Phytoplankton Community Structure of the Makassar Strait, Indonesia

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Abstract. Makassar Strait is a unique oceanic ecosystem influenced by Indonesian Throughflow (ITF) and acted as a geographical barrier for Asian and Australasian ecozones. Those characteristics could form the diversity of phytoplankton in the strait. Thus, this research aimed to describe the phytoplankton community structures and determine the longitudinal or latitudinal shift in the Makassar Strait community. Specimen collection was carried out in 2013 from 20 stations along the Makassar Strait during the Widya Nusantara Expedition (EWIN). There were 165 phytoplankton species identified in this study, which consists of 1 cyanobacterium, 97 diatoms, and 67 dinoflagellates. The cyanobacteria, Trichodesmium spp., was dominating the phytoplankton communities, with a relative density of >60%. Aside from Trichodesmium spp, the diatoms, Chaetoceros lorenzianus, Thalassionema nitzschioides, Bacteriastrum furcatum, Chaetoceros curvisetus, and Chaetoceros dichaeta were also the most abundant species in Makassar Strait. There was no extreme species assemblage shifting along the latitudinal and longitudinal gradients in the Makassar Strait. The phytoplankton community structure in all stations was similar, with noticeable differences only found at stations 8, 21, and 29 that are located in proximity to the Kalimantan coastline. However, a southward decrease in the density and diversity of phytoplankton was noticed in this study. It was confirmed that Makassar Strait was not a barrier for phytoplankton dispersal, which is shown in an indistinct shift in the phytoplankton community structure both latitudinally and longitudinally. However, ITF might be an important factor that controls the latitudinal trend in phytoplankton diversity and cell density in this research.

1. Introduction
Makassar Strait is a unique area that serves as a geographical barrier that separated the biogeographic realms of Indonesia into Indo-Malayan and Australasian, or a barrier between the Sunda-Shelf-Philippines and Wallacea bioregion [1]. The strait is also thought to have created the 'Ocean Wallace line' for several coral reef-related organisms, such as mantis shrimp Haptosquilla pulchella [2]. Besides, the Makassar Strait is one of Indonesian Throughflow (ITF) pathways, which transport around 8 Sv of water masses and contributes to around 80% of the ITF system’s total flow[3, 4]. The presence of ITF also affects marine organisms’ diversity in the strait by acting as the dispersal agent for its planktonic larvae, such as the mantis shrimp (Haptosquilla pulchella) [5]. On the other hand,
the seasonal runoff from the large rivers, such as the Mahakam River in Kalimantan, into the Makassar Strait could influence the surface water’s salinity and nutrient level in the strait [6]. Thus, it also affects the dynamic of marine organisms communities in the Makassar Strait water columns, particularly the planktonic organism.

As the marine ecosystem’s primary producer and foundation, the abundance, and diversity of phytoplankton can regulate other marine organism’s population at the higher trophic levels [7, 8, 9]. Phytoplankton is also an important component that drives the ocean’s biogeochemical cycle, such as in the carbon sequestration process [10]. The importance of phytoplankton was particularly high in the oligotrophic oceanic water and could contribute to up to 90% of the total chlorophyll-a concentration in the ecosystem [8]. Furthermore, the phytoplankton diversity has a stabilizing effect on the community structure and regulating the rate of usage of natural resources in the planktonic communities, which then also affecting the biogeochemical cycle in the ecosystem [11, 12].

Even though oceanic plankton has no definitive barrier of dispersal, there is a trend of decreasing abundance [13] and increasing diversity [10, 14] in the oceanic ecosystem closer to the equatorial regions. In this case, the equatorial oceanic ecosystems should have a high diversity of phytoplankton, but in much lower abundance or cell density compared to the one in the temperate and polar regions [10, 13, 14]. However, physical heterogeneity and the existence of landmasses, like islands or continent, could potentially limit the distribution of marine phytoplankton species across the pelagic ecosystems [13].

Changes in the species composition, distribution range, and disappearance or appearance of certain phytoplankton species could act as a proxy to quickly detect the disturbances or anomalies that occurred in the marine ecosystems [15]. Thus, understanding the shift in phytoplankton communities across geographical distances is important to detect any changes in the studied community due to disturbances caused by anthropogenic activities, naturally occurred anomalies, or climate changes [16]. It also helps to understand how those changes affect other organisms at the higher trophic level and those changes affect the function of many unique oceanic or coastal ecosystems within the Makassar Strait. Therefore, this study aimed to describe the phytoplankton community structure in the Makassar Strait and determine the longitudinal or latitudinal shift in the phytoplankton community within the strait. In addition, it was hypothesized that the Makassar Strait should not become a geographical barrier in the distribution of phytoplankton. However, ITF, which is known as a dispersal agent for many planktonic organisms, should have a much higher influence on the distribution of phytoplankton in the Makassar Strait and might cause latitudinal differences in the phytoplankton communities within the strait.

