Spatial and temporal distribution of phytoplankton in the Gorontalo Bay, Indonesia

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Abstract. Phytoplankton has an important role in coastal ecosystems due to its ability to process photosynthesis as the base of producer for the aquatic food chain. The purpose of this study is to determine the spatial and seasonal distribution pattern of phytoplankton in Gorontalo Bay, Indonesia. The samples were taken from 5 sampling sites in the Gorontalo Bay, Indonesia in three different seasons: west monsoon season (in May), transition season (in June) and east monsoon season (in July). The results showed that ecological dynamics in the Gorontalo Bay was indicated by the various physics and chemical characteristics of waters spatially and seasonally. Based on the abundance of phytoplankton in the waters during the study, the east monsoon season was the most productive time in the Gorontalo Bay with an average of number of phytoplankton of 673026 cells L^{-1} followed by transition and west monsoon season with the average counts of phytoplankton of 352704 and 3839 cells L^{-1} respectively. Spatially, the highest abundance of phytoplankton was found in the station 3 with an average of 9891 cell L^{-1}, followed by station 4 with an average of 8770 cell L^{-1}, station 1 with an average of 7493 cell L^{-1}, station 2 with an average of 6343 cell L^{-1}, and, finally, station 5 with the average of 2651 cell L^{-1}.

Key Words: monsoon season, phytoplankton distribution, Gorontalo Bay.

Introduction. Tomini Bay is relatively fertile and rich in natural marine potential (Yusron & Edward 2000). It is also known as a marine tourism region and has a variety of potential pelagic fish resources (Wiadnyana 1998). The Bay of Gorontalo is part of Tomini Bay area which goes into the administrative area of Gorontalo City, Indonesia. The geographic conditions of the bay give consequences for the mass circulation of water between the waters within the bay and the surrounding as it is directly related to the Maluku Sea, Tolo Bay and the Celebes Sea (Setyadji & Priatna 2011). The existence of phytoplankton in the Gorontalo Bay is one of the ecological studies that need to be conducted regularly to monitor and ensure aquatic ecosystem balance.

Phytoplankton has an important role in coastal ecosystems due to its ability to process photosynthesis. Most of marine organisms depend on phytoplankton as a base producer for the aquatic food chain (Townsend et al 2000). Phytoplankton forms the essential base of the aquatic food web and plays a major role in aquatic productivity and ecosystem health (Nursuhayati et al 2013). The abundance and composition of phytoplankton in waters can be used as an indication of the fertility rate and water conditions changes (Karydis & Tsirtsis 1996; Thoha & Amri 2011; Radiarta 2013). Phytoplankton availability influences the distribution of consumer organisms especially the herbivore zooplankton. The high nutritional contents make phytoplankton become the valuable feed items in the aquatic food chain (Natrah et al 2007; Khatoon et al 2009; Banerjee et al 2010).

The phytoplankton distribution in the Gorontalo Bay is influenced by the dynamics occurring within and outside the water. Internal factors such as ecological interactions that take place in the bay waters and external factors such as seasons and human activities around the bay have the potential to affect the stability of the aquatic ecosystem. The purpose of this study is to determine the spatial and seasonal distribution pattern of phytoplankton in the Gorontalo Bay, Indonesia.

Material and Method

Description of the study sites. The study area was localized throughout the Gorontalo City coastal region called as Gorontalo Bay. This research was carried out in west monsoon (in May), transition (in June) and east monsoon season (in July) in the year 2017. Samplings were performed in 5 stations, all displaying diverse types of land use. In the main land near from site 1 there are rare resident settlements and a steep cliff close to site 2 with no human activities. Moreover, land use near from the site 3 is Bone River estuary. In the site 4 there is an oil port and in the site 5 there are densely populated settlements. Sampling in each station was performed out in 3 sub-stations by dragging the line-transect toward the offshore as presented on the map on the Figure1.

