Salinity and temperature regulations on the genus *Trichodesmium* in Pombo Island national marine park environment, Central Maluku, during the easterly monsoon

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Abstract. Genus *Trichodesmium* is a wide-spread planktonic cyanobacteria in the world ocean that has an ability to fix nitrogen (N) from the atmosphere in N-starved marine environments. Thus, the presence of the genus in a marine environment plays an important role in sustaining marine life by providing key nutrient elements via biogeochemical cycles. The present study aimed to investigate *Trichodesmium* dynamics and their responses to environmental drivers in a national marine park, Pombo Island, during the easterly monsoon. Phytoplankton samples were collected using a plankton net during a fortnightly-campaign scheme between June and August, during which sea surface temperature, salinity, nitrate, phosphate and water transparency were measured from seven stations. *Trichodesmium*'s filaments were recorded in all stations during the observation, representing between 13 and 59% of the total phytoplankton community. During the observation, low sea surface temperature (27.42-28.36°C) and high salinity (31.78-34.18 PSU) levels were recorded, indicating that Banda Sea's upwelling reached Pombo Island. The principal component analysis revealed that during the upwelling period, *Trichodesmium* abundances were positively correlated with increased salinity, yet inversely correlated with temperature. Meanwhile, nutrient concentrations showed no impacts on the abundance. This study revealed that physical properties mainly governed dynamics of the genus during the easterly monsoon. Further annual dynamics need to be investigated in order to fully understand environmental regulations on the genus as well as on N fixing processes and nutrient cycles.
Key Words: cyanobacteria, nitrogen, upwelling, Banda Sea, southeast monsoon.

Introduction. The diazotrophic, a blooming-forming, cyanobacteria *Trichodesmium* are a ubiquitous marine species that is widely distributed in the tropical and subtropical oceans. *Trichodesmium* cells develop as filaments, which are known as trichomes that can be accumulated as colonies in millimeter-sized of fusiform (tuft) and radial (puff) shapes during bloom conditions (Klawonn et al 2020; Wang et al 2022). Their filaments have strong intracellular gas vesicles that support buoyancy ability to migrate from 200 m depth to the surface where they often form blooms, visible to the naked eye and conspicuous from space (Heimann & Cirés 2015; Wang et al 2022). *Trichodesmium* filaments contain unique pigments such as phycourobilin (PUB) and phycoerythrobilin (PEB) that allow satellite to distinguish their bloom range colors from other different cyanobacteria (Ani et al 2023).

The genus plays an important role in providing bioavailable nitrogen (N) to support basic food web producers by elevating the primary productivity and the carbon flux in the oligotrophic near-surface oceans (Held et al 2020). *Trichodesmium* supplies its N requirements by fixing N_2 (dinitrogen) from the atmosphere and releases it into the water by a remineralization process to provide basic nutrient elements for the growth of other phytoplankton (Wang et al 2022; Ani et al 2023). The conversion of N_2 to ammonium and the nitrification of nitrate and nitrite elevate bioavailability of N in the water column (Klawonn et al 2020). This ability makes the genus responsible for

approximately 50% production of the reactive nitrogen in oligotrophic oceans every year (Eichner et al 2020; Gardner et al 2023).

The trend of Harmful Algal Bloom (HAB) events has increased recently, and responses of HAB species have shown relationships with the alteration of environmental drivers such as sea surface temperature and salinity, nutrient inputs, stratification, upwelling and precipitation (Wells et al 2015). In particular, *Trichodesmium* proliferations were regularly recorded during calmer/low wind periods (Krishnan et al 2007; Kuganathan et al 2023), and the influences of environmental drivers were different among locations. Previous studies have shown that rapid growth and surface blooms of the species occurred in the presence of high concentrations of surface nutrients such as phosphorus (P) and iron (Fe) (Orchard et al 2010; Bergman et al 2013; Walworth et al 2016; Frischkorn et al 2018; Rouco et al 2018). *Trichodesmium* in the northern Great Barrier Reef benefited from a relatively high phosphate, increased temperatures of 22°C to 30°C, an elevated nitrogen and carbon fixation in the ambient (Qu et al 2019). In the East China Sea, *Trichodesmium* blooms were associated with temperature, dissolved inorganic phosphate and P/N ratios (Yue et al 2021).

