.62±0.48 μg L^{-1} and 0.71±0.32 μg L^{-1} at Yan (Fig. 2) and KR (Fig. 3), respectively. Distribution of Chl *a* throughout the water column at both Yan and KR revealed a similar pattern of higher Chl *a* concentration nearshore and lower concentration offshore. It was also observed that nearshore bottom waters showed elevated Chl *a* concentration, suggesting the occurrence of benthic disturbance and resuspension.

Chl *a* size fractionation of surface water samples revealed that the >20 μm fraction had the highest Chl *a* concentration, and was a major fraction at both Yan (0.37±0.45 μg L^{-1}) and KR (0.45±0.33 μg L^{-1}) (Figs. 4 and 5). Chl *a* concentration in the 2–20 μm was 0.14±0.11 μg L^{-1} at Yan and 0.11±0.10 μg L^{-1} at KR, whereas the <2 μm fraction averaged 0.11±0.09 μg L^{-1} at Yan and 0.15±0.06 μg L^{-1} at KR. Post-hoc Tukey's test showed that relative to the >20 μm fraction, Chl *a* concentration in the 2–20 μm and <2 μm fractions were significantly lower at Yan (q>7.87, $p<0.001$) and KR (q>12.25, $p<0.001$). Interestingly, an overall increase in the <2 μm Chl *a* fraction was observed along the Yan transect in May 2017 which coincided with a significant decrease in salinity (Paired t-test: t=9.54, $p<0.001$), and at KR in Sep 2017 which coincided with a decrease in NH_4 (Paired t-test: t=2.50, $p<0.05$).

Distribution of Picocyanobacteria

Picocyanobacteria abundance at Yan and KR was 6.8 ± 6.5×10^3 cells mL^{-1} and 1.8 ± 1.9×10^4 cells mL^{-1}, respectively. At Yan, *Synechococcus* ranged from 170 to 3.3×10^4 cells mL^{-1} whereas at KR, *Synechococcus* ranged from 100 to 8.5×10^4 cells mL^{-1}. For *Prochlorococcus*, it ranged from 70 to 1.2×10^4 cells mL^{-1} at Yan, and ranged from 350 to 2.2×10^4 cells mL^{-1} at KR. Water column distribution of *Synechococcus* and *Prochlorococcus* at both Yan and KR did not exhibit temporal (monthly) and spatial (from the shoreline) variations. As water column distribution of *Synechococcus* and *Prochlorococcus* revealed no clear pattern, we calculated their depth integrated abundance at both Yan (Fig. 6) and KR (Fig. 7). All stations were integrated to 15 m depth, and we observed that *Prochlorococcus* predominated at Yan (24 out of 38 occasions) whereas *Synechococcus* predominated at KR (47 out of 59 occasions).

