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Temporal shifts in phytoplankton communities in Cam Ranh Bay

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ABSTRACT

Phytoplankton communities can change rapidly in response to shifting environmental conditions. A dataset of phytoplankton and environmental factors in Cam Ranh Bay was analyzed to assess the temporal shifts in phytoplankton communities over both short-term (days, weeks) and long-term (seasons) periods. In this Bay, changes in phytoplankton compositions were insignificant found in short-term, while there was no clear pattern in abundance and biomass variation. Seasonally, significant changes in dominant phytoplankton were also observed, with dinoflagellates and diatoms predominating in the dry and wet seasons, respectively. Diatoms abundance and biomass were higher during the wet season, whereas dinoflagellate abundance was higher in the dry season. The dominant analysis revealed that some species prevailing throughout sampling periods, including *Chaetoceros* spp., *Bacteriastrum* sp., *Coscinodiscus* sp., *Thalassionema frauenfeldii*, *Pleurosigma* sp., and *Protoperidinium* spp. The pattern was clear seasonally, such as *Chaetoceros diversus*, *Dictyocha fibula*, and *Tripos setaceus* dominant in the dry season, and *Guinardia striata*, *Leptocylindrus danicus*, and *Chaetoceros compressus* in the wet season. Multidimensional scaling statistical analysis (NMDS) indicated both nitrate and nitrite impact on a diatom group, Bacillariophyceae, during the dry season, while other diatom groups, Mediophyceae, with phosphate and ammonium and Coscinodiscophyceae with temperature. In the wet season, Bacillariophyceae were closely related to nitrite, nitrate, and phosphate, whereas Mediophyceae were associated with ammonium and DIN. The density of Dinophyceae was inversely related to silicate, salinity, and fluorescence. Our results provide insights into how and which types of nutrients and temperature and salinity variations, influence the rapid changes in phytoplankton communities within coastal tropical embayment.

Keywords: Temporal shift of phytoplankton, SIMPER analysis, Cam Ranh Bay.

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INTRODUCTION

Phytoplankton communities are vital to aquatic ecosystems, and crucial in the biogeochemical cycles and food webs. Understanding how these communities respond to environmental changes is essential for predicting ecosystem health and resilience. While controlled experimental studies offer valuable insights into the short-term responses of phytoplankton to specific environmental factors, extrapolating these findings to understand long-term and ecosystem-scale dynamics remains challenging [1]. Temporal variability in phytoplankton community structure and function is critical for aquatic system metabolism [2]. Aquatic environments exhibit high temporal variability, with frequent shifts in species composition and relative abundance driven by interactions among physical, chemical, and biological variables [3].

Environmental perturbations, such as turbulence and variability in water column stability, significantly influence phytoplankton community structure, affecting diversity, dominance, and biomass [4–6]. Physical instability in the water column is typically regarded as a primary driver of changes in species composition [3, 6]. Various biotic and abiotic factors, including water mixing, light availability, temperature, nutrients, and interactions with heterotrophic microorganisms, pathogens, parasites, and herbivores, shape phytoplankton communities [7–9].

Cam Ranh Bay, located in Khanh Hoa Province, Viet Nam, is one of the deep-water shelters in Viet Nam. The bay supports intensive aquaculture, hosting a variety of marine organisms. In the shallower areas, shrimp and macroalgae are dominant, while lobster cages are in the deeper regions, particularly near Binh Ba Island. Despite its ecological importance, there has been a lack of comprehensive studies on the phytoplankton communities in Cam Ranh Bay. This study aims to assess the shifts in phytoplankton community structure over short-term (days, weeks) and long-term (seasonal) periods, thereby enhancing our understanding of phytoplankton dynamics and the environmental factors driving these changes in this key marine ecosystem.

METHODS AND MATERIALS

Time and sampling sites

Samples were collected on days 1–3, day 5, day 10, day 15, day 20, and day 30 during June (dry season) and on days 1–3, day 5, day 20, and day 30 during November (wet season) in Cam Ranh Bay (Fig. 1) at two-four depths (surface, middle and near bottom layers). Additionally, sampling at an anchored station (St. 3) was conducted every three hours over 24-hours on day 20. Sixty qualitative and 187 quantitative phytoplankton samples collected.

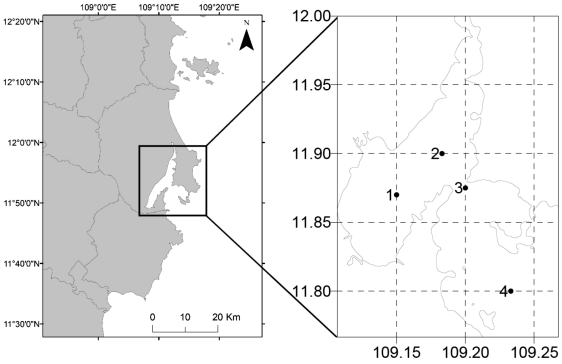

Figure 1. Maps showing studied areas (left) and sampling stations in Cam Ranh Bay (right)

Sampling and analysis methods

Qualitative samples

Qualitative phytoplankton samples were collected using a plankton net with a 25 µm mesh size, slow-towed vertically from the bottom to the surface. Samples were then fixed with 5% formalin and stored in the dark for later analysis in the laboratory. Species identification and cell-size measurement were conducted under a light microscope (Leica LDMB, Germany). The Calcofluor White M2R method [10] was employed to identify armored dinoflagellates, and observations were made using an epifluorescence microscope (Leica LDMB, Germany).

The identification of the phytoplankton species was based on published descriptions from a range of authoritative sources, including

[11–21]. The scientific names and ranks of the species were updated as in Guiry & Guiry [22].