Pombo Island is one of uninhabited small islands in Maluku Province, Central of Maluku Regency that has been appointed as a Marine Park Sanctuary by the Indonesian Ministry of Agriculture since 1973, encompassing the land, coral reef flats and a lagoon with a total of 1000 hectare area. The island lies between Ambon Island and Haruku Island, which is known as Haruku Strait. Seram Sea and Banda Sea adjoin Pombo Island in the north and the south, respectively. Upwelling in Banda Sea occurs during the southeast (easterly) monsoon from May to September, during which the sea surface temperature (SST) reaches the lowest level at 26.5°C in August (observation between 1982 and 2000) (Gordon & Susanto 2001). This SST is regularly detected in small island waters located near Banda Sea such as Ambon Bay, Buru Island and Lease Islands including Haruku Strait (Saputra & Lekalette 2016; Tubalawony et al 2023). During the easterly monsoon, Banda Sea's upwelling supports higher phytoplankton biomass and increases primary productivity in surrounding local coastal waters, including the Marine Park Pombo Island (Moore et al 2003). Yet, *Trichodesmium* observations in the area were completely lacking. Given the fact that this cyanobacterium species plays important roles in the marine environment, but studies on the species lack, it is important to conduct a basic observation regarding the ecology of the species in this marine park. Thus, the present study aimed to investigate the dynamics of this cyanobacteria species and its responses to environmental drivers during the easterly monsoon.

Material and Method. The campaign was conducted during the easterly monsoon between June and August at seven stations, of which two were located in the lagoon (Figure 1).

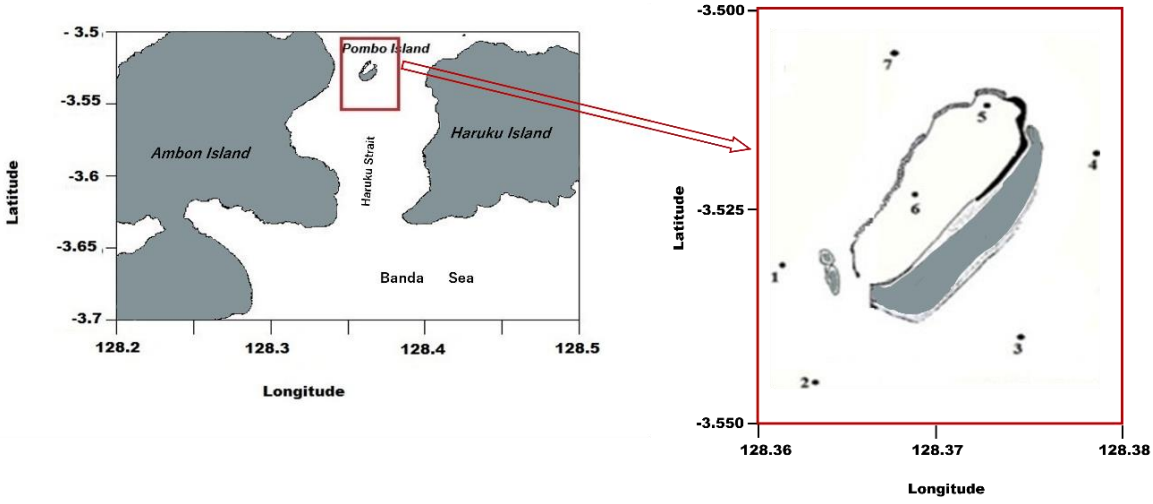

Figure 1. Pombo Island map and stations (1-7).