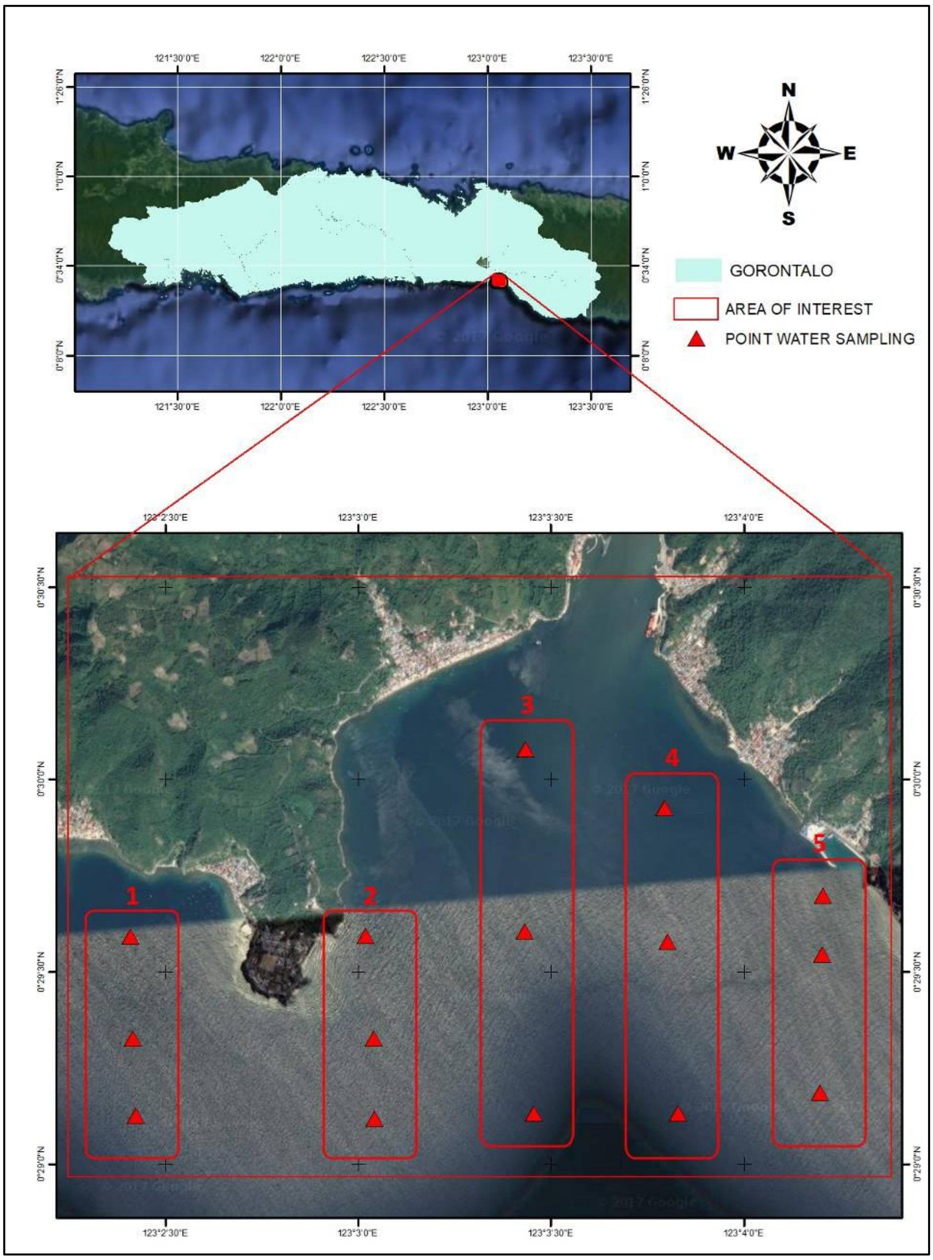

Figure 1. Map of the study area showing the locations of stations.

Physical and chemical parameters establishment. Physical parameters such as temperature, salinity, pH, and dissolved oxygen were conducted *in situ* in each station, while chemical parameters performed *ex situ* and determined using spectrophotometry according to the APHA (APHA 2012) methods consist of chlorophyll-*a*, nitrate, ammonium and orthophosphate.

The water sample for phytoplankton analysis purpose was collected using plankton-net (25 µm in mesh size) by horizontally towing at 15 points then compiled into 5 sample bottles preserved with a 10% lugol solution. In the meantime, water samples for chemical parameters measuring purpose were taken in depth ranging from 0 to 2 m from the surface in every site.