2. Materials and Methods

2.1. Study Area

This research was conducted in 2013 as a part of the Expedition of Widya Nusantara (E-WIN) in the Makassar Strait. The plankton sampling was conducted at 20 sampling stations during the 10 days cruise from 07th to 17th of June 2013 (Figure 1). Initially, there were 29 sampling stations in this expedition, but we obtained samples only from 20 stations due to time constraints and bad weather conditions. The sampling stations were situated along the strait by taking account of the topographic characteristic at the bottom of Makassar Strait and the known flow pattern of ITF along the strait. Stations 1-3 located along the Labani Channel that connects the South Makassar Basin to the North Makassar Basin, while stations 4-21 were situated across the North Makassar Basin, and stations 22-29 were located at the entrance to the strait from the Celebes Sea (Figure 1).
Figure 1. Sampling stations of the 2013 EWIN cruise in the Makassar Strait. The unusual numbering of stations at 20 stations is due to the absence of several stations that are not exemplified from the original 29 sampling stations. Scale in nautical miles (NM).

2.2. **Field Sampling**
Phytoplankton samples were collected by a 150m vertical haul using Kitahara plankton net (Ø 31cm; length 1 m, mesh size 80 µm). An analog TSK flowmeter was fitted at the Kitahara net’s mouth to measure filtered water volume using the formula as described in Arinardi (1997) [17]. After each haul, the plankton net was soaked with seawater to release entangled cells from the mesh of the net. The filtered sample collected in the net’s cod end or sample ‘bucket’ was then moved into a 250mL plastic bottle and preserved by adding 2 mL formaldehyde (40%) per 100 mL sample [18].

2.3. **Identification and Enumeration**
A fraction method [17, 19] was used in the identification and enumeration of phytoplankton species of this study. About 1 to 1.5 mL subsample was taken from a carefully preserved phytoplankton sample and placed in the Sedgewick Rafter Counting Chamber (SRCC). Subsamples were then observed, counted, identified, and documented under the Nikon Diaphot inverted phase-contrast microscope, connected with Canon 500D Digital Single Lens Reflex camera. The number of counted phytoplankton cells was then converted into cells.m-3 using a modified formula [17, 20]. Whenever possible, Phytoplankton was identified up to species level by observing the cells’ morphological and morphometrical characters under the light microscope (LM) with the aid of several identification guides [21-28]. An online taxonomic database, the Algaebase [29], was also used to correct the scientific names from the older publications and match with the most recent and accepted scientific names.
2.4. Data Analysis

This study used several statistical analyses, such as non-metric multidimensional scaling (nMDS), clustering analysis using Unweighted Pair Group Method with Arithmetic mean (UPGMA), and non-linear regression. All statistical analysis was conducted in RStudio using ‘vegan’ [30] and ‘fANCOVA’ [31] packages. A non-parametric estimator of species richness, the 2nd order Jackknife (Jackknife-2) [32] was used to estimate the number of missing species from the effort (number of sampling station) in this study. To visually observed a shift in phytoplankton species composition or assemblages, the cell density data of each species were converted into relative density (RD) based on the formula described by Cox (1976) [33]. Furthermore, to find out the most important species based on its abundance (Relative Density/RD) and distribution (Relative Frequency of occurrence/RF), the Importance Value (IV) of each phytoplankton species was also calculated [33].

The LOESS (Locally Weighted Regression Smoother) smoother [34, 35] was used to observe the latitudinal and longitudinal trends in the density and diversity of phytoplankton in the study area. To avoid bias in the selection of span parameters in LOESS, Generalized Cross-Validation (GCV) analysis [35, 36] was used to obtain a robust value of span for the LOESS smoothing of each dependent variable. However, since LOESS cannot calculate the statistical significance of the trend, Generalized Additive Model (GAM) with the Poisson log link function was used to determine the phytoplankton’s latitudinal and longitudinal trends data [35]. Analysis of the differences and similarities of the phytoplankton communities from the study sites was done using nMDS and UPGMA with Bray-Curtis dissimilarity index [35, 37, 38]. Aside from the STRESS value, a Shepard diagram was then used to determine the goodness of fit of the nMDS result [35, 37].

3. Results

3.1. Phytoplankton Community Structure

There were 165 species of phytoplankton were identified consisting of 1 species of cyanobacteria (Phylum: Cyanobacteria), 97 species of diatoms (Phylum: Bacillariophyta), and 67 species of dinoflagellates (Phylum: Miozoa) (Figure 2). The largest genera with the highest number of member species were Chaetoceros (diatoms) and Tripos (dinoflagellates), with 24 member species each. As a note, the analysis using 2nd order Jackknife (Jackknife-2) non-parametric estimators of species richness suggested that at least 47 phytoplankton species were estimated to be missing from the current sampling effort.