Samples were collected six times in a fortnightly scheme campaign, and the final total of 42 samples were obtained. Phytoplankton samples were collected using a modified-plankton net (Ø=30 cm, length=120 cm and mesh size=20 µm) mounted with a flowmeter, and deployed horizontally for 2 minutes with a constant boat speed. Phytoplankton samples were transferred to 500 mL bottles and adjusted to 300 mL final volume, and subsequently fixed with formaldehyde at 4% final concentration. Approximately 50 mL of subsamples were separated for the *Trichodesmium* inspection, and 1 mL was placed on a Sedgwick Rafter cell chamber for filament determinations and calculations under a Nikon Eclipse 50*i* microscope with 100× and 200× magnifications. *Trichodesmium* filaments were expressed in cells m^{-3}.

A compact Alec CTD ASTD 687 was used to measure temperature and salinity, and the average of 0 m and 2 m data were used to express the surface values from the seven stations. Water transparency was measured using a Ø 30 cm Secchi disc, deployed at each station. Water samples for nutrient analysis were collected using a 3.5 L Niskin Bottle at 1 m depth, and transferred to 300 mL dark bottles. In the lab, water samples were filtered immediately through 0.45 µm pore size, 47 mm Ø membrane filters using a vacuum pump. Filtered samples were stored in a freezer at -20°C until the determinations. Phosphate and nitrate were analyzed using a spectrophotometer UV-Vis Shimadzu 1700, according to Strickland & Parsons (1972) guidance.

The Minitab 21.1 was employed to conduct statistical analysis, in which all data were used to reveal the relationship between *Trichodesmium* filament abundances and environmental parameters. The loading plot of the Principal Component Analysis (PCA) and the non-parametric Spearman Rank analysis were performed to investigate correlations among parameters. Before conducting the ordination in the PCA, all data were standardized to eliminate physical dimensions according to Legendre & Birks (2012).

Results

Water physicochemical properties. The average of sea surface temperature (SST) values varied during the observation and showed unclear trend. Overall data showed that SST ranged between 27.42°C and 28.36°C, with the highest was at the end of the sampling period in the second week of August and the lowest was at the second week of July (Figure 2A). A similar unclear trend was also found for the sea surface salinity (SSS) value in Pombo Island waters. SSS was stable at the beginning of sampling period between the first week of June and July, yet decreased drastically at the second week of July to reach the lowest value (Figure 2A). The average of salinity values ranged between 31.78 and 34.18 PSU in Pombo Island during the easterly monsoon (wet season). Meanwhile, Secchi dish measurement for water transparency average values ranged between 10.43 m and 19.29 m. The average Secchi dish depth was deep in June (19.15 m) and it gradually became shallow in July to reach 10 m at the second week (Figure 2B). Subsequently, the water transparency increased to 17.28-17.57 m in August.

The average of surface nitrate concentrations showed a stable range during the observation, with values ranging between 0.03 to 0.05 µM (Figure 3). Yet, a peak was found in the second week of July as the highest value, which was 0.09 µM. Inversely, the lowest phosphate value was found during the peak of nitrate. Phosphate concentrations showed an increase trend between the first week of June and July, after which the concentration declined drastically in the second week of July and remained constant to end of sampling period (Figure 3). Phosphate concentrations during the sampling period ranged between 0.01 and 0.09 µM.