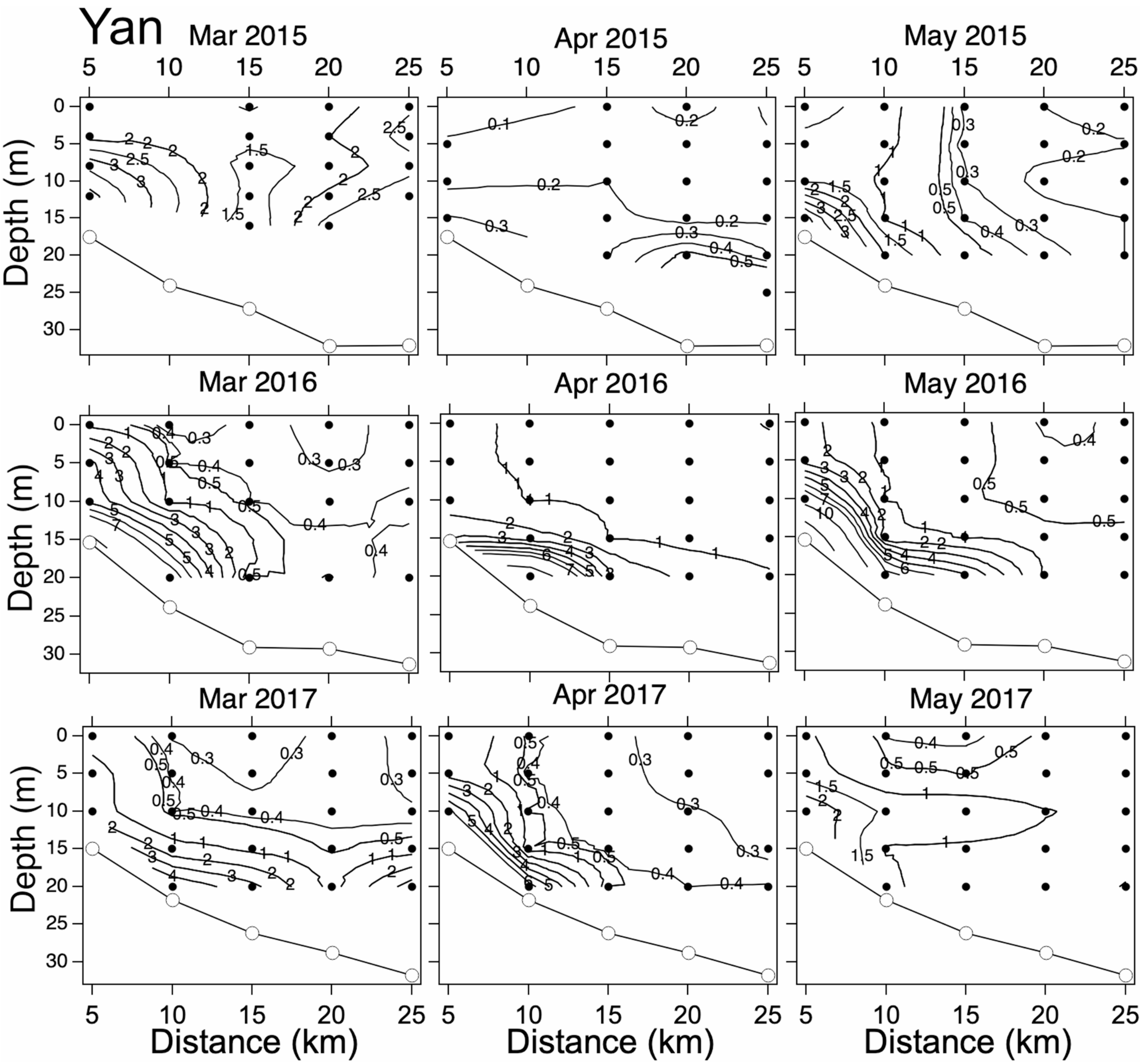

Fig. 2 Spatial distribution of Chl *a* concentration along the Yan during 2015–2017. Sampling points are filled circles. Depth at each station is indicated by an open circle

Discussion

Environmental Variables

Despite the temporal offset between the Yan and KR transects, this study provided representative snapshots of coastal hydrography during contrasting monsoonal periods around Peninsular Malaysia (Akhir and Chuen 2011). Seawater temperature was relatively high and typical for waters around Peninsular Malaysia (Shaari and Mustapha 2017). From the CVs of temperature and salinity, the waters studied were generally homogeneous, except when the occasional freshwater inflow was substantial. This is consistent with regional CTD observations made during similar monsoonal period (Roseli et al. 2022), where average CVs for temperature and salinity in both the Strait of Malacca and the southern South China Sea ranged from 0.3 to 5.4% and 0.4–3.1%, respectively. Roseli et al. (2022) also showed that the upper 20 m of the water column studied is typically homogeneous. DO levels were generally at healthy levels (DOE 2011), whereas TSS was low compared to nearshore waters (Lee and Bong 2008).

Salinity varied over a slightly wider range at Yan than KR, as there is increased river discharge from both Sumatra,

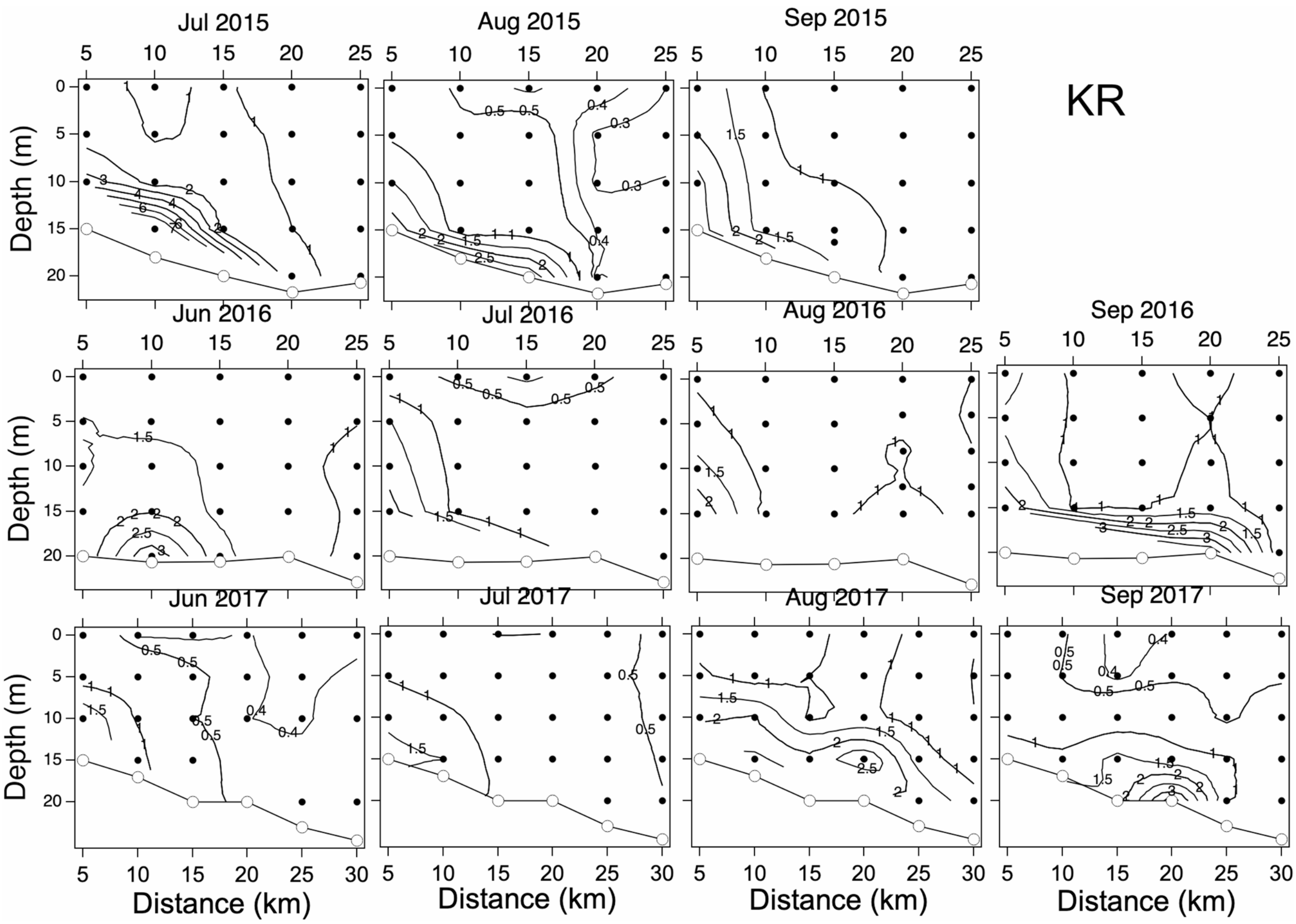

Fig. 3 Spatial distribution of Chl *a* concentration along the KR during 2015–2017. Sampling points are filled circles. Depth at each station is indicated by an open circle