In general, Trichodesmium spp. (Cyanobacteria) dominated the Makassar Strait’s phytoplankton community, with a relative density of up to 62% of the total cell density of phytoplankton. The total density of Trichodesmium spp. was between $3 \times 10^4$ cells.m$^{-3}$ and $1.62 \times 10^5$ cells.m$^{-3}$. Besides, Trichodesmium spp. was also considered the most important species within the phytoplankton communities in Makassar Strait, with an IV over 30% (Figure 2). Five most abundant species of diatoms in the water column of Makassar Strait after Trichodesmium spp. were Bacteriastrum furcatum, Chaetoceros curvisetus, Chaetoceros dichaeta, Chaetoceros lorenzianus, and Thalassionema nitzschioides. The total density of those most abundant species was up to $1.55 \times 10^5$ cells.m$^{-3}$, $1.51 \times 10^5$ cells.m$^{-3}$, $7.1 \times 10^4$ cells.m$^{-3}$, $5.1 \times 10^4$ cells.m$^{-3}$, and $3.6 \times 10^4$ cells.m$^{-3}$, respectively. Interestingly, not all of the most abundant diatoms were widespread in the Makassar Strait. Besides Trichodesmium spp., only B. furcatum and T. nitzschioides could be found in all sampling stations in this study. Other species that have the widest distribution range were two diatoms species, Proboscia alata, Thalassiothrix longissima, and one dinoflagellate species, Tripos
trichoceros. The total density of those species were $3.3 \times 10^4 \text{cells.m}^{-3}$, $1.5 \times 10^4 \text{cells.m}^{-3}$, and $7.6 \times 10^3 \text{cells.m}^{-3}$, respectively.

In general, phytoplankton in the Makassar Strait was more abundant in areas closer to the mainland than in areas in the middle of the strait (Figure 5). Even so, more species were found in the stations at the northern entrance of the strait compared to the other area in this study (Figure 5B). Low diversity (Shannon H’) and evenness (Shannon J) (Figure 5C & 5D) in the area with a high number of phytoplankton species (Figure 5B) were also observed. Most likely due to over-dominance of cyanobacteria, *Trichodesmium* spp. in that area (Figure 3A & 4A). Even so, the diversity and evenness within the phytoplankton community were higher in stations closer to Kalimantan compared to the stations closer to Sulawesi (Figure 5C & 5D). Diatoms were more abundant at stations closer to the Kalimantan coastal area compared to the area at the centre of the strait or area closer to the Sulawesi coastal area (Figure 5E). On the other hand, dinoflagellates were more abundant in the area with a low density of diatoms and have a centre of distribution around the northern area and the entrance of Makassar Strait (Figure 5E & 5F). Cyanobacteria (Figure 5G) has a similar distribution pattern with dinoflagellates (Figure 5F) and were found at its highest density at stations 9, 14 and 29.

3.2. Species Composition at Different Latitude and Longitude

Complete analysis at species level showed subtle changes in the species composition across different latitude and longitude in Makassar Strait. However, due to the over-dominance of *Trichodesmium* spp. in all study sites in this study (Figure 3A & Figure 4A), a separate histogram without the cell density of *Trichodesmium* spp. was created to emphasize the species composition within the diatoms and dinoflagellates groups (Figure 3B & Figure 4B).

Longitudinally, there was no drastic change in phytoplankton species assemblages in the Makassar Strait (Figure 3). The phytoplankton assemblages found in areas near Kalimantan were similar to those in areas near Sulawesi (Figure 3B). There were no gradual and drastic changes in the composition of phytoplankton species from Kalimantan to Sulawesi. However, the Bray-Curtis nMDS ordination and the UPGMA clustering analysis clearly showed that the three stations (stations 8, 21, 29) (Figure 6) near the Kalimantan coastline (Figure 6) did have a very different phytoplankton community structure compared to other stations in Kalimantan. Station 21 had a unique phytoplankton community where diatoms generally replaced the predominance of cyanobacteria in the water column (Figure 3A). It was also the only station in which *C. curvisetus* was the most abundant species within the phytoplankton community (Figure 3A). Aside from station 21, distinct species assemblages were found in station 1 and 17 located around the Makassar Strait center. Station 1 had a phytoplankton community without *C. lorenzianus*, while *Thalassiosira* spp. and *P. alata* were found at higher relative density in station 17 than the other stations (Figure 3B).

Similar to longitudinal trends, there were no drastic changes in the phytoplankton community along the latitudinal gradients in Makassar Strait (Figure 4). However, the species assemblages at the northernmost station were very different from the southernmost station in this study (Figure 4B). As shown in Figure 4A & B, aside from *Trichodesmium* spp., the other most abundant species at the northernmost station (station 29) were *C. lorenzianus*, *T. nitizschioides*, and *B. furcatum*. However, this is not the case at the southernmost station (station 1), where no diatoms or dinoflagellates had a very prominent dominance in the phytoplankton community (Figure 4B). At station 1, there were five diatoms, *Chaetoceros affinis*, *Cylindrotheca closterium*, *P. alata*, *Rhizosolenia imbricata*, and *T. nitizschioides*, were found with the highest cell density compared to the other diatoms and dinoflagellates. In addition, according to the Bray-Curtis ordination and UPGMA clustering analysis, station 29 (the northernmost site) has a unique phytoplankton community structure (Figure 6).
A combination of nMDS ordination and UPGMA clustering analysis, based on Bray-Curtis dissimilarity of phytoplankton species assemblages in each station, is shown in Figure 6. Based on the result of nMDS analysis, there were three distinct phytoplankton groups at the study sites and a unique phytoplankton community structure at stations 8, 21, and 29 (Figure 6A). Note that the grouping of stations in the nMDS ordination plot (Figure 6A) was based on the UPGMA analysis (Figure 6B) to avoid subjectivity in the grouping process. The first group in the nMDS plot consisted of station 1, 17, 19, and 25, which had different phytoplankton community structure than the second group (stations 12 and 27), and the third group (stations 2, 3, 4, 6, 9, 11, 15, 22, 23, and 24) (Figure 6A). Note that the STRESS value of the nMDS result was lower than 0.05, which indicated an excellent configuration of the plotted model (Figure 6A).