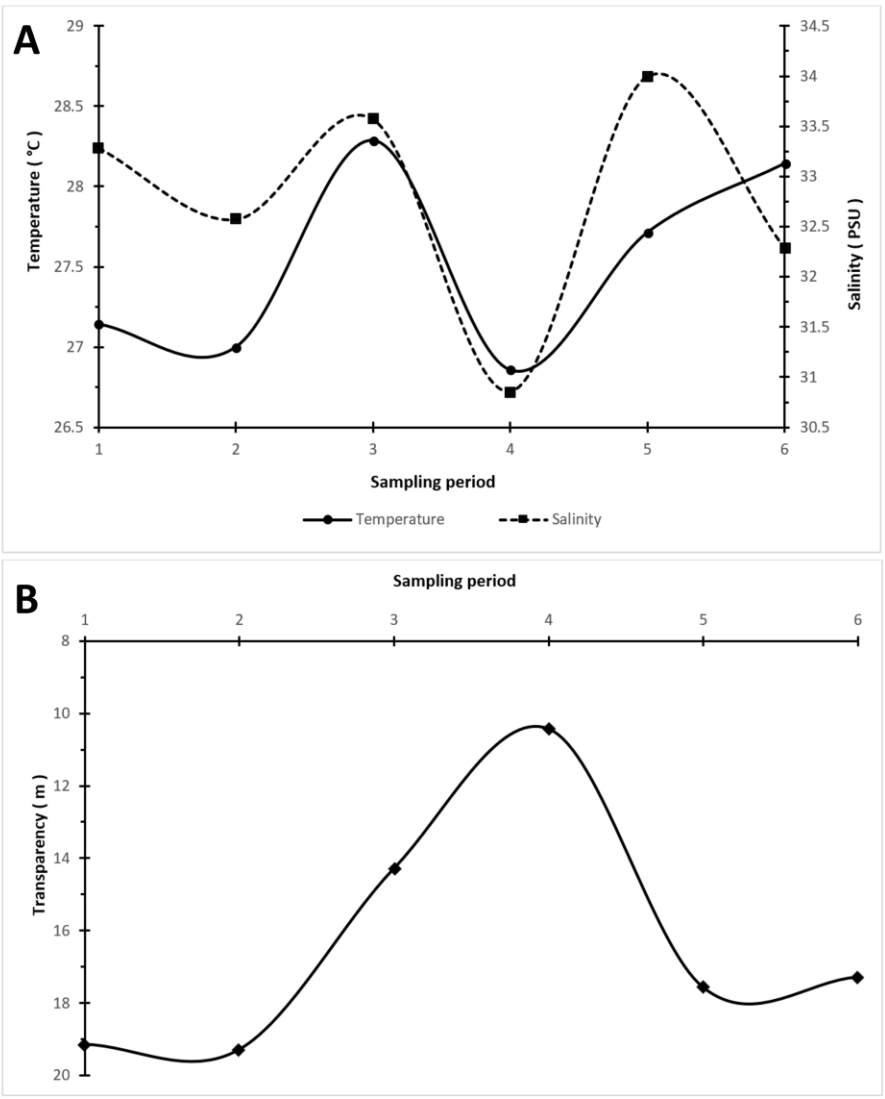

Figure 2. Temporal variability of physical properties in Pombo Island during the easterly monsoon. A) Temperature and salinity; B) Water transparency of Secchi dish.