Indonesia and the west coast of Peninsular Malaysia during the Northeast monsoon (November to March) (Chua et al. 2000). Located about 25 km south of Yan, the Merbok River has a discharge rate > 100 m^3 s^{-1} (Fatema et al. 2014), and during the Northeast monsoon, the current in the Straits of Malacca flows northward (Wibowo et al. 2022). As rivers are known to transport nutrients to estuaries and nearshore waters (Lim et al. 2018; Lee et al. 2020), contributions from rivers could explain the spatial variation of NO_2+NO_3 and PO_4 observed at Yan. Predominance of NH_4 (51 ± 25% of the dissolved inorganic nitrogen) at Yan, also affirms the anthropogenic impact on the Straits of Malacca (Chua et al. 2000) as NH_4 is known to predominate in polluted waters (Edwards et al. 2024).

At KR, dissolved inorganic nutrients measured were within the range of published report (Aziz et al. 2019). The Southeast coast of Peninsular Malaysia experiences less rainfall and drier conditions during Southwest monsoon (May to September) (Daryabor et al. 2014). Although Rompin River is located nearby, it has a low discharge rate during Southwest monsoon, about 30 to 90 m^3 s^{-1} (Akhtar et al. 2020), and this could explain the lack of spatial variation in the nutrients measured. NO_2+NO_3 predominated at KR, attributing up to 53 ± 25% of dissolved inorganic nitrogen, and this suggested cleaner and healthier waters at KR (Wang et al. 2018).

Distribution of Chlorophyll a (Chl a)

Chl *a* is commonly used as a proxy for phototrophic biomass (Roesler and Barnard 2013), and total Chl *a* measured in this study were within range of published data in this region (Lim et al. 2018; Amin et al. 2021). Chl *a* concentration was higher nearshore and at bottom waters, probably due to nearshore physical processes that stimulate phytoplankton growth e.g., sediment resuspension that releases nutrients into the overlying waters, or nutrient runoff from agriculture and urban areas that enhances nutrient availability (Siswanto and Tanaka 2014; Shaari and Mustapha 2017; Lim et al. 2021).

To better understand Chl *a* dynamics, size-fractionation of Chl *a* was carried out in 2016 and 2017 samplings.