**Figure 6.** The Importance Value (IV) of each species in the groups of (A) diatoms, (B) dinoflagellates, and (C) cyanobacteria in the Makassar Strait. Values of IV were calculated by taking into account the abundance and distribution of each species.
Figure 3. Phytoplankton community structure expressed as the relative density of each species within a sampling station. The stations were ordered from left to right based on the stations’ longitude. (A) bar graph of all species; (B) bar graph without *Trichodesmium* spp. (cyanobacteria).
Figure 4. Phytoplankton community structure expressed as the relative density of each species within a sampling station. The stations were ordered from top to bottom based on the stations’ latitude. (A) bar graph of all species; (B) bar graph without *Trichodesmium* spp. (cyanobacteria).
Figure 5. Contour map showing the spatial trend of (A) phytoplankton total density, (B) number of species, (C) diversity (Shannon H’), (D) equitability or evenness (Shannon J), (E) diatoms density, (F) dinoflagellates density, and (G) cyanobacteria density in Makassar Strait.
3.3. Trends in Phytoplankton Density and Diversity Across Geographical Gradients

The longitudinal trends of the diversity and density of phytoplankton groups in this study were different from the latitudinal trends (Figure 7 & 8). In addition, the latitudinal trend in phytoplankton cell density differed from the diversity of phytoplankton (Figure 7). In general, phytoplankton cell density was very high ($2.8 \times 10^5$ cells.m$^{-3}$) in the area closest to the Kalimantan coastal area. The density was sharply declined in the station further from the coastline and reached the lowest density ($6.7 \times 10^4$ cells.m$^{-3}$) at higher longitude, or closer to Sulawesi island (Figure 7A). Similarly, the density of diatoms, dinoflagellates, and cyanobacteria were higher around Kalimantan coastal area compared to the area close to the Sulawesi coast (Figure 7E–F). However, phytoplankton diversity has the opposite trends compared to the cell density of phytoplankton (Figure 7B–D). Despite the obvious increasing trend eastward, the number of species within the community did not change drastically along the longitude (Figure 7B). However, both diversity and evenness reached their maximum at the stations closest to the two mainlands (Figure 7C & 7D). The Shannon H’ (diversity index) and Shannon J (evenness index) values were the lowest in the middle part of Makassar Strait (Figure 7C & 7D).
Figure 7. Longitudinal trend in the data of (A) total phytoplankton density, (B) number of species, (C) diversity (Shannon H’), (D) evenness or Shannon equitability (Shannon J), (E) diatoms density, (F) dinoflagellates density, (G) cyanobacteria density. The span value for each graphic was determined based on the result of the GCV analysis.

Latitudinally, the density and diversity of phytoplankton cells were decreased southward of the Makassar Strait (Figure 8). The phytoplankton cell density, either the total density or the density of each phytoplankton groups, was very high at the northernmost station and then decreased southward and reached its lowest density at the southernmost station (Figure 8A, Figure 8E–G). Unlike cell density, the number of phytoplankton species, diversity, and evenness, did not start from the highest point of the northernmost station, instead, it started around the median value and then declined sharply at the southern stations closest to the equator (Figure 8B–D). The maximum number of species, diversity, and evenness were observed at stations positioned between latitude -1 to -1.5, but the value was then quickly decreased and reached one of its lowest value at the southernmost station (Figure 8B–D).
Figure 8. Latitudinal trends in the data of (A) total phytoplankton density, (B) number of species, (C) diversity (Shannon H’), (D) evenness or Shannon equitability (Shannon J), (E) diatoms density, (F) dinoflagellates density, (G) cyanobacteria density. The span value for each graphic was determined based on the result of the GCV analysis.

4. Discussions

4.1. Species Assemblages in the ITF-influenced Makassar Strait

Unlike in the coastal area, which commonly dominated by diatoms [39], the phytoplankton communities in the Makassar Strait were mainly dominated by cyanobacteria, particularly *Trichodesmium* spp. The dominance of cyanobacteria in the oceanic ecosystems was observed in another area in Indonesia, such as the Banda Sea during a study in November 1999 [40]. *Trichodesmium* spp was also the most important species within the phytoplankton community of Makassar Strait in this study. *Trichodesmium* spp’s importance was reflected in its highest IV value, which indicated its high abundance and wide distribution across the study areas. For the record, species with low IV values are not necessarily insignificant or of little importance, because the IV values only reflect the distribution and cell density of species in the study area. In this case, species with low abundance or limited distribution can act as keystone species in the phytoplankton
community. For example, some toxic phytoplankton species, such as *Chrysocromulina polylepis*, was regarded as keystone species that helps maintain the coexistence of many non-toxic species by affecting the competition rate and regulating the grazing pressure despite its low cell density in the community [41].