Quantitative samples

Quantitative water samples (1 L) were collected using a 5-liter Niskin bottle at each station's surface and bottom layers. The samples were stored in PET plastic bottles and fixed with a neutral Lugol solution. To concentrate the samples, a series of settling steps were performed over 48 hours, reducing the volume from 1,000 mL to a final 3 mL using graded cylinders. A 1000 µL aliquot of each concentrated sample was then loaded onto a Sedgwick-Rafter counting chamber for phytoplankton cell enumeration, following the UNESCO method [23]. One drop of 0.5 mg/mL of Calcofluor was added to each sample to identify and enumerate of dinoflagellates [16].

Estimating diversity of phytoplankton community

PRIMER software version 6 (PRIMER-E Ltd, Plymouth, United Kingdom) was used to calculate diversity indices and perform community analysis. The following equations were employed in these analyses:

Bray-Curtis similarity index [24]:

$$BC_{ij} = 1 - \frac{2C_{ij}}{S_i + S_j}$$

where: i and *j*: are the two sites; n_i: cell number of species counted on site *I*; *S*: a total of the number of species in a sample; C_{ij}: a total of similar species found in both sites; S_i and S_j: the number of species counted on each site.

A master list of all species was recorded in the study waters. All taxa were hierarchically arranged into species, genera, families, orders, classes, and phylum. This hierarchical arrangement was used to determine the indices below:

Average taxonomic distinctness (AvTD) (Δ^+) [25, 26]:

$$\Delta^+ = \frac{\sum\sum_{i<j} \omega_{ij}}{s(s-1)/2}$$

Variation in taxonomic distinctness (VarTD) Λ^+ [25, 26]:

$$\Lambda^+ = \frac{\sum\sum_{i\neq j} \left(\omega_{ij} - \varpi\right)^2}{s(s-1)/2}$$

where: s is the number of species present; ω_{ij} is the 'distinctness weight' given to the path length linking species *i* and *j* in the taxonomy.

Water environmental parameters

In this study, water environmental parameters were collected in June and November 2006 from 187 samples in Cam Ranh Bay. All samples were maintained in the dark at a cool temperature (4°C) before transportation to the Department of Hydro-Geochemistry, Institute of Oceanography, for analysis. The parameters measured included salinity, total suspended solids (TSS), phosphate (PO_4^{3-}), nitrite (NO_2^-), nitrate (NO_3^{2-}), ammonia ($NH_{3,4}$), silicate (SiO_4^{4-}) were measured following standard methods [27] - Total Suspended Solids: dried at 103–105°C (2540-D); Phosphate: Ascorbic Acid Method (4500-P); Nitrate: Cadmium Reduction Method (4500-NO_3); Nitrite: Colorimetric Method (4500-NO_2); Ammonia: Phenate Method (4500-NH_3); Silicate: Molybdosilicate Method (4500-SiO_2).

Data analysis

Phytoplankton data were extracted from the PLANKTONSYS database (BioConsult A/S). Excel Microsoft Office 365 was used for data treatment and plotting, while R v4.4.2/RStudio was employed for drawing graphs and performing basic statistical analyses. The R packages "pgirmess" [28], ggplot2 [29], vegan [30], "coin" [31], and "ggrepel" [32] were used.

Similarity percentage analysis (SIMPER) was conducted to identify key species in various sampling areas or groups based on the Bray-Curtis similarity index. This analysis involved pairwise comparisons of sampling unit groupss, determining each species' average contributions to the overall Bray-Curtis similarity (dissimilarity). Non-metric multidimensional scaling (NMDS) assessed similarity among

phytoplankton assemblages based on abundance, biomass, and environmental data. Welch t-tests and Fisher-Pitman permutation tests were performed for parametric and non-parametric data to determine significant seasonal differences, respectively.

Using PRIMER software v.6 (PRIMER-E Ltd, Plymouth, United Kingdom), Funnel plot analysis was employed to identify sites with Δ^+ and Λ^+ values. This analysis utilized 1000 simulation subsamples to calculate expected Δ^+ and Λ^+ values from a master list of phytoplankton, creating 95% probability intervals to evaluate the uncertainty based on differences between observed and expected values against species numbers [25, 26].

RESULTS

Environmental characteristics

Environmental factors exhibited some differences between the dry and wet seasons. Water was warmer and less salty in the wet season ($p < 0.01$). Fluorescence and conductivity levels were insignificant between the two seasons. Nutrient concentrations showed varied trends: nitrite, nitrate, and dissolved inorganic nitrogen (DIN) were significantly higher in the dry season, whereas phosphate and silicate were just elevated in the wet season. The ammonium levels remained consistent in both seasons (Fisher-Pitman permutation test) (Table 1).

Composition and abundance of phytoplankton community

This study recorded 245 taxa with 221 taxa in the dry season and 202 taxa in the wet season belonging to 8 classes: Bacillariophyceae (38 taxa - dry season, 31 taxa - wet season, 40 taxa - total), Coscinodiscophyceae (31, 31, 35), Mediophyceae (60, 62, 71), Dinophyceae (85, 72, 92), Noctilucophyceae (1, 1, 1), Cyanophyceae (3, 3, 3), Dictyochophyceae (2, 2, 2), Thecofilosea (1, 0, 1). Generally, the number of species varied less during the sampling days in either the dry or wet seasons (Table 2).

Short-term variations in the phytoplankton community's density and biomass were observed on the specific sampling days. The abundance and biomass of phytoplankton groups changes in days and weeks, more clearly at stations CR1, CR2 and CR3 (Figs. 2, 3). These variations exhibited an insignificant pattern and were provided in Appendix 1.