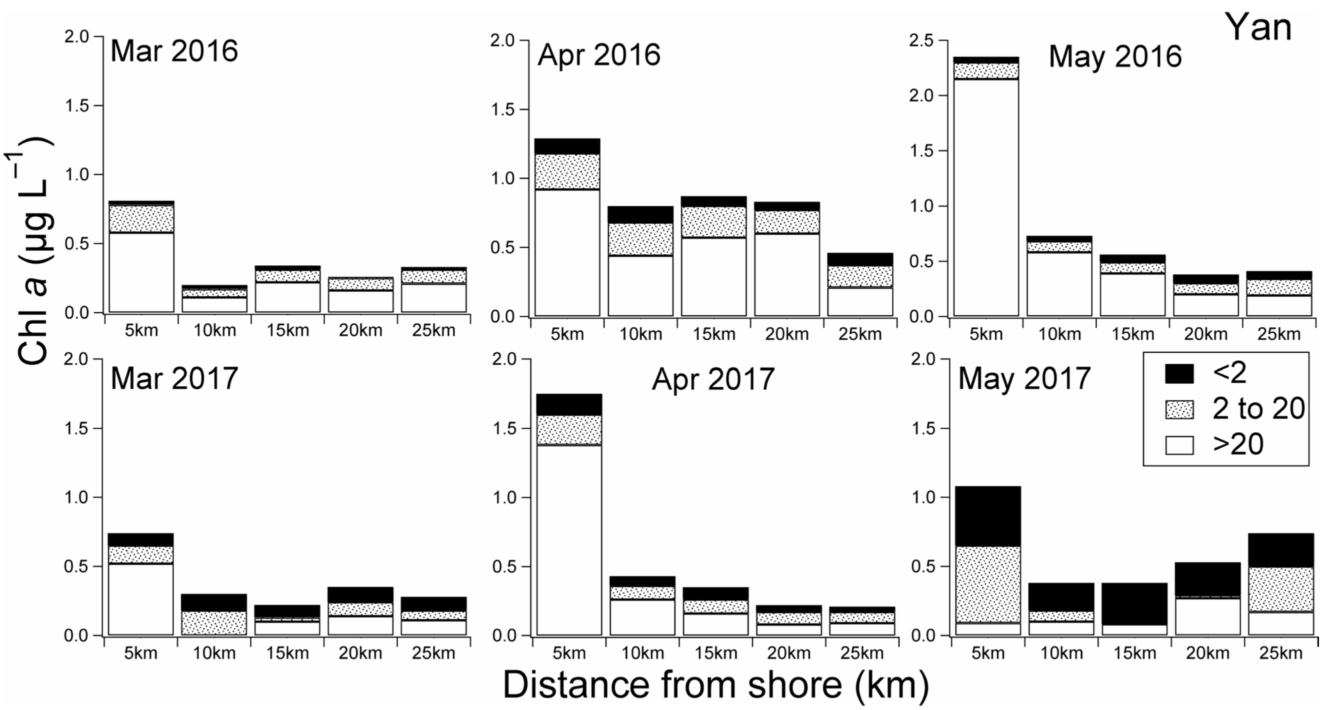

Fig. 4 Chl *a* size fractionation at Yan in 2016 and 2017

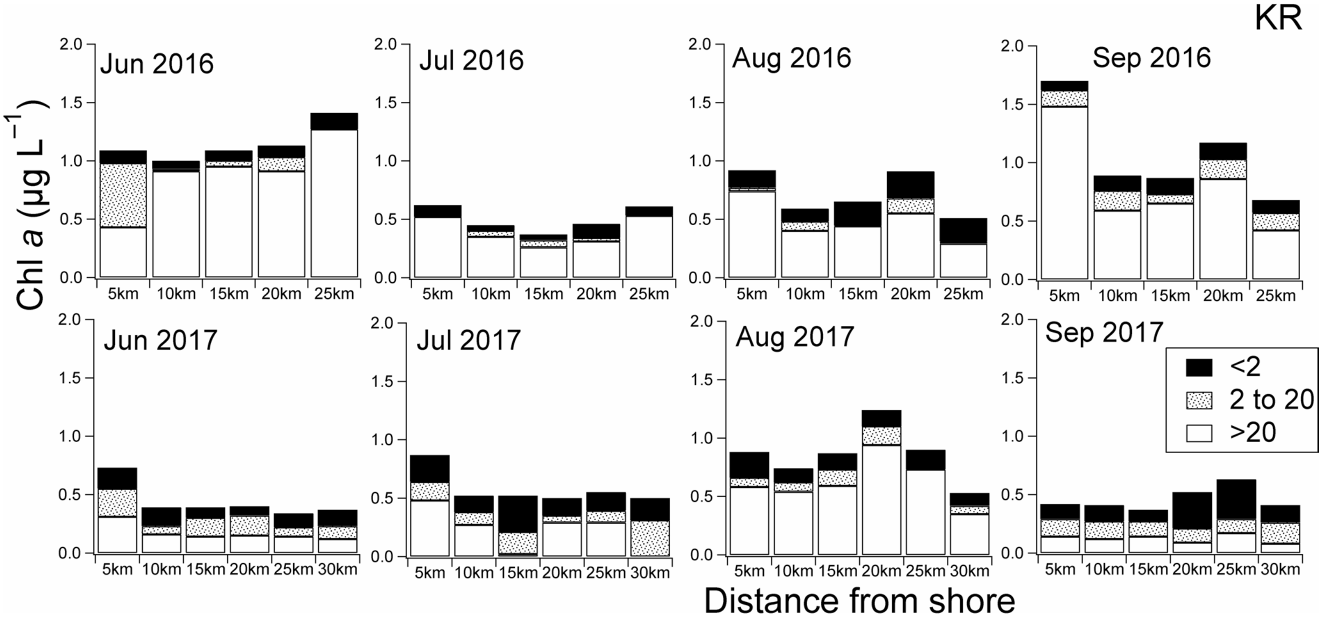

Fig. 5 Chl *a* size fractionation at KR in 2016 and 2017

Although size-fractionation was limited to surface waters, the relative homogeneity of the water column (Roseli et al. 2022) allowed reasonable extrapolation of the results to the upper layer. The > 20 µm fraction was the predominant fraction and made up 86 ± 6% of total Chl *a* at Yan and nearly all of the total Chl *a* at KR (97 ± 6%). Several studies have shown that diatoms or the > 20 µm fraction are predominant along the Straits of Malacca, and South China Sea (Lim and Lee 2017; Lim et al. 2021; Sohaimi et al. 2024). This was consistent with the inverse correlation observed between the > 20 µm fraction and SiO_4 (Table 4), suggesting silicate uptake during diatom growth. At KR, the > 20 µm fraction also correlated positively with NH_4 and PO_4, whereas at Yan, no significant correlations with inorganic nutrients were observed. These differences may reflect contrasting nutrient regimes between the two sites, with KR waters