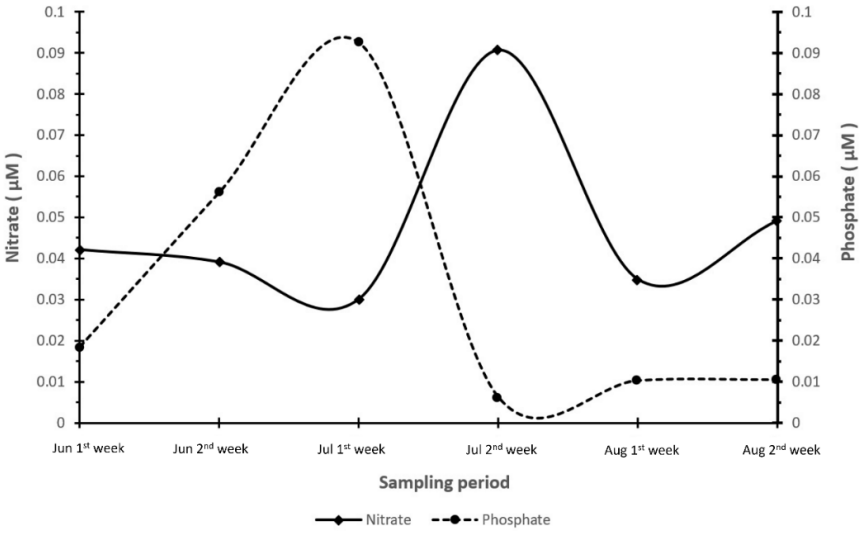

Figure 3. Temporal variability of dissolved nutrients in Pombo Island during the easterly monsoon.

Trichodesmium abundances. The general average abundance of the genus showed a downward trend during the sampling period (Figure 4). The highest *Trichodesmium* abundance was found in the second week of June with the average value of 43.72 × 10^3 cells m^{-3}, and it was subsequently followed by a sharp decline in the first week of July, reaching its lowest value (9.41 × 10^3 cells m^{-3}). During the last three sampling periods, *Trichodesmium* abundances decreased gradually, ranging between 26.77 × 10^3 cells m^{-3} and 17.07 × 10^3 cells m^{-3}. High average abundances were found at the stations one and two, with values of 30.41 × 10^3 cells m^{-3} and 33.96 × 10^3 cells m^{-3}, respectively (data not shown). Meanwhile, other stations showed similar *Trichodesmium* cell abundances, ranging between 16.12 × 10^3 cells m^{-3} and 23.40 × 10^3 cells m^{-3}.

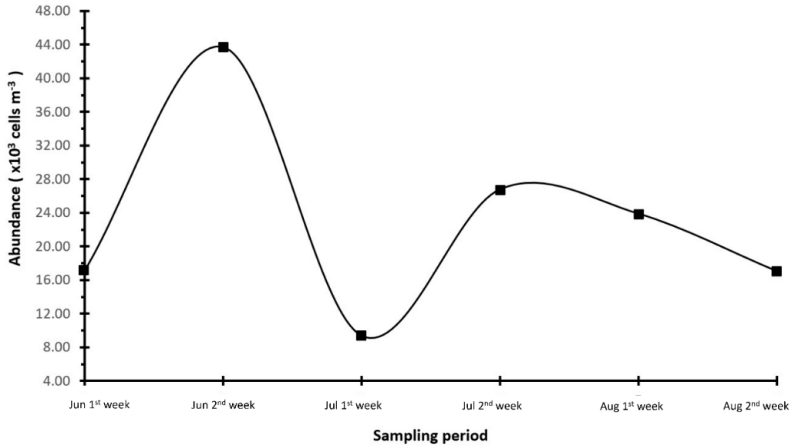

Figure 4. Temporal variability of *Trichodesmium* abundances in Pombo Island during the easterly monsoon.

Environmental influences. The grouping of the first and second component of the PCA analysis accounted for 63.40% of the total variance in the data set. The loading plot PCA analysis showed a positive correlation between *Trichodesmium* abundances and salinity levels. Meanwhile, temperature showed an inverse correlation with the filament abundance (Figure 5). Correlations were not found between *Trichodesmium* cells abundance and nutrient concentrations. Spearman Rank analysis revealed similar results as found by PCA (Table 1). *Trichodesmium* abundances was positively correlated with salinity and negatively related to temperature during the sampling period ($r=0.37$; $p< 0.01$, and $r=-0.40$; $p<0.01$).