Phytoplankton performace. Phytoplankton was identified taxonomically using light microscope referred to Davis (1955) taxonomical guide. Phytoplankton abundances were measured using Lackey drop-transect method. Biological diversity index (H') and dominance index (D) were calculated according to the following equation (Shannon & Wiener and Sampson index 1949 in Odum 1998).

$$H' = -\sum_{i=1}^{s}\left(\frac{N_i}{N}\right)\ln\left(\frac{N_i}{N}\right)$$

$$D = \sum_{i=1}^{s}\left(\frac{N_i}{N}\right)^2$$

Where N_i symbol is individual amount of the phytoplankton species, and N is total individual amount, then s is a total phytoplankton species.

Data analysis. The variety of water parameters and counts of phytoplankton species in every sampling site and different season were performed descriptively. Furthermore, the correlation between physico-chemical water parameters and the abundance of phytoplankton in the Gorontalo Bay were analyzed using Microsoft Excel.

Results

Physico-chemical characteristics. Physico-chemical characteristics and chlorophyll-*a* in the Gorontalo Bay were studied parallel to the phytoplankton performance at the same time in the sampled stations. The results are showed in Table 1.

Tomini Bay water surface temperature varied with a minimum of 26.5^{o}C at station 3 in the east monsoon season and a maximum of 29.8^{o}C at station 1 in the west monsoon season. Although water temperature effect on communities and ecosystem processes is debated, it affects phytoplankton growth rates strongly (Edwards et al 2016). Renaud et al (2002) mentioned that phytoplankton tolerate a range of temperature 20-30°C and optimum temperature to phytoplankton development is 27-30°C.

The pH value showed maximum of 6.67 during transition season and a minimum of 5.67 at stations 2, 4 and 5 in in the west monsoon season. Marine phytoplankton in general is resistant to climate change in terms of ocean acidification and does not increase or decrease in its growth rate according to ecological relevant ranges of pH and CO_2 (Berge et al 2010).

The salinity is the main physical parameter that can be attributed to the plankton diversity and acting as a limiting factor, which influences the distribution of plankton communities (Sridhar et al 2006). The salinity ranged between 30.93 and 34.80 ppt. The minimum salinity was observed at station 5 in transition monsoon, while the maximum level was detected at station 1 in west monsoon period.

The dissolved oxygen (DO) concentration in water depends on its temperature and salinity. The quantity of organic matter presenting in the aquatic environment also depends on DO in water. If the decomposition of organic matter is in great proportion then it will absorb of DO in water too much (Shakweer 2003). The DO varied between a maximum of 6.15 mg L^{-1}in west monsoon period at station 4 and a minimum of 3.59 mg L^{-1} in east monsoon season at station 3. Phytoplankton are responsible for dissolved oxygen level in surface water, which upturns due to photosynthesis (Ramaraj et al 2010). Concentration of DO naturally associates with microalgae densities in waters (Kunlasak et al 2013).

Table 1

Waters characteristics of Gorontalo Bay in three different seasons in year 2017

Parameters	*West monsoon season*					*Transition season*					*East monsoon season*				
	1	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*
Temperature	29.80	29.70	28.43	29.07	29.50	29.40	28.17	26.73	28.27	26.83	29.60	28.40	26.50	27.27	28.40
pH	6.00	5.67	6.00	5.67	5.67	6.00	6.00	6.00	6.00	6.67	6.00	6.00	6.00	6.00	6.00
Salinity	34.8	34.13	34.63	35.03	34.03	32.73	32.37	31.53	31.9	30.93	32.10	32.9	33.27	30.87	31.8
DO	6.00	5.40	5.36	6.15	6.14	5.32	4.85	5.38	5.63	5.76	4.45	4.35	3.59	4.41	4.46
NO_3	0.058	0.060	0.146	0.042	0.084	0.089	0.132	0.079	0.098	0.126	0.061	0.051	0.084	0.117	0.144
NH_3	0.057	0.069	0.142	0.117	0.122	0.130	0.063	0.206	0.035	0.105	0.051	0.073	0.193	0.054	0.336
PO_4	0.026	0.057	0.038	0.024	0.044	0.003	0.046	0.013	0.024	0.006	0.059	0.052	0.094	0.137	0.088
Chlorophyll-*a*	1.789	1.536	1.175	0.651	0.821	1.806	1.610	1.377	1.182	0.984	1.806	1.969	2.332	3.744	1.775

1-5: stations.