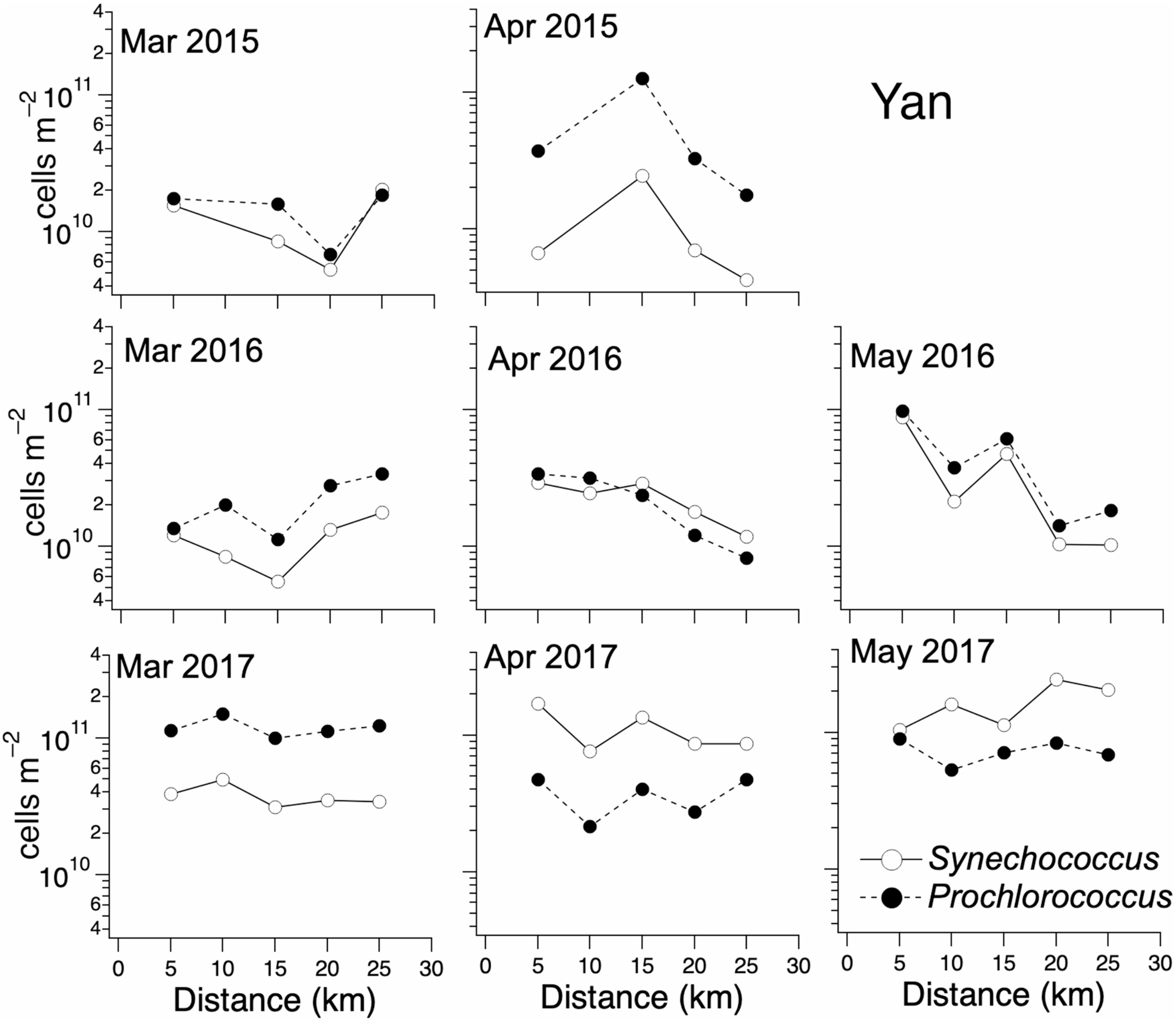

Fig. 6 Water column depth-integrated picocyanobacteria (*Synechococcus* and *Prochlorococcus*) abundance at Yan

being relatively more oligotrophic than Yan. The contrasting significance of DO and TSS between Yan and KR could also reflect site-specific physical processes that were not captured in this study.

At Yan, the 2–20 µm fraction was also important and made up to 23 ± 3% of total Chl *a*, but no significant correlations with environmental variables were detected. Although the 2–20 µm fraction was a minor component at KR, it was positively correlated with NO_2^-+NO_3^- and inversely correlated with salinity. This suggests that riverine outflow at KR reduced salinity while increasing NO_2^-+NO_3^- concentrations, thereby stimulating phytoplankton growth in the 2–20 µm fraction. The observed differences between Yan and KR could be attributed to variations in phytoplankton community composition, although further investigation is needed to confirm this. Although the 2–20 µm and <2 µm fractions were minor components relative to the >20 µm fraction (Lim et al. 2021), they could still be ecologically important for their contribution to primary productivity (Jang et al. 2018) and for their contribution to the resilience of the phytoplankton community especially with environmental change (Sanchez-Gallego et al. 2025).

At Yan, the <2 µm fraction was inversely correlated with salinity, TSS, PO_4 but positively correlated with SiO_4, while at KR, NH_4 and PO_4 showed significant inverse relationships with the <2 µm fraction (Table 4). These relationships were consistent with the observed increase in <2 µm fraction at Yan in May 2017 and at KR in Sep 2017. When compared with the relationships observed in the predominant > 20 µm fraction, correlations observed in the <2 µm