Aside from the cyanobacteria, the other most abundant phytoplankton in Makassar Strait were the chain-forming diatoms, such as *B. furcatum*, *C. curvisetus*, *C. dichaeta*, *C. lorenzianus*, and *T. nitzschioides*. Although slightly different, previous research by Thoha [42] also reported a co-dominance of *Chaetoceros*, *Rhizosolenia*, *Thalassiothrix*, and *Nitzschia* in the oceanic systems of Makassar Strait. As a note, a high abundance of *Chaetoceros* in the Indonesian oceanic ecosystem has been reported from other oceanic ecosystems, such as the Banggai Sea [43] and Banda Sea [40]. *Chaetoceros* generally was considered as a cosmopolitan diatoms genus and could be found in almost all marine ecosystems. It usually is more abundant and formed blooms in coastal areas with a higher trophic condition, such as in the highly eutrophic coastal waters of Jakarta Bay [44]. Several species found in Makassar Strait of this study, such as *Alexandrium* sp., *Gonyaulax* sp., *Prorocentrum lima*, *Pseudo-nitzschia* spp., *Skeletonema costatum*, *Chaetoceros* spp., including the dominant cyanobacteria in this study, *Trichodesmium* spp., were considered as potentially harmful and bloom-forming species [45, 46, 47].

Similar to other marine ecosystems, the oceanic system generally has limited productivity due to the limitation of nitrogen (N) input to the ecosystem [6, 8, 48]. In this study, the surface waters of the Makassar Strait was classified as oligotrophic based on the total density of phytoplankton that was lower than the oligotrophic threshold \(<4.16 \times 10^6 \text{cells.m}^{-3}\) or \(<4,160 \text{cells.L}^{-1}\) [49]. The oligotrophic condition of Makassar Strait based on the nutrient concentration in the water column was also described by Khasanah [50] in the 2013 EWIN report. Data in the report showed that the surface water of Makassar Strait was oligotrophic, with a nitrogen (N) concentration between 0.009-0.067 mg.L\(^{-1}\) and phosphate concentration between 0-0.007 mg.L\(^{-1}\). Meanwhile, the silicate concentration at the surface layer of Makassar Strait in 2013 was ranging between 0.136-0.282 mg.L\(^{-1}\) [50]. Furthermore, the distribution of those three key nutrients for phytoplankton growth was homogenous at the Makassar Strait’s surface layer [50]. Those findings implied that all phytoplankton species in all stations were subjected to the same nutrient level at the surface layer of the Makassar Strait, with some negligible latitudinal or longitudinal variations.

The oligotrophic and N-limited water column might be the cause of a much lower density of diatoms and dinoflagellates because the water condition was not suitable to sustain a large population of those groups. In this case, the dominance of cyanobacteria in the phytoplankton community was typical in the oligotrophic and N-limited tropical oceanic ecosystems, since those conditions give a great advantage to the cyanobacteria species with N2-fixation ability, such as *Trichodesmium* spp. [48, 51, 52, 53]. Interestingly, the Makassar Strait’s surface water in 2013 seems to be more P-limited rather than N-limited due to the very low concentration of phosphate [50]. This condition was also favourable for *Trichodesmium* spp., which was also known for its unique ability to overcome the limited availability of phosphorus (P) by maximizing phosphorus uptake, adjusting its intracellular N:P ratio, or by utilizing its buoyancy-regulating mechanism to scavenge P in the water column [53]. Phototrophic cyanobacteria also belonged to the group of “gleaners” which were generally more successful in dominating the ecosystem with a low and stable nutrient concentration or supply [9]. Note that the density of *Trichodesmium* spp. was much lower at some stations with a higher density of diatoms, such as station 21 that was located near the mouth of a large river in Sangkulirang, East Kalimantan.
4.2. Phytoplankton Community Shift Across Geospatial Gradients within the Makassar Strait

As explained earlier, Makassar Strait is a unique ecosystem, which creates a boundary between two ecozones and is heavily influenced by the ITF current [1, 3, 4]. But unlike terrestrial organisms, in which distribution was limited by the presence of a geographical barrier, such as a strait, distribution of phytoplankton species should not be limited by the Makassar Strait. In addition, compared to benthic and sessile organisms, oceanic phytoplankton is known to have no clear barriers to their distribution in various marine ecosystems [13]. Thus, the community structure of phytoplankton on the Kalimantan coast should be similar to that of the Sulawesi coast. This hypothesis is supported by longitudinal species composition data in this study which shows that there are no significant differences in phytoplankton communities in the coastal areas of Kalimantan and Sulawesi, in this case, the strait is not a barrier to the spread of phytoplankton species.