The maximum concentration of phosphate (0.137 mg L^{-1}) was shown at station 4 east monsoon season, while the minimum value (0.003 mg L^{-1}) was recorded at station 1 transition period. The role of dissolved inorganic phosphorus could be considered as an important nutrient for marine phytoplankton in the oligotrophic settings and the need for evaluating nutrient limitation at the taxa and/or single cell level, rather than inferring it with nutrient concentrations and ratios or bulk enzyme activities (Mackey et al 2007).

Nitrate is the most stable form of inorganic nitrogen in the oxygenated waters (Nassar et al 2014). Dissolved nitrate attained a maximum of 0.146 in west monsoon season at station 3 and a minimum of 0.042 at station 4. Nitrate and phosphate are primary nutrients for algae growth (Haag 2007). Reduction of nitrogen and phosphorus concentrations also can be a limiting factor to phytoplankton growth (Freeman 2002).

Ammonium is the nitrogenous end product of the bacterial decomposition of natural organic matter containing nitrogen. In the presence of high ammonium concentrations, the phytoplankton productivity could be high or even higher if the cells are using NH_4^+ rather than NO_3^- (Dugdale et al 2007). The maximum concentration of ammonium (0.336 mg L^{-1}) occurred in east monsoon season at station 5 while the minimum (0.035 mg L^{-1}) was found in transition monsoon season at station 4. Hutchinson (1967) stated that Chlorophyta and diatom preferred nitrogen form of nitrate and ammonia.

Ocean phytoplankton production plays a considerable role in the ecosystem. Primary production can be indexed by chlorophyll concentration (Gui & Subrahmanyam 2018). Chlorophyll-*a* is the most commonly used indicator of phytoplankton biomass in the marine environment. It is relatively simple and cost effective to measure when compared to phytoplankton abundance and is thus routinely included in many surveys (Davies et al 2018). The highest chlorophyll-*a* occurred in east monsoon season with the number of average 3.744 mg L^{-1}. Season is one of some factors that can affect the variability of Chlorophyll–*a* concentration in the water. The upwelling in Gorontalo Bay generally occurs in the east season. The mass of water in the upper layers of the waters is driven by the eastern winds then the vacuum of this coated water is filled by the water mass from the nutrient-rich bottom. In addition, Al-Azri et al (2010) stated that the highest concentrations of chlolophyll-*a* (3 mg m^{-3}) were recorded during the southwest monsoon when upwelling is active along the coast of Oman.

Spatial distribution and composition of phytoplankton. The phytoplankton of Gorontalo Bay was represented by 39 taxa from 7 classes and 3 divisions: Chrysophyta (30 taxa), Chlorophyta (7 taxa) and Cyanophyta (2 taxa). Chrysophyta was the most dominant group, since it constitutes about 63.3% of the total average phytoplankton abundance of 182.326 cell L^{-1}, mainly due to the flourishing of *Chaetoceros affinis* (average of 25.441 cell L^{-1}), *Bacteriastrum hyalinum* (average of 19.624 cell L^{-1}), *Chaetoceros brightwelli* (average of 17.539 cell L^{-1}), *Chaetoceros messanensis* (average of 17.007 cell L^{-1}) and *Bacteriastrum delicatulum* (average of 15.660 cell L^{-1}). Cyanophyta was the second dominant group forming about 22.7% of the total average phytoplankton with 65.334 cell L^{-1} and a relative high occurrence of *Oscillatoria limosa* (average of 42.140 cell L^{-1}) and *Anabaena* sp. (average of 23.194 cell L^{-1}). Whereas, the other algae division, Chlorophyta as the least dominant group forming collectivity about 14.1% (total average 40.558 cell L^{-1}) with relative high occurrence of *Pediastrum simplex* (average of 17.381 cell L^{-1}) and *Pediastrum duplex* (average of 11.708 cell L^{-1}).

Recording of 39 phytoplankton species in this study is considered to be high since compared to the previous study that was reported by Kadim & Arsad (2016) that in the west of Tomini Bay founded 29 species of phytoplankton which dominated by Chrysophyta. In addition, Setyadji & Priatna (2011) stated that in the eastern part of Tomini Bay there were 33 species phytoplankton was recorded and dominated by Bacillariophyceae.