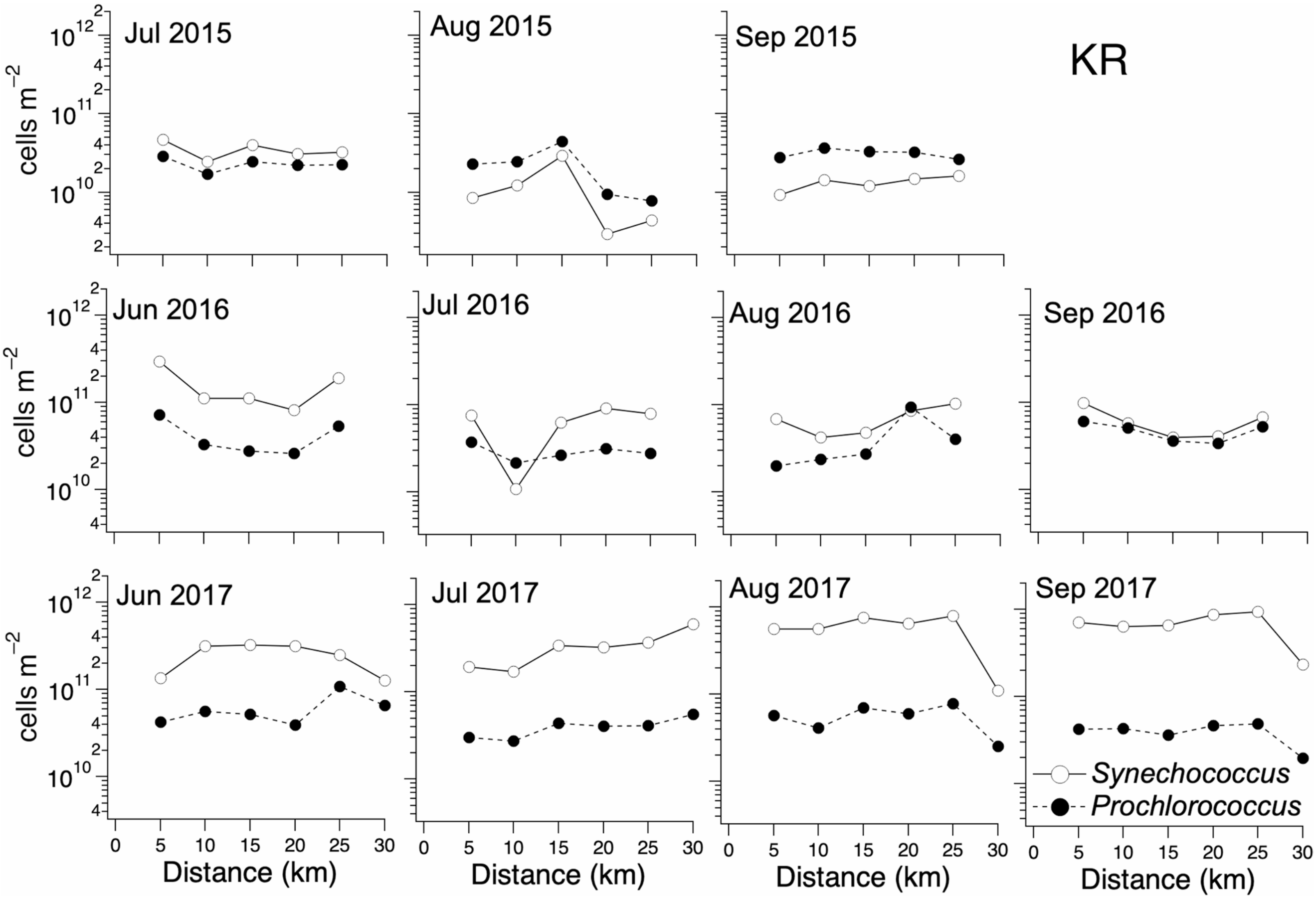

Fig. 7 Water column depth-integrated picocyanobacteria (*Synechococcus* and *Prochlorococcus*) abundance at KR

Table 4 Correlation indices (R^2) of size-fractionated Chl *a* concentration against selected environmental parameters. * indicates $p<0.05$, ** indicates $p<0.01$ whereas *** indicates $p<0.001$

Yan	Salinity (ppt)	DO (μM)	TSS (mg L^{-1})	PO_4 (μM)	SiO_4 (μM)
>20 μm	—	–0.200*	0.149*	—	–0.215**
2–20 μm	—	—	—	—	—
<2 μm	–0.249**	—	–0.209*	–0.175*	0.166*
KR	Salinity (ppt)	NH_4 (μM)	NO_2+NO_3 (μM)	PO_4 (μM)	SiO_4 (μM)
>20 μm	–0.095*	0.319***	—	0.177**	–0.113*
2–20 μm	–0.167**	—	0.382***	—	0.099*
<2 μm	—	–0.130*	—	–0.116*	—

fraction were probably a consequence of compensatory dynamics (Agawin et al. 2000) between the two size classes.

Distribution of Picocyanobacteria

Synechococcus measured at Yan was within the range reported by Lee et al. (2013) and Heng et al. (2017). However, the *Prochlorococcus* abundance at Yan is the first report for Straits of Malacca. For KR, *Synechococcus* and *Prochlorococcus* abundance measured were within the range reported by Amin et al. (2021). Depth integrated abundance at both Yan and KR suggested site-specific differences, whereas statistical testing via paired t-test showed that *Prochlorococcus* predominated at Yan (55 ± 22% of picocyanobacteria) (Paired t-test: $t=2.88$, $p<0.01$) during the late Northeast Monsoon and inter-monsoon transition, and *Synechococcus* predominated at KR (68 ± 23% of picocyanobacteria) (Paired t-test: $t=13.07$, $p<0.001$) during the Southwest Monsoon.

We also found that only *Prochlorococcus* correlated significantly with the <2 μm Chl *a* fraction at Yan ($R^2=0.221$, $p<0.01$) (Fig. 8) while at KR, only *Synechococcus* correlated with the <2 μm Chl *a* fraction ($R^2=0.135$, $p<0.05$). Although picoeukaryotes could also occupy the <2 μm Chl *a* fraction (Tamm et al. 2022), we did not measure them in this study. Amin et al. (2021) have shown that in the South China Sea, picoeukaryotes are minor components (about 6%) of the total picophytoplankton population. Therefore, their exclusion is unlikely to affect the conclusions for KR. However, we do not know the contribution of picoeukaryotes at Yan, and more studies should be carried out.