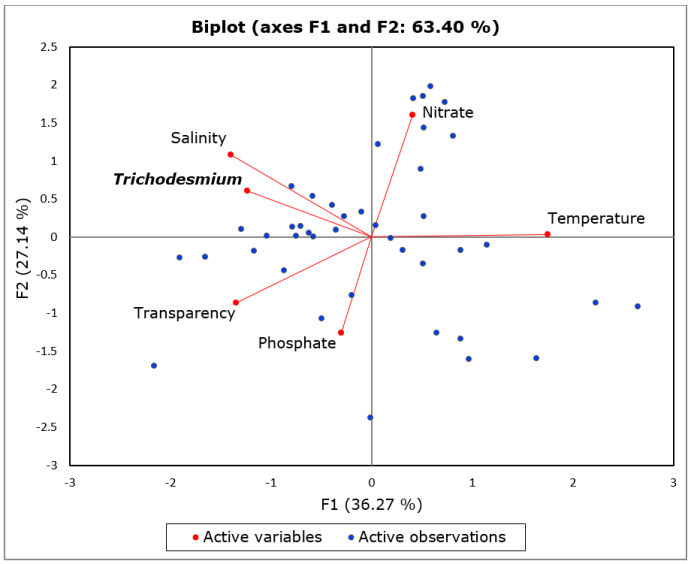

Figure 5. Loading plot PCA analysis between *Trichodesmium* and environmental drivers.

Table 1
Spearman rank analyses between *Trichodesmium* abundances and environmental drivers at the confidence level of 95%

Parameters	*Trichodesmium*	*Nitrate*	*Phosphate*	*Temperature*	*Salinity*
Nitrate	0.12				
Phosphate	0.01	-0.24			
Temperature	-0.40**	0.17	-0.19		
Salinity	0.37**	0.24	-0.23	-0.61	
Transparency	0.22	-0.43	0.18	-0.44	0.23

** $p<0.01$

Discussion. The study showed that low SSTs and high SSSs in Pombo Island during the easterly monsoon indicated the arrival of upwelled water from Banda Sea to the island, through the Haruku Strait. Similar conditions were also found by a recent study during the same period in Haruku Strait (Tubalawony et al 2023). They found that the average SST and SSS for the stations near Pombo Island during the easterly monsoon were approximately 27.03°C and 34.00 PSU, respectively. Low levels of SST and SSS in our study during the second week of July occurred as the result of high precipitation during the sampling period. This was also supported by the shallowest water transparency, indicating high runoff triggered by high precipitation in the second week of July. Cold-saline water from Banda Sea was also observed in Ambon Bay during the upwelling season between June and August (Saputra & Lekalette 2016; Likumahua et al 2019). These imply that Banda Sea water properties during the easterly monsoon influence surrounding waters of local small islands in Maluku Province, including Pombo Island.

Upwelled water is a nutrient-rich water that is distributed from deep ocean to the surface water. A previous study found that during the upwelling period in Banda Sea, phosphate and nitrate concentrations in the upper 5 m were 0.10 µM and 0.30 µM, respectively (Wetsteyn et al 1990). These nutrient levels were higher than the levels observed in the present study in Pombo Island. Nutrient uptake by phytoplankton and other macroalgae such as seagrass and seaweed might be the reason of the low levels of nutrients in the island. During the easterly season in Ambon Bay, phosphate and nitrate showed increase trends and the concentration were higher than at Pombo Island (Likumahua et al 2019). High population in Ambon Island generates massive organic matter inputs to the bay through runoffs, which are coupled with upwelling resulting in nutrient enrichment. Meanwhile, Pombo Island waters is influenced mainly by upwelling since the surrounding islands have fewer human populations. High concentrations of the genus at station one and two, located near Ambon Island, indicated the contribution of the land inputs such as nutrient and mineral loads through river runoffs, and of the air-borne minerals sourced from Ambon Island. Unfortunately, studies regarding these contributions are lacking for the area, which thus hinders a complete understanding of *Trichodesmium* dynamics in conjunction with land inputs and cultural eutrophication. However, many studies have revealed that Fe from dust plays crucial roles in regulating *Trichodesmium* cell growth and N fixation both in marine waters and laboratory experiments (Tovar-Sanchez et 2006; Zhang et al 2019; Kessler et al 2020; Shaked et al 2023).