During the dry season, phytoplankton abundance generally remained below 30×10^3 cells/L, except at days 10 (Sta CR1) and 30 (St CR2-CR4). The main compositions of phytoplankton were the classes Dinophyceae, Mediophyceae, Coscinodiscophyceae, and Bacillariophyceae (Fig. 2). At station CR1, located within Cam Ranh Bay, abundance peaked at over 150×10^3 cells/L, the highest among all sampling stations, with Dinophyceae being dominant on the 10th day. Stations CR2, CR3, and CR4 peaked on the 30th day with Dinophyceae, and Mediophyceae predominating at CR2 and CR3, while Bacillariophyceae was the predominant group at CR4. The biomass variations at stations CR1, CR3, and CR4 followed similar patterns to their respective densities. Station CR1 showed the highest value on the 10th day, mainly due to the high abundance of Dinophyceae. At station CR3, Dinophyceae dominated from the 1st to the 20th day, succeeded by Mediophyceae on the 30th day. In station CR4, the biomass was mainly derived from Dinophyceae, Mediophyceae, and Bacillariophyceae, showing predominance on the 30th day, with a minor proportion of Cyanobacteria. For station CR2, the biomass peaked on the 3rd day with the dominant species of Dinophyceae and Coscinodiscophyceae, and the latter group shifted to Mediophyceae on the 30th day (Fig. 3).

During the wet season, diatoms (classes Coscinodiscophyceae, Mediophyceae, and Bacillariophyceae) were predominant in abundance. Stations CR1, CR2, and CR3 showed apparent shifts in groups and fluctuating abundances. In contrast, station CR4 showed less fluctuation in abundance, with Mediophyceae being the major composition throughout all sampling days (Fig. 4). The patterns of biomass change were similar to those of density. However,

Dinophyceae remained as a main component at station CR1 (Fig. 5). At the anchored station, the abundance, biomass, and composition showed less variation during the observation period, with a high abundance of Mediophyceae and Bacillariophyceae, and a high biomass of Mediophyceae and Dinophyceae (Fig. 6).

Table 1. Environmental parameters (Mean ± Standard Deviation) from four stations in the dry and wet seasons, with p-value from Fisher-Pitman permutation test comparing between seasonal values ('-' = *p*-value > 0.05; '*' = *p*-value < 0.05; '**' = *p*-value < 0.01; '***' = *p*-value < 0.001)

Environmental parameters		*p*-value	CR1	CR2	CR3	CR4
Temperature (^{o}C)	Dry	**	28.38 ± 2.02 (*n* = 20)	27.86 ± 2.57 (*n* = 18)	27.08 ± 2.30 (*n* = 26)	25.56 ± 2.14 (*n* = 33)
	Wet		28.49 ± 0.47 (*n* = 12)	27.78 ± 0.36 (*n* = 11)	27.60 ± 0.34 (*n* = 43)	27.64 ± 0.43 (*n* = 23)
Salinity	Dry	**	34.06 ± 0.14 (*n* = 20)	34.05 ± 0.18 (*n* = 18)	34.10 ± 0.10 (*n* = 26)	34.14 ± 0.08 (*n* = 33)
	Wet		33.08 ± 0.25 (*n* = 12)	33.38 ± 0.17 (*n* = 11)	33.35 ± 0.18 (*n* = 43)	33.50 ± 0.14 (*n* = 23)
Fluorescence (mg/m^3)	Dry	-	0.23 ± 0.11 (*n* = 20)	0.17 ± 0.07 (*n* = 18)	0.15 ± 0.05 (*n* = 26)	0.10 ± 0.03 (*n* = 33)
	Wet		0.16 ± 0.08 (*n* = 12)	0.14 ± 0.04 (*n* = 11)	0.16 ± 0.11 (*n* = 43)	0.27 ± 0.45 (*n* = 23)
Conductivity (mS/cm)	Dry	-	55.29 ± 2.00 (*n* = 20)	54.74 ± 2.51 (*n* = 18)	54.01 ± 2.30 (*n* = 26)	52.51 ± 2.11 (*n* = 33)
	Wet		53.98 ± 0.52 (*n* = 12)	53.70 ± 0.40 (*n* = 11)	53.48 ± 0.38 (*n* = 43)	53.73 ± 0.38 (*n* = 23)
Nitrite (µg/L)	Dry	*	1.86 ± 1.72 (*n* = 20)	1.63 ± 1.29 (*n* = 18)	1.93 ± 1.51 (*n* = 26)	2.57 ± 1.83 (*n* = 33)
	Wet		0.80 ± 0.80 (*n* = 12)	0.86 ± 0.86 (*n* = 11)	2.22 ± 1.60 (*n* = 43)	1.62 ± 2.09 (*n* = 23)
Nitrate (µg/L)	Dry	***	7.56 ± 3.47 (*n* = 20)	6.67 ± 2.19 (*n* = 18)	8.55 ± 4.91 (*n* = 26)	10.78 ± 9.76 (*n* = 33)
	Wet		0.77 ± 0.50 (*n* = 12)	0.76 ± 0.65 (*n* = 11)	1.80 ± 1.71 (*n* = 43)	2.54 ± 3.04 (*n* = 23)
Ammonium (µg/L)	Dry	-	13.85 ± 7.32 (*n* = 20)	11.58 ± 6.49 (*n* = 18)	13.15 ± 9.24 (*n* = 26)	10.54 ± 7.76 (*n* = 33)
	Wet		14.84 ± 18.01 (*n* = 12)	18.28 ± 22.96 (*n* = 11)	13.31 ± 11.19 (*n* = 43)	10.29 ± 15.61 (*n* = 23)
DIN (µg/L)	Dry	**	23.28 ± 9.43 (*n* = 20)	19.89 ± 6.94 (*n* = 18)	23.64 ± 10.58 (*n* = 26)	23.90 ± 14.26 (*n* = 33)
	Wet		16.22 ± 18.72 (*n* = 12)	19.64 ± 23.72 (*n* = 11)	17.20 ± 11.89 (*n* = 43)	14.02 ± 16.57 (*n* = 23)
Phosphate (µg/L)	Dry	***	6.98 ± 3.66 (*n* = 20)	5.81 ± 2.95 (*n* = 18)	6.90 ± 3.58 (*n* = 26)	5.60 ± 2.87 (*n* = 33)
	Wet		9.59 ± 5.99 (*n* = 12)	9.63 ± 5.76 (*n* = 11)	11.57 ± 5.57 (*n* = 43)	8.72 ± 4.48 (*n* = 23)
Silicate (µg/L)	Dry	***	361.54 ± 158.05 (*n* = 20)	326.57 ± 197.91 (*n* = 18)	306.29 ± 152.10 (*n* = 26)	229.36 ± 122.32 (*n* = 33)
	Wet		599.79 ± 522.37 (*n* = 12)	510.63 ± 479.69 (*n* = 11)	476.9 ± 427.36 (*n* = 43)	485.76 ± 312.21 (*n* = 23)