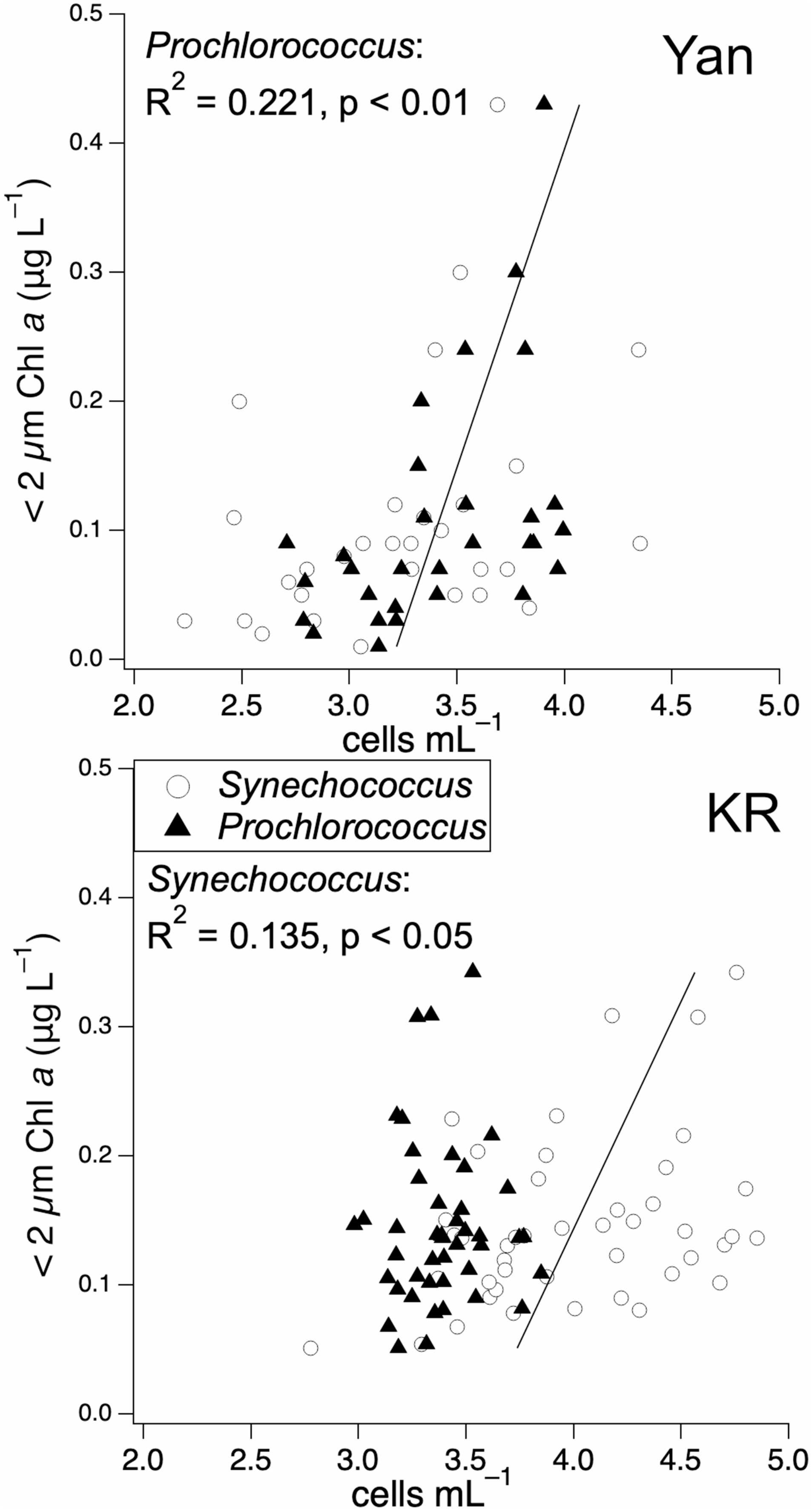

Fig. 8 Relationship of picocyanobacteria (*Synechococcus* and *Prochlorococcus*) against <2 μm Chl *a* concentration, with correlation statistics and regression line when significant