This research shows that the highest abundance of phytoplankton found in the station 3 with an average of 9891 cell L^{-1} followed by station 4 with an average of 8770 cell L^{-1}, station 1 with an average of 7493 cell L^{-1} and station 2 with an average of 6343 cell L^{-1}. Furthermore, the lowest population density of phytoplankton was recorded at station 5 with the average of 2651 cell L^{-1}. This may be due to rising up of organic materials which entered the river. The sewage discharge can cause phytoplankton productivity growth where sewage was the main source of nitrogen and phosporus (Burford et al 2012). The distribution and abundance of phytoplankton in tropical waters varied substantially because of the environmental flunctuations during the seasons (Rajkumar et al 2009).

Species diversity index (H') of phytoplankton population during this research varied from 0.433 to 2.712 and the dominance index (D) ranged between 0.071 and 0.302 (Table 2). In the west monsoon period, H' values with an average of 1.287-2.262 were recorded. Meanwhile, in the transition period, H' increased with the average from 2.268 to 2.712. In general, based on Shannon-Wiener diversity index, these two seasons performed an average diversity condition. On the other hand, the lower diversity value recorded during the east monsoon season with an average of 0.433 to 0.904. Diversity depends on key ecological processes such as competition, predation, succession and therefore changes in these processes can alter the species diversity index trough changes in evenness (Stirling & Wilsey 2001). The species diversity index of plankton communities can serve as an indicator that the ecosystem is under the influence of pollution or eutrophication (Telesh 2004 in Nassar & Gharib 2014). An increasing in diversity values means the water quality is recovered. Lower species diversity indicated influence of pollution (Nassar & Gharib 2014). According to the dominance index value (D) in the west monsoon to east monsoon seasons, there is no species domination in Gorontalo Bay.

Table 2

Diversity index (H') and dominance index (D) of phytoplankton in the Gorontalo Bay

Seasons	*Index*	*Stations*				
		1	*2*	*3*	*4*	*5*
West monsoon	H'	1.890	2.034	1.287	2.262	1.813
	D	0.177	0.171	0.302*	0.121	0.180
Transition	H'	2.304	2.469	2.268	2.712*	2.284
	D	0.190	0.131	0.129	0.078	0.142
East monsoon	H'	0.723	0.904	0.433	0.874	0.760
	D	0.103	0.071	0.096	0.110	0.118

Note: * maximum values.

Seasonal fluctuation of phytoplankton. Result of phytoplankton analysis according to their abundance, spatial-seasonal fluctuation is successively presented on Table 3 and Figures 2 and 3.

The total phytoplankton in the whole investigated areas showed the highest counts during east monsoon season with an average of 673026 cell L^{-1} followed by transition season with an average of 352704 cell L^{-1} and west monsoon season with an average of 3839 cell L^{-1}. It can be seen from Table 3 that in the Gorontalo Bay the east monsoon season was the most productive season. Awwaludin et al (2005) stated that in the east monsoon season, phytoplankton distribution was concentrated in the north part of Tomini Bay with the abundance ranged between 80010 and 1082520 cell m^{-3} which consisted of 45 species and dominated by Bacillariophyceae. In the transitional season, the number of phytoplankton cell tends to be homogeny recorded as 26 taxa with the abundance ranged from 25000 to 1500000 cell m^{-3} dominated by *Chaetoceros* and *Rhizosolenia* (Wiadnyana 1998).

In this study, the high abundance of phytoplankton during east monsoon season was associated with high flourishing of *Anabaena* sp. (61863 cell L^{-1} in average), *Oscillatoria limosa* (59902 cell L^{-1} in average), *Chaetoceros affinis* (53724 cell L^{-1} in average), *Chaetoceros messanensis* (44783 cell L^{-1} in average) and *Bacteriastrum hyalinum* (42086 cell L^{-1} in average). On the other hand, some phytoplankton species showed their maximum abundance during transition season. These taxa are namely

Oscillatoria limosa (average of 66366 cell L^{-1}), *Chlorella* sp. (average of 7817 cell L^{-1}) and *Rhizosolenia imbricata* (average of 7732 cell L^{-1}).