Table 2. The number of species on sampling days during the dry and wet season in Cam Ranh Bay

Groups/Classes	Dry season (DS)								Total	Wet season (WS)						Total	Total
	1	2	3	5	10	15	20	30	in DS	1	2	3	5	20	30	in WS	
Diatoms	67	69	69	71	86	89	95	94	*129*	98	79	89	86	105	85	*124*	146
Bacillariophyceae	17	19	18	22	22	25	20	22	*38*	20	16	22	20	24	16	*31*	40
Coscinodiscophyceae	22	20	21	20	21	24	25	25	*31*	27	19	21	25	28	24	*31*	35
Mediophyceae	28	30	30	29	43	40	50	47	*60*	51	44	46	41	53	45	*62*	71
Dinoflagellates	52	49	51	48	52	60	57	50	*86*	49	42	36	42	56	52	*73*	93
Dinophyceae	52	49	50	48	52	60	57	50	*85*	49	41	36	42	56	52	*72*	92
Noctilucophyceae	0	0	1	0	0	0	0	0	*1*	0	1	0	0	0	0	*1*	1
Cyanophyceae	3	3	3	3	3	3	3	3	*3*	1	0	0	1	3	2	*3*	3
Dictyochophyceae	1	1	2	1	2	2	2	2	*2*	2	2	1	1	2	1	*2*	2
Thecofilosea	0	0	0	0	0	0	1	0	*1*	0	0	0	0	0	0	*0*	1
Total	123	122	125	123	143	154	158	149	221	150	123	126	130	166	140	202	245

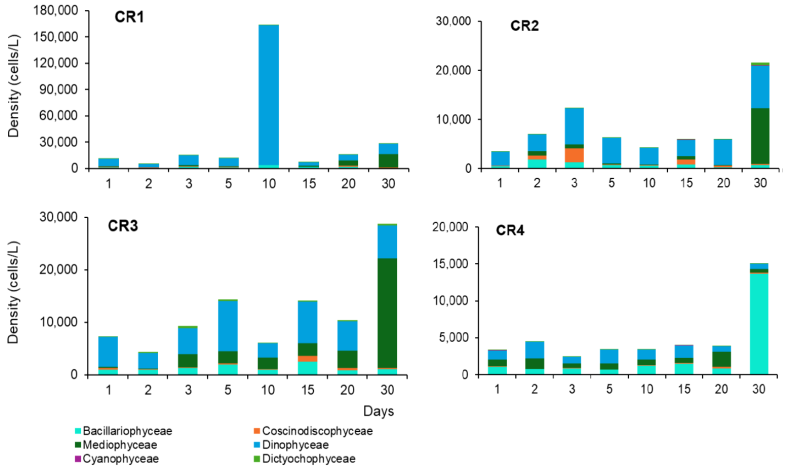

Figure 2. Variation in density of phytoplankton groups from day 1 to day 30 during dry season of 2006 at four stations of Cam Ranh Bay

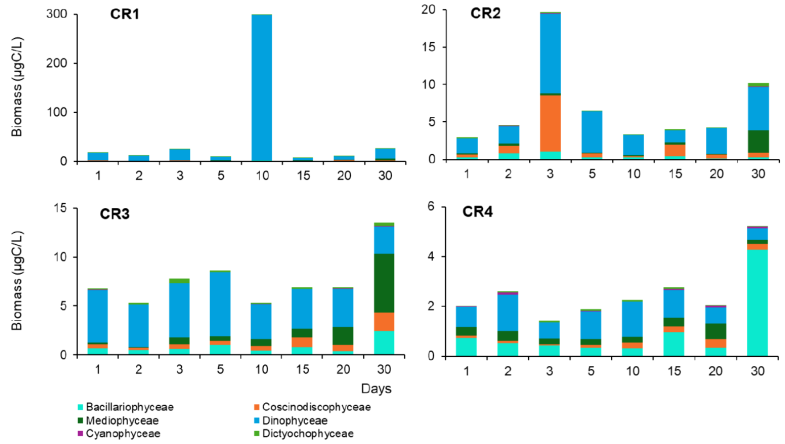

Figure 3. Variation in biomass of phytoplankton groups from day 1 to day 30 during the dry season of 2006 at four stations of Cam Ranh Bay

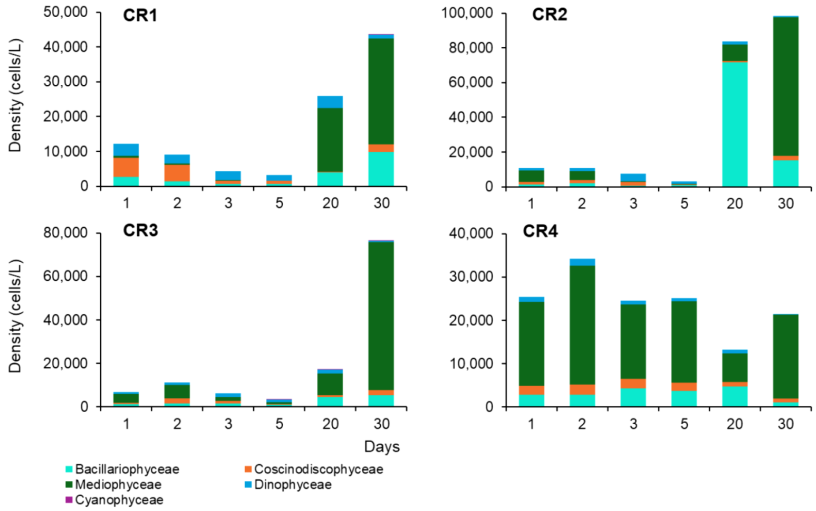

Figure 4. Variation in average density of phytoplankton groups from day 1 to day 30 during the wet season of 2006 at four stations of Cam Ranh Bay