However, spatial trends in the abundance or cell density of phytoplankton in this study generally show a higher density of cells in the area closer to Kalimantan compared to that of the Sulawesi coastal area. That trend might be related to a much higher riverine input from the large rivers in Kalimantan, particularly from Mahakam River, which supplies more nutrients to support a higher density of phytoplankton in the area closer to its coastal area. River discharge and surface run-off have long been known to greatly affecting the density and diversity of phytoplankton in the coastal area by supplying the necessary nutrients to increase its primary production and population growth [6]. The influence of river discharge from the Kalimantan island might also be the reason for unique phytoplankton communities in stations 8, 21, and 29, which are located closer to the Kalimantan coastal area. Station 8 and 21, particularly station 21, do not have the dominance of *Trichodesmium* spp. as seen at other stations in this study. Instead, diatoms *Chaetoceros subtilis* were dominant in the phytoplankton community at station 21.

In general, many taxa of marine organisms, including phytoplankton, follows a declining trend in its diversity along with increasing latitude and are commonly found at its highest diversity around the equatorial area [10, 14]. Unfortunately, such a trend can’t be observed clearly in phytoplankton data in this study, most likely due to the limited latitudinal range that was sampled (only approx. 6° Lat.). However, the data did shows a gradual southward decrease in the abundance and diversity of phytoplankton. That trends were suspected to be influenced by the presence of two mainlands that supply the nutrient to the Makassar Strait, and the ITF that distribute the nutrient and planktonic organism along the Strait. The ITF, which known to flow southwest and turn to the southeast along with the bathymetry at the southernmost area of the strait [54] would distribute the nutrients from the riverine inputs from the mainlands along the strait. Although the surface layer of Makassar Strait was nutrient-poor, the strait’s bottom layer was nutrient-rich, with the concentration of nitrate between 0.238-0.583 mg.l⁻¹, phosphate between 0.038-0.098 mg.l⁻¹, and silicate between 0.551-3.879 mg.l⁻¹ [50].

On the other hand, ITF flow patterns and Western Boundary Current’s existence that causing turbulence around the northern entrance of the Makassar Strait [54, 55] might be the reason for a high number of phytoplankton species found around that area (stations 22, 23, 24). It is known that phytoplankton diversity hotspot often found in the area with high turbulence and low stability water columns [12]. The turbulence caused by ocean currents could also produce a spatial gradient that regulates the diversity of phytoplankton in oceanic ecosystems [13]. The Makassar Strait was found to have medium to high turbulence in the water column [55]. This factor could increase the productivity and biomass of phytoplankton in the surface layer by distributing the nutrient-rich deep water into the surface layer via upwelling process. The upwelling process can break through the strong thermocline layer that commonly present in tropical waters. However, despite the high number of species, the
diversity (Shannon $H'$) and equitability (Shannon $J$) in the northern entrance of Makassar Strait were low due to the over-dominance of several phytoplankton species, particularly the cyanobacteria *Trichodesmium* spp, which occupied more than 60% of total cell density in the phytoplankton community. Interestingly, similar to diatoms and dinoflagellates, a southerly downward trend in cell density was also found in the cyanobacteria group. That implies that driving factors of the trend were similar in all three phytoplankton groups in this study.

5. Conclusion

It can be concluded from this research that the Makassar Strait is not a geographical barrier for the distribution of phytoplankton. The lack of distinct differences between the phytoplankton communities on the latitudinal and longitudinal gradients supports those statements. However, the southward flowing ITF might play a great role in the variation within the phytoplankton communities across different latitudes. A general southward decrease was observed in both cell density and species diversity of all phytoplankton groups. In addition, differences in riverine inputs from two mainland areas, Kalimantan and Sulawesi, can cause differences, particularly in different phytoplankton groups’ cell density. On the other hand, the oligotrophic nature of the surface layer of the Makassar Strait provides an advantage for *Trichodesmium* spp., which is known to be able to withstand both N and P limited conditions, and allows it to dominate the phytoplankton community in the strait.