Table 3

Seasonal fluctuation of phytoplankton abundance (cell L^{-1}) in the Gorontalo Bay

Class	*Species*	*West monsoon*	*Transition*	*East monsoon*
Division: Chlorophyta				
Trebouxiophyceae	*Chlorella* sp.	141	7817	5761
Zygnematophyceae	*Cosmarium* sp.	118	2042	2533
	Hyalotheca mucosa	76	1880	5533
	Spirogyra sp.	223	1196	4258
Chlorophyceae	*Pediastrum duplex*	282	8202	26641
	Pediastrum simplex	0	12858	39283
	Golenkinia sp.	94	2734	0
Division: Chrysophyta				
Bacillariophyceae	*Achnanthes brevipes*	94	4955	3146
	Dyitylum criophilum	203	1126	4331
	Synedra gailonii	218	4836	11956
	Synedra montana	249	6519	6832
	Synedra ulna	102	6092	7257
	Pleurosigma formosum	24	0	5598
	Amphora obtusa	235	3913	8581
	Cymbella cistula	24	1196	2942
	Gyrosigma sp.	12	352	1136
	Nitzschia sp.	326	5801	6178
	Rhizosolenia castracanei	317	5784	8711
	Rhizosolenia imbricata	642	9665	7020
	Rhizosolenia pungens	509	3238	9766
	Rhizosolenia shrubsolei	353	2136	5720
	Surirella sp.	142	2691	9725
	Corethron hystrix	0	162	597
	Thalassionema nitzschioides	0	8031	11147
	Thalassiothrix frauenfeldii	0	5895	14056
	Trachyneis aspera	352	0	2243
Mediophyceae	*Biddulphia aurita*	141	85	8989
	Hemiaulus membranaceus	355	3845	11858
	Lauderia anulata	106	5468	5042
	Bacteriastrum delicatulum	176	13456	36039
	Bacteriastrum hyalinum	212	16575	42086
	Chaetoceros affinis	1752	20846	53724
	Chaetoceros brightwelli	690	12986	38940
	Chaetoceros messanensis	0	6237	44783
Coscinodiscophyceae	*Coscinodiscus eccentricus*	259	3904	4944
	Coscinodiscus radiatus	74	1837	3906
	Coscinodiscus sp.	86	940	2860
Division: Cyanophyta				
Cyanophyceae	*Anabaena* sp.	142	7577	61863
	Oscillatoria limosa	153	66366	59902

Chaetoceros as a group from Bacillariophyceae appeared frequently in the waters. It has high tolerance in waters salinity fluctuation (Kennish 1990), has segmented cell form where each segment is self-contained, and more adaptable to its environment and is a phytoplankton group favored by fish and shrimp larvae. In addition, *Anabaena* and *Oscillatoria* from Cyanophyceae class also appeared in the waters with a high frequency. They can survive in unfavorable environmental conditions since they have ability to fixing nitrogen in the air directly (Meeks & Elhai 2002; Conradie et al 2008).

The spatial distribution of abundance of phytoplankton species varied substantially among all seasons (Figure 2). The fluctuation of total phytoplankton abundance among sub stations located in front of estuary has alteration with a cyclic-like pattern. In west monsoon season, the higher abundance of total phytoplankton species was separate between in front of estuary and western waters. It was move and being fully concentrated at western waters during transition season. The fully concentrated in front of estuary is back later in east monsoon. The continually lower abundances were located in eastern waters of Gulf Gorontalo (predominantly at sub stations XIII, XIV, and XV).