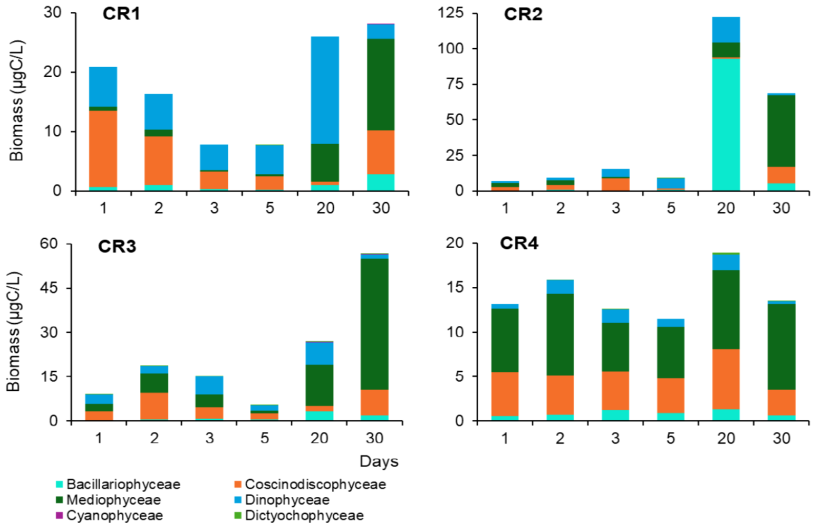

Figure 5. Variation in average biomass of phytoplankton groups from day 1 to day 30 during wet season of 2006 at four stations of Cam Ranh Bay

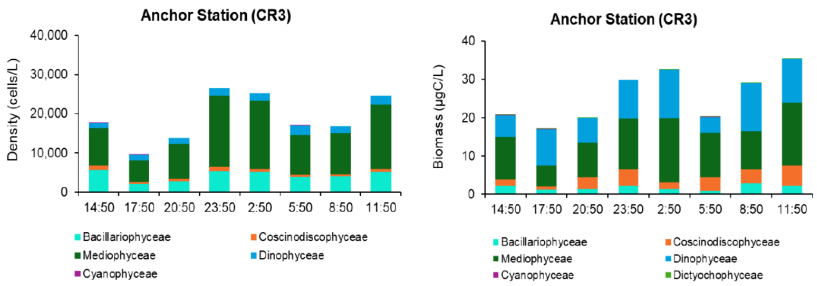

Figure 6. Variation in abundance and biomass of phytoplankton groups in 24 hours in wet season of 2006 at anchored station

Seasonally, despite the higher total abundance in the wet season (p-value < 0.01), the total biomass did not differ significantly between the two seasons (p-value > 0.05). The abundance and biomass of diatoms, including Bacillariophyceae, Coscinodiscophyceae, and Mediophyceae, were significantly higher in the wet season (p-value < 0.01). Meanwhile, the abundance of Dinophyceae increased markedly in the dry season (p-value < 0.001). However, there was no significant difference in the biomass of dinoflagellates between the two seasons (p-value > 0.05, Fisher-Pitman permutation test).

Succession of dominant species

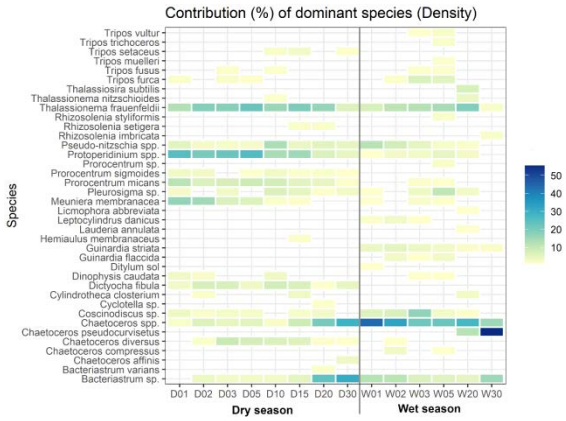

Figure 7. Contribution percentage of dominant species in SIMPER analysis based on density data from day 1 to 30 during dry and wet seasons in Cam Ranh Bay

The similarity percentage (SIMPER) analysis based on abundance indicated that certain species are dominant during the sampling period in both seasons. These species include centric diatoms forming chain and setae (*Chaetoceros* spp., *Bacteriastrum* sp.), centric diatoms with solitary cells (*Coscinodiscus* sp.), harmful diatoms (*Pseudo-nitzschia* spp., pennate diatoms (*Thalassionema frauenfeldii*, *Pleurosigma* sp.), and dinoflagellate *Protoperidinium* spp. *Protoperidinium* spp. were dominant in the dry season, while *Chaetoceros* spp. were in the wet season. Some other species were found more abundance in specific seasons, such as *Chaetoceros diversus*, *Dictyocha fibula*, and *Tripos setaceus* in the dry season, and *Guinardia flacida*, *Guinardia striata*, *Leptocylindrus danicus*, and *Chaetoceros compressus* in the wet season (Fig. 7). Analysis on biomass data further showed the clearer contribution of *Protoperidinium* spp., *Thalassionema frauenfeldii*, *Coscinodiscus* sp., *Chaetoceros* spp., and *Pleurosigma* sp. in both seasons. Notably, *Protoperidinium* spp. contributed approximately 30–65% during the dry season. *Chaetoceros* spp. and *Coscinodiscus* sp. exhibited higher contributions during the wet season. Some species, such as *Oscillatoria* sp. (Cyanobacteria), *Trieres chinensis*, and *Trieres mobiliensis* (Mediophyceae), were not dominant in abundance but had significant contributions to the biomass (Fig. 8).