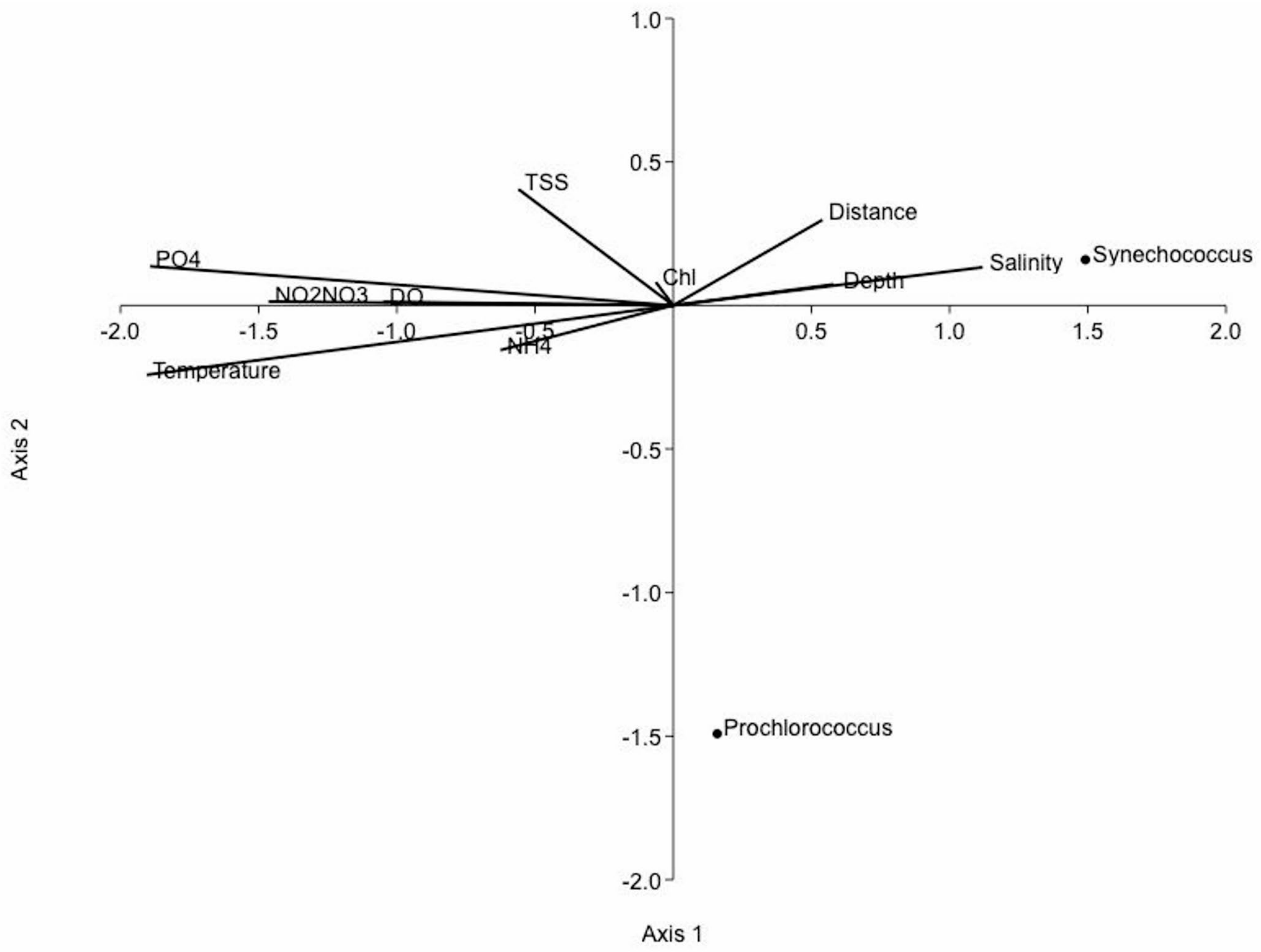

Fig. 9 *Synechococcus* and *Prochlorococcus* ordination via Redundancy Analysis Plot with environmental variables

Environmental Drivers for Picocyanobacteria

We investigated possible physico-chemical drivers for picocyanobacterial distribution via the ordination method of Redundancy Analysis (RDA) for both Yan and KR data. Although there are temporal offsets between Yan and KR sampling, the RDA was to identify key environmental drivers across coastal waters around Peninsular Malaysia. The RDA produced a cumulative explanatory of 13.95% where Axis 1 explicated 13.33% while Axis 2 explicated 0.62%. Despite the low explanatory power, the RDA model was significant via permutation test ($n = 999$) ($F = 6.920$, $p = 0.001$) (Fig. 9).

Synechococcus exhibited a strong affinity along Axis 1 (RDA coordinates: 0.99, 0.11), exhibiting a direct relationship (explanatory variable score >|0.100|) with salinity and inverse relationship to temperature, PO_4, NO_2+NO_3 and DO. This pattern suggested that *Synechococcus* thrived in colder, more saline and cleaner waters, typical of offshore waters away from freshwater influence. This concurred with studies that have shown *Synechococcus* adaptation to less eutrophic conditions, and is consistent with its known ecological niche in tropical marine systems (Moore et al. 2013; Fu et al. 2016). Meanwhile the inverse correlation with DO implied re-oxygenation events, possibly driven by freshwater inputs that also contribute nutrients, and do not favor *Synechococcus* proliferation (Cai et al. 2007).

Complementary correlation analyses between *Synechococcus* and *Prochlorococcus* abundances and physico-chemical parameters further supported these observations. Significant relationships ($R^2 > 0.100$) were only observed at KR, where *Synechococcus* abundance was inversely correlated with NH_4 ($R^2 = -0.107$, $p < 0.001$) and $NO_2^- + NO_3^-$ ($R^2 = -0.116$, $p < 0.001$). These negative associations reinforce the interpretation that elevated inorganic nutrient concentrations may stimulate the growth of larger phytoplankton such as diatoms, thereby reducing the competitive advantage of *Synechococcus*, which typically flourishes under nutrient-depleted conditions (Moore et al. 2013; Fu et al. 2016).

In contrast, *Prochlorococcus* was nearer to Axis 2 (RDA coordinates: 0.11, −0.99), and clearly separated from *Synechococcus* in the RDA plot. This reflected microbial niche differentiation (Flombaum et al. 2013). However, the relatively low explanatory power of Axis 2 suggested that the RDA analysis was missing additional factors for *Prochlorococcus* such as light quality, micronutrients (e.g. iron) or top-down pressure (e.g. grazing by protozoa or lysis by phages) (Partensky et al. 1999; Denis et al. 2000; Coleman and Chisholm 2007; Flombaum et al. 2013).

Our findings demonstrated that subtle shifts in temperature, salinity and nutrient availability can profoundly restructure picocyanobacterial communities, emphasizing the sensitivity of tropical marine ecosystems to environmental variability, and demonstrate that predominance is shaped not by a single driver but by a combination of temperature, salinity and nutrients. Future work incorporating year-round sampling at both sites would strengthen the resolution of spatial versus seasonal effects. Nonetheless, this present study provides a useful first comparison of picocyanobacteria and chlorophyll partitioning across two monsoon-influenced coastal systems of Peninsular Malaysia.

Conclusion

This study is the first comparative effort to examine picocyanobacterial distribution, Chl *a* size partitioning, and associated environmental variables across two monsoon-influenced coastal systems of Peninsular Malaysia. Despite temporal offsets between sampling at Yan (Straits of Malacca) and Kuala Rompin (South China Sea), our findings revealed clear spatial patterns. *Prochlorococcus* predominated at Yan during the late Northeast Monsoon and inter-monsoon transition, whereas *Synechococcus* predominated at KR during the Southwest Monsoon. RDA revealed that *Synechococcus* showed positive relationship with salinity and inverse relationships with temperature, DO, PO_4, and NO_2+NO_3, suggesting preference for cooler, more saline and less eutrophic waters. In contrast, *Prochlorococcus* aligned along a separate axis, suggesting the influence of other unmeasured variables such as micronutrients or top-down pressure.

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Author Contributions JH Lim: Formal analysis, Investigation, Data Curation, Writing Original Draft. CW Lee, CW Bong: Conceptualization, Validation, Resources, Data curation, Writing, Review and Editing, Supervision, Project administration, Funding acquisition. YY Wong: Sampling, Formal analysis, Project administration. X Pan, K Narayanan, EUH Sim, TY Ho, GTF Wong: Reviewing and Editing, Data Curation, Validation.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Ethics approval No ethical approval is required.

Competing interests The authors declare no competing interests.

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