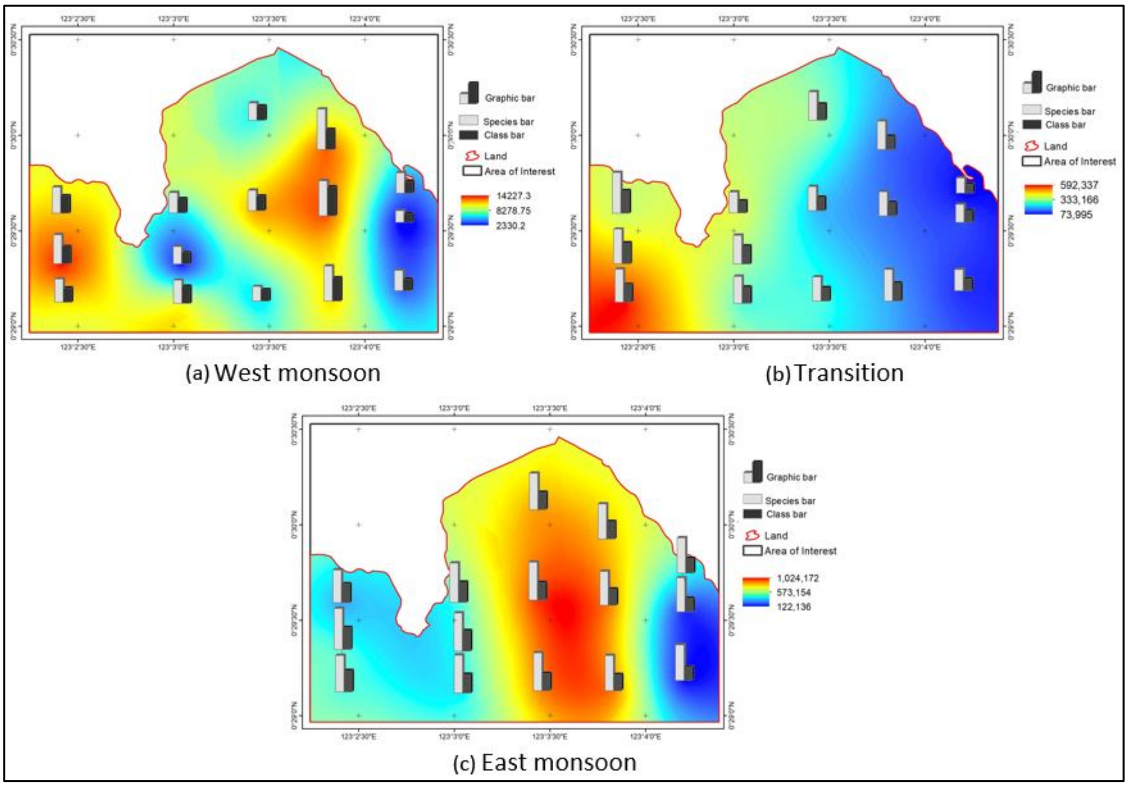

Figure 2. Tempo-spatial variations of phytoplankton distribution and species-class fluctuation during different season: (a) west monsoon, (b) transition and (c) east monsoon. The interpolation map was constructed by GIS software using the kriging method.

In general, the average of species and class occurrence was rise from time to time of season (Figure 3). Further analysis to comparison in term of ratio between occurrence of average amount of classes and their member of species has also a rising pattern. While in east monsoon the higher ratio was significant, the lag distance (i.e. differences value between ratios) from west monsoon to transition season was higher than transition to east monsoon season.

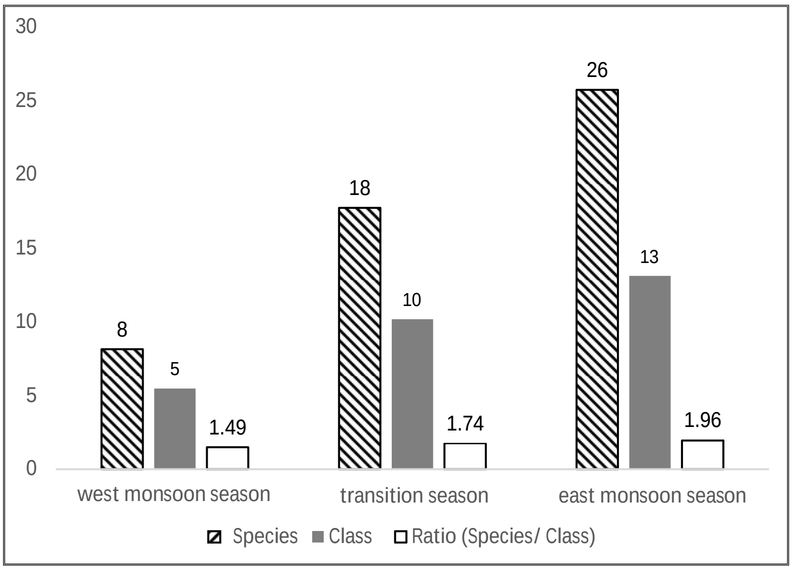

Figure 3. Average of total abundance of phytoplankton species and classes and their ration of comparison during three phase of season.

Bacillariophyceae and Mediophyceae from Chrysophyta division have a high species presence variety in Gorontalo Bay. Nybakken (1993) stated that phytoplankton species dominated by Chrysophyta mainly from Bacillariophyceae. The marine phytoplankton community