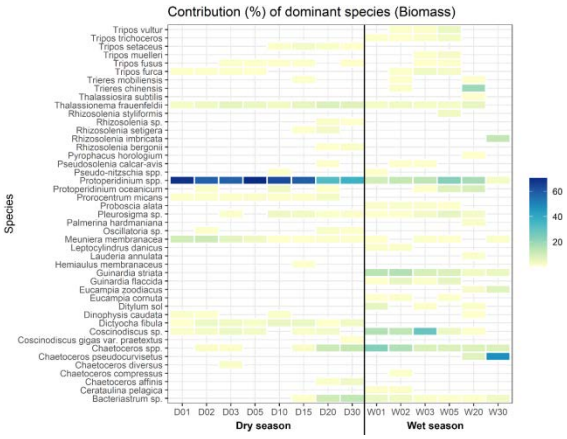

Figure 8. Contribution percentage of dominant species in SIMPER analysis based on biomass data from day 01 to 30 during dry and wet seasons in Cam Ranh Bay

Taxonomic Diversity index

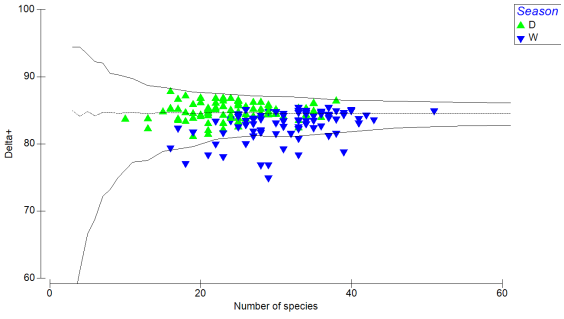

Figure 9. Funnel plot of Δ^+ index of samples at four stations during dry (D) and wet (W) seasons

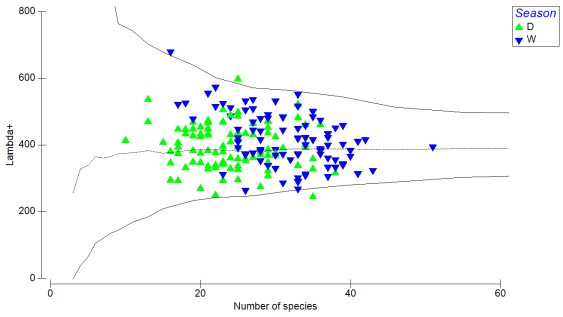

Figure 10. Funnel plot of Λ^+ index of samples at four stations during dry (D) and wet (W) seasons

The analysis of taxonomic indices using funnel plots, including average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+), revealed significant seasonal differences. The Δ^+ values were significantly higher during the dry season (p-value < 0.001, Fisher-Pitman permutation test), suggesting a higher level of taxonomic diversity in this period. Conversely, there was no significant difference in Λ^+ values between seasons (p-value > 0.05, Welch t-test, α = 0.05), indicating that the variation in taxonomic distinctness remained consistent throughout the year. Most samples from the wet season exhibited lower Δ^+ values, with some samples from station CR4 falling below the simulated 95% probability funnel threshold, indicating reduced taxonomic diversity (Fig. 9). Furthermore, while Λ^+ values did not differ significantly overall, specific samples such as CR1 on the 5th day at the surface (wet season) and on 30th day at surface (dry season) were above the 95% funnel, whereas CR3 on 20th day at bottom (dry season) fell below it, pointing to individual variations in taxonomic distinctness (Fig. 10).

Impacts of environmental factors on phytoplankton communities

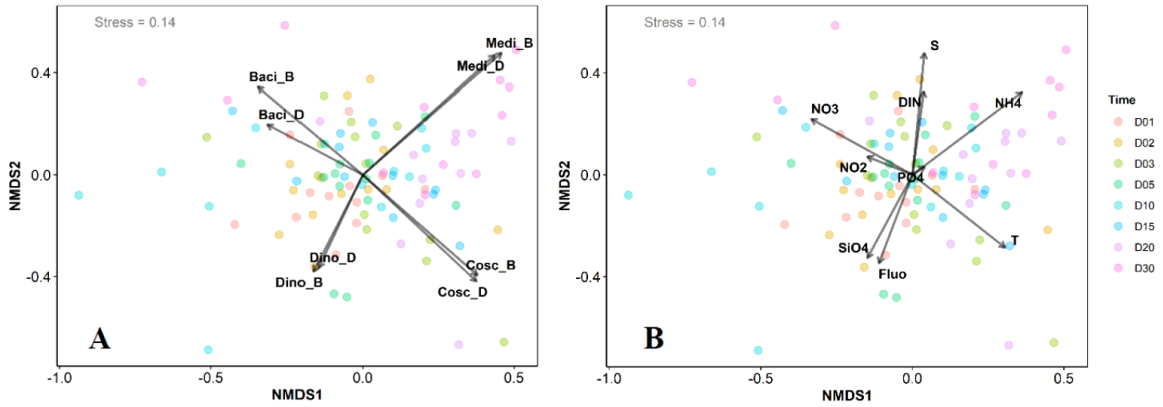

Figure 11. Non-metric Multi-dimensional Scaling (NMDS) ordination plot of Bray–Curtis community dissimilarities based on abundance and biomass values of phytoplankton (A) and environmental variables (B) following distance matrix of sampling days during the dry season. Abbreviations in (A) plot: Baci_D = Bacillariophyceae, Cosc_D = Coscinodiscophyceae, Medi_D = Mediophyceae, Dino_D = Dinophyceae based on abundance values, Baci_B = Bacillariophyceae, Cosc_B = Coscinodiscophyceae, Medi_B = Mediophyceae, Dino_B = Dinophyceae based on biomass values; (B) plot: S = salinity; T = temperature; Fluo = fluorescence; NO_2 = nitrite, NO_3 = nitrate; NH_4 = ammonium, PO_4 = phosphate, DIN = dissolved inorganic nitrogen, SiO_4 = silicate

The NMDS plot (Figs. 11A, 12A) revealed positions between the abundance and biomass of Bacillariophyceae, Coscinodiscophyceae, Mediophyceae, and Dinophyceae. During the dry season, the abundance and biomass of these groups exhibited a strong correlation with one another. Specifically, Bacillariophyceae were associated with nitrate and nitrite content, Mediophyceae with phosphate and ammonium, Coscinodiscophyceae were influenced by temperature, and Dinophyceae corresponded with chl-a concentration (fluorescence) (Fig. 11).