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References

[1] Jepson P and Whittaker R J 2002 Ecoregions in Context: a Critique with Special Reference to Indonesia *Conserv. Biol.* 16 42-57
[2] Barber P H, Palumbi S R, Erdmann M V and Moosa M K 2000 A marine Wallace's line? *Nature* 406 692-3
[3] Gordon A L, Susanto D, Huber B A, Sulistyo B and Supangat A 2010 Seven years of measuring the Makassar Strait throughflow—the primary component of the Indonesian Throughflow *P. Ocean. Obs.* 9 21-5
[4] Sprintall J 2009 Encyclopedia of Ocean Sciences (Second Edition), ed J H Steele (Oxford: Academic Press) pp 237-43
[5] Barber P H, Palumbi S R, Erdmann M V and Moosa M K 2002 Sharp genetic breaks among populations of Haptosquilla pulchella (Stomatopoda) indicate limits to larval transport: patterns, causes, and consequences *Mol. Ecol.* 11 659-74
[6] Kinkade C, Marra J, Langdon C, Knudson C and Ilahudet A G 1997 Monsoonal differences in phytoplankton biomass and production in the Indonesian Seas: tracing vertical mixing using temperature Deep Sea Research Part I: Oceanographic Research Papers 44 581-92
[7] Lalli C and Parsons T R 1997 Biological oceanography: an introduction (Oxford: Elsevier)
[8] Redden A M, Kobayashi T, Suthers I, Bowling L, Rissik D and Newton G 2019 Plankton: A Guide to Their Ecology and Monitoring for Water Quality, p 1
[9] Lévy M, Jahn O, Dutkiewicz S, Follows M J and d’Ovidio F 2015 The dynamical landscape of marine phytoplankton diversity J. Roy. Soc. Interface 12 20150481
[10] Righetti D, Vogt M, Gruber N, Psomas A and Zimmermann N E 2019 Global pattern of phytoplankton diversity driven by temperature and environmental variability Sci. Adv. 5 1-10
[11] Ptcenik R, Solimini A G, Andersen T, Tamminen T, Brettum P, Lepistö L, Willén E and Rekolainen S 2008 Diversity predicts stability and resource use efficiency in natural phytoplankton communities P. Nat. Acad. Sci. 105 5134-8
[12] Clayton S, Dutkiewicz S, Jahn O and Follows M J 2013 Dispersal, eddies, and the diversity of marine phytoplankton Limnol. Oceanogr.: Fluids Environ. 3 182-97
[13] Chust G, Irigoien X, Chave J and Harris R P 2012 Latitudinal phytoplankton distribution and the neutral theory of biodiversity J. of Glob. Ecol. Biogeogr. 22 531-43
[14] Barton A D, Dutkiewicz S, Flierl G, Bragg J and Follows M J 2010 Patterns of diversity in marine phytoplankton Science 327 1509-11
[15] Beaugrand G, Harlay X and Edwards M 2014 Detecting plankton shifts in the North Sea: a new abrupt ecosystem shift between 1996 and 2003 Mar. Ecol. Prog. Ser. 502 85-104
[16] Ibarbalz F M, Henry N, Brandão M C, Martini S, Bussen G, Byrne H, Coelho L P, Endo H, Gasol J M, Gregory A C, Mahé F, Rigonato J, Royo-Llonch M, Salazar G, Sanz-Sáez I, Scalco E, Soviadán D, Zayed A A, Zingone A, Labadie K, Ferland J, Marec C, Kandels S, Picheral M, Dimier C, Poulin J, Pisarev S, Carmichael M, Pesant S, Acinas S G, Babin M, Bork P, Boss E, Bowler C, Cochrane G, de Vargas C, Follows M, Gorsky G, Grimsley N, Guidi L, Hingamp P, Hudicone D, Jaillon O, Kandels S, Karp-Boss L, Karsenti E, Not F, Ogata H, Pesant S, Poultion N, Raes J, Sarket C, Speich S, Stemmman L, Sullivan M B, Sunagawa S, Wincker P, Babin M, Boss E, Hudicone D, Jaillon O, Acinas S G, Ogata H, Pelletier E, Stemmman L, Sullivan M B, Sunagawa S, Bopp L, de Vargas C, Karp-Boss L, Wincker P, Lombard F, Bowler C and Zinger L 2019 Global Trends in Marine Plankton Diversity across Kingdoms of Life Cell 179 1084-97.e21
[17] Arinardi O 1997 Metode analisis air laut, sedimen dan biota, ed H Hutagalung, et al. (Indonesia: Pusat Penelitian dan Pengembangan Oceanologi) pp 143-52
[18] Edler L and Elbrächter M 2010 Microscopic and molecular methods for quantitative phytoplankton analysis, ed B Karlson, et al. (Paris: UNESCO) pp 13-20
[19] LeGresley M and McDermott G 2010 Microscopic and molecular methods for quantitative phytoplankton analysis. UNESCO (IOC Manuals and Guides), ed B Karlson, et al. pp 25-30
[20] Semina H 1978 Phytoplankton manual, ed C R Tomas and G R Hasle (San Diego: Academic Press) pp 5-584
[21] Steidinger K A and Jangen K 1997 Identifying Marine Phytoplankton, (San Diego: Academic Press) pp 387-584
[27] Praseno D P and Sugestiningsih 2000 *Retaid di perairan Indonesia* (Jakarta: Pusat Penelitian dan Pengembangan Oceanologi-LIPI)

[28] Al-Kandari M, Al-Yamani F and Al-Rifaie K 2009 *Marine phytoplankton atlas of Kuwait’s waters* (Kuwait: Kuwait Institute for Scientific Research)

[29] Guiry M D and Guiry G M 2020 GreenBase. (Galway: National University of Ireland)

[30] Oksanen J, Blanchet F G, Kindt R, Legendre P, Minchin P R, O'Hara R B, Simpson G L, Solymos P, Stevens M H H and Wagner H 2015 *vegan: Community Ecology Package.*

[31] Wang X-F 2010 fANCOVA: Nonparametric Analysis of Covariance.