The abundance of *Trichodesmium* in this study was lower than it was found in other Indonesian waters. In Ambon Bay, the abundance of the genus ranged between 0.2 × 10^5 cells m^{-3} and 1.5 × 10^5 cells m^{-3} during the easterly season, between June and August (Likumahua 2013). The genus was reported to form blooms in several waters in western Indonesia such as Jakarta Bay and Lampung Bay, and these events were frequently associated with massive fish kills (Sidabutar et al 2021; Sidabutar et al 2022). Regardless of low abundances found in this present study, the genus may form bloom events in Pombo Island due to regular upwelling of Banda Sea coupled with runoffs from surrounding islands. The combination of these nutrient sources has shown contributions in promoting *Trichodesmium* blooms in many waters around the world (Ramos et al 2005; Voss et al 2006; Foster et al 2009; Singh et al 2021). *Trichodesmium* can develop

rapidly in marine waters and subsequently release essential nutrient elements upon their death and decay, fueling the phytoplankton growth as the food for herbivores and carnivores, which is thus crucial for marine biota in protected areas and parks, including Pombo Island (Sarangi et al 2004; Wang et al 2022; Ani et al 2023).

The results implied that nutrients were not the only limiting factor during the upwelling season (easterly monsoon), but the influences of the water physical properties on the *Trichodesmium* cell abundance in Pombo Island were also significant. In the northern Pacific Ocean, physical drivers such as temperature, salinity and eddies regulated the diversity and abundance of diazotroph populations, while high abundances were found during low N/P ratios and phosphate concentrations (Wang et al 2022). Similar water property roles on regulating this species were observed during a monitoring scheme in a neighborhood bay near Pombo Island. A seven-month investigation of *Trichodesmium* in Ambon Bay showed that temperature correlated with its cells abundance and no relationships were found with phosphate and nitrate concentrations (Likumahua 2013). A winter bloom of *Trichodesmium* was recorded in the Bay of Bengal, and salinity showed a positive correlation with the abundance, while the latter was inversely related to temperature levels (Shaika et al 2023). These relationships were similar to our present results during the cool easterly monsoon in Pombo Island, which thus indicated that water physical properties had the main role in regulating *Trichodesmium* abundances. Other previous studies have shown the importance of temperature in regulating this diazotrophic cyanobacterium species (Qu et al 2019; Chinnadurai et al 2021; Yue et al 2021). Suitable temperatures for *Trichodesmium* abundance and distribution in the northern Pacific Ocean ranged between 26°C and 30°C (Wang et al 2022). High abundance of *Trichodesmium* cells were frequently recorded in the tropical regions with the approximate temperature ranging between 27°C and 30°C (Cheung et al 2020; Wang et al 2022). These ranges are similar to the SST in Pombo Island during the easterly monsoon found in this study, implying that this marine park is a suitable area for *Trichodesmium* to develop and proliferate.

Given the fact that other water physical properties such as horizontal advection, winds and upwelling have been observed to induce *Trichodesmium* distribution in the global ocean (Wang et al 2022), water physical dynamics of Banda Sea and its connectivity with the waters surrounding small islands may regulate the dynamics of the genus and other phytoplankton species in the area. Hence, an annual observation combined with a bi-monthly sampling scheme is a priority for advancing the knowledge on the general phytoplankton community dynamics, including bloom forming species.

Conclusions. The filaments of planktonic cyanobacteria *Trichodesmium* were found abundant and dominate the phytoplankton community in the marine park Pombo Island during the easterly monsoon. The upwelling of Banda Sea was detected in the waters and revealed influences on *Trichodesmium*, judging from the relationships among filament abundances, temperature and salinity. Further research and field observations are needed to reveal annual dynamics of the species and their responses to the environmental drivers.

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Conflict of interest. The authors declare no conflict of interest.

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