Conversely, in the wet season, there was a high correlation between the abundance and biomass of these groups, except for Dinophyceae. Bacillariophyceae were closely related to nitrite, nitrate, and phosphate, whereas Mediophyceae were associated with ammonium, DIN and chl-a concentration (fluorescence). The density of Dinophyceae was negative correlated to silicate, salinity, and chlo-a concentration (fluorescence). Coscinodiscophyceae did not show any correspondence to any environmental factors. Additionally, temperature showed lesser influence on the abundance and biomass of all phytoplankton groups (Figs. 12A, B).

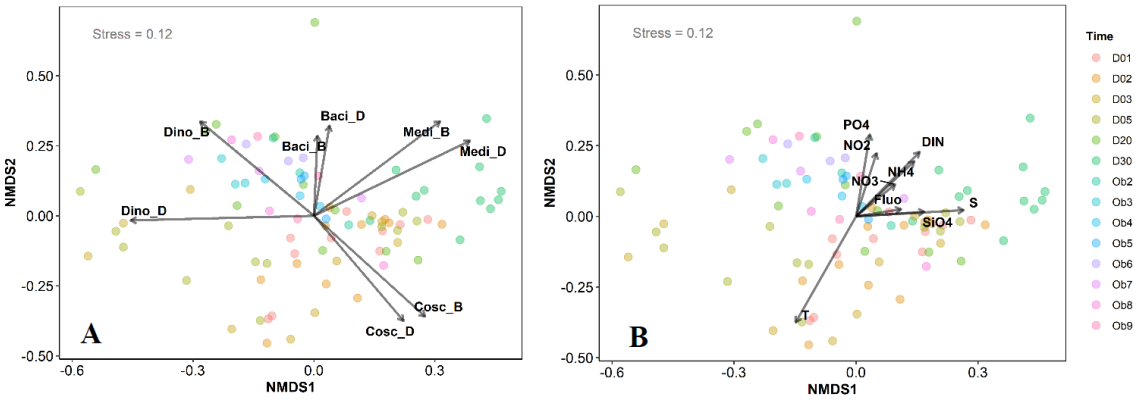

Figure 12. Non-metric Multi-dimensional Scaling (NMDS) ordination plot of Bray–Curtis community dissimilarities based on abundance and biomass values of phytoplankton (A) and environmental variables (B) following distance matrix of sampling days/observations during wet season. Abbreviations in (A) plot: Baci_D = Bacillariophyceae, Cosc_D = Coscinodiscophyceae, Medi_D = Mediophyceae, Dino_D = Dinophyceae based on abundance values, Baci_B = Bacillariophyceae, Cosc_B = Coscinodiscophyceae, Medi_B = Mediophyceae, Dino_B = Dinophyceae based on biomass values; (B) plot: S = salinity; T = temperature; Fluo = fluorescence; NO_2 = nitrite, NO_3 = nitrate; NH_4 = ammonium, PO_4 = phosphate, DIN = dissolved inorganic nitrogen, SiO_4 = silicate

DISCUSSION

It was observed that temperature, nitrate, salinity, and conductivity had greater variability among layers during the dry season, while these parameters were less variation among layers in the wet season. This observation suggests that water mass mixing was less effective in the dry season compared to the wet season. Besides, salinity, ammonium, DIN, phosphate, and silicate concentrations demonstrated stronger fluctuations among sampling days during the wet season, notably in the 20th and 30th days at stations CR1 and CR2, which are closer to the shore, implying that runoff from land contributed to the variations in salinity and the nutrients. Additionally, the lower salinity levels and higher concentrations of phosphate and silicate observed during the wet season were likely influenced by terrestrial flows. When compared with other waters, Chut Cape and the Cua Be estuary in Nha Trang Bay, nitrate concentrations in the study area were much lower [33]. Based on the Redfield ratio, nitrogen was a limited factor in the study area across both seasons. In subtropical coastal regions, nutrient limitations alternate between nitrogen and phosphorus, influenced by freshwater inflows and the spatial distribution of nutrients driven by river discharge dynamics [34].

The species richness was significantly lower in the dry than wet season (p-value < 0.001, Fisher-Pitman permutation test). Despite this, the total number of species observed in the dry season (221 taxa) exceeded that in the wet season (202 taxa), suggesting that the dissimilarity of species composition (heterogeneity) among dry season samples was more pronounced than in wet season samples. Results of similarity analysis based on

abundance data also revealed lower values in the dry season, with an average similarity of 25.9 and 31.9% in the dry and wet seasons, respectively. This pattern of higher species richness in the dry season was consistent with findings from the Cua Be estuary in Nha Trang Bay [33] and Thi Nai Lagoon [35], located in central Vietnam.