[32] Colwell R K and Coddington J A 1994 Estimating Terrestrial Biodiversity through Extrapolation *Philosophical Transactions: Biological Sciences* **345** 101-18

[33] Cox G W 1976 *Laboratory manual of general ecology 3rd ed.* (Iowa: Wm C. Brown Company Pub)

[34] Logan M 2011 *Biostatistical design and analysis using R: a practical guide* (UK: John Wiley & Sons)

[35] Zuur A F, Smith G M and Ieno E N 2007 *Analysing ecological data* (New York: Springer)

[36] Borcard D, Legendre P and Gillet F 2011 *Numerical Ecology with R* (New York: Springer)

[37] Oksanen J 2010 Multivariate analysis of ecological communities in R: vegan tutorial. R package version. R Foundation for Statistical Computing Vienna, Austria)

[38] Oseji O F, Chigbu P, Oghenekaro E, Waguespack Y and Chen N 2018 Spatiotemporal patterns of phytoplankton composition and abundance in the Maryland Coastal Bays: The influence of freshwater discharge and anthropogenic activities *Estuar. Coast. Shelf Sci.* **207** 119-31

[39] Sediadi A 2004 Dominasi cyanobacteria pada musim peralihan di perairan Laut Banda dan sekitarnya *Makara J. Sci.* **8** 1-14

[40] Chakraborty S, Ramesh A and Dutta P S 2016 Toxic phytoplankton as a keystone species in aquatic ecosystems: stable coexistence to biodiversity *Oikos* **125** 735-46

[41] Thoha H 2004 *Biodiversitas organisme planktonik dalam kaitannya dengan kualitas perairan dan sirkulasi massa air di Selat Makassar*, ed E A Sopaheluwakan: Pusat Penelitian Oseanografi, Lembaga Ilmu Pengetahuan Indonesia) pp 26-8

[42] Thoha H and Rachman A 2013 The Abundance and Spatial Distribution of Plankton Communities in Banggai Islands Waters *Jurnal Ilmu dan Teknologi Kelautan Tropis* **5**

[43] Adnan Q 1992 *Marine Coastal Eutrophication*, ed R A Vollenweider, et al. (Amsterdam: Elsevier) pp 809-18

[44] Praseno D and Wiadnyanah N 1996 HAB organisms in Indonesian waters *Can. Tec. Rep. Fish Aquat. Sci.* **69** 69-75

[45] Praseno D, Fukuyo Y, Widiarti R, Badrudin Y E and Pain S 1999 The HAB/red tide blooms in Indonesian waters 1997/1998. In: *Proceedings of the Fourth ASEAN-Canada Technical Conference on Marine Sciences, Malaysia*, pp 432-7

[46] Praseno D, Fukuyo Y, Widiarti R and Sugestiningsih 2003 Red tide occurrences in Indonesian waters and the need to establish a monitoring system. In: *Proceedings of Workshop on Red Tide Monitoring in Asian Coastal Waters* , pp 87-90

[47] Yurkovskis A, Kostrichkina E and Ikauniece A 1999 *Seasonal succession and growth in the plankton communities of the Gulf of Riga in relation to long-term nutrient dynamics.* (Dordrecht: Springer Netherlands) pp 83-94

[48] Spatharis S and Tsirtsis G 2010 Ecological quality scales based on phytoplankton for the implementation of Water Framework Directive in the Eastern Mediterranean *Ecol. Indic.* **10** 840-7

[49] Khasanah E N 2013 *Exploring the Deep Sea of Makassar Strait*, ed Susetiono (Jakarta, Indonesia: Research Center for Oceanography, Indonesian Institute of Sciences) pp 25-34
[51] Capone D G, Zehr J P, Paerl H W, Bergman B and Carpenter E J 1997 *Trichodesmium*, a Globally Significant Marine Cyanobacterium *Science* **276** 1221-9

[52] O’Neil J M, Davis T W, Burford M A and Gobler C J 2012 The rise of harmful cyanobacteria blooms: The potential roles of eutrophication and climate change *Harmful Algae* **14** 313-34

[53] Bergman B, Sandh G, Lin S, Larsson J and Carpenter E J 2013 *Trichodesmium* – a widespread marine cyanobacterium with unusual nitrogen fixation properties *FEMS Microbiol. Rev.* **37** 286-302

[54] Horhoruw S, Atmadipoera A, Purba M and Purwandana A 2015 Current Structure and Spatial Variation of Indonesian Throughflow in Makassar Strait Under Ewin 2013 (Struktur Arus dan Variasi Spasial Arlindo di Selat Makassar dari Ewin 2013) *ILMU KELAUTAN: Indonesian J. Mar. Sci.* **20** 87-100

[55] Prihatini D, Purba M, Naulita Y and Purwandana A 2016 Vertical Turbulent at Thermocline Layer in Makassar Strait *Int. J. Mar. Sci.* **6** 1-10