In the dry season, the average abundance and biomass of phytoplankton at station CR1 reached abnormally high values on the 10th day, mainly due to the outbreak of *Tripos fusus*, which accounted for over 300,000 cells.L^{-1} at the surface. When considering the related environmental factors on this day, there were no significant differences compared to other days, except for the surface temperature, which was measured at a depth of 0–3 meters. The temperatures on other days ranged from 28.5^{o}C to 31^{o}C, while the surface temperature on the 10th day decreased to 28^{o}C and 28.5^{o}C. This anomaly in surface temperature may have contributed to the observed increase in phytoplankton abundance and biomass. Experiments with *Tripos fusus* also revealed optimal growth rates between 26^{o}C and 28^{o}C [36].

The study demonstrated remarkable seasonal shifts in phytoplankton composition, with dinoflagellates being the most abundant during the dry season and diatoms predominating in the wet season. This finding is consistent with earlier research by Nguyen et al., [33] in the Cua Be estuary, where dinoflagellates showed a peak abundance during the dry season. The pattern of higher dinoflagellate abundance in the dry season was also observed at all locations in a tropical Karstic coastal zone [37]. Despite the higher overall abundance of phytoplankton in the wet season observed in this study, there was no significant variation in total biomass. This discrepancy suggests that biomass, which depends on cell concentration and volume, varies with seasonal changes in species composition. Typically, during the dry season, larger cells of *Protoperidium* spp. contributed about 17% to total abundance but accounted for approximately 56% of total biomass. Conversely, in the wet season, smaller chain-forming diatoms such as *Chaetoceros* spp. and *Bacteriastrum* sp. contributed around 27% and 9% to total abundance, yet only 12% and 4% to total biomass, respectively. Additionally, while the abundance of Dinophyceae was higher in the dry season, their biomass did not differ significantly between the two seasons, indicating that dinoflagellates may include larger species in the wet season. This study recorded higher encounter frequencies of larger dinoflagellates from quantitive samples in the wet season, such as *Blepharocysta splendor-maris*, *Dinophysis* sp., *Protoperidinium oceanicum*, *Pyrophacus horologium*, *Tripos fusus*, *Tripos muelleri*, *Tripos trichoceros*, and *Tripos vultur*.

The study identified several dominant phytoplankton species in the study area across both seasons, including the diatoms *Chaetoceros* spp., *Bacteriastrum* spp., *Coscinodiscus* spp., *Thalassionema frauenfeldii*, *Pleurosigma* sp., and the heterotrophic dinoflagellate *Protoperidinium* spp. The genera *Chaetoceros* and *Coscinodiscus* are prevalent worldwide, even in high latitudes such as the western subarctic Pacific Ocean, exhibiting temporal succession and year-round dominance [38]. Beyond these consistently dominant species, the succession of other species showed more pronounced changes during the wet season, as highlighted by SIMPER analysis on biomass. This analysis revealed that the number of dominant species based on density (38 taxa) was lower than those based on biomass (45 taxa). During the dry season, *Protoperidinium* spp. contributed significantly to the total biomass, accounting for approximately 33–70% during sampling days. In contrast, the wet season showed an equal contribution from multiple dominant species, including *Protoperidinium* spp., *Chaetoceros* spp., *Guinardia striata*, *Coscinodiscus* sp., and *Thalassionema frauenfeldii*, each contributing a maximum of 29% of the total biomass. Some small dominant species, like the harmful *Pseudo-nitzchia* spp. contributed significantly to the total abundance but not to the total biomass. Hence, assessing dominant species based on abundance and biomass provides a more comprehensive understanding. Additionally,

seasonal changes in dominant species were evident, with diatom genera such as *Guinardia*, *Eucampia*, and *Ditylum* being predominant in the wet season and the genus *Rhizosolenia* dominating the dry season. The dominance of *Rhizosolenia* during the dry season suggests less mixing of waters, as this genus is commonly found in stable water masses [39].

The lower Δ^+ values observed at station CR4 during the wet season indicate that the phytoplankton assemblage possessed lower hierarchical levels despite having a similar number of species compared to other stations. This observation aligns with findings by [40] reporting the lowest Δ+ values in the most polluted part of their study area. The nutrient content analysis at CR4 in the wet season revealed that average nitrite and nitrate values were higher than at other stations, and one-third of the samples from CR4 exhibited silicate content above the average for the entire area. These findings suggest that nutrient enrichment, particularly elevated levels of nitrite, nitrate, and silicate, may have contributed to the reduced taxonomic distinctness at CR4, reflecting the impact of nutrient pollution on the phytoplankton community structure.

The present study revealed significant seasonal variations in the relationship between phytoplankton abundance/biomass and environmental factors. Clear correlations were identified between Bacillariophyceae and nitrate and nitrite levels and between Mediophyceae and ammonium across both seasons. Also, phosphate was closely related to Mediophyceae in the dry season and Bacillariophyceae in the wet season. However, it was not a limiting factor in the study area as per the Redfield ratio. Besides, Dinophyceae exhibited a positive correlation with silicate and fluorescence during the dry season but an inverse correlation with these factors in the wet season. Fluorescence, closely related to chlorophyll-a or autotrophic phytoplankton, is influenced by heterotrophic Dinophyceae species that prey on autotrophic species, explaining their relationship with fluorescence. Dinoflagellates also showed a negative relationship with salinity and silicate, likely due to the salinity fluctuation and silicate increase during the wet season. Additionally, Coscinodiscophyceae significantly correlated with temperature in the dry season but had no significant relationship with any environmental variables in the wet season. Although the data indicated that diatoms predominated during the wet season, coinciding with decreased salinity and increased levels of temperature, phosphate, and silicate, results from the NMDS analysis only highlighted a strong relationship between Bacillariophyceae and phosphate. Another possible explanation for these findings is the decline in Dinophyceae abundance, which is known to be a high-salinity species under reduced salinity conditions [41]. Meanwhile, diatoms adapted to lower salinity likely led to a higher proportion of diatoms in the total abundance in the wet season.

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Appendix 1. Variations in phytoplankton abundance and biomass at four stations CR1, CR2, CR3, and CR4 in Cam Ranh Bay in the dry and wet seasons. *Note:* numbers in the graphs indicated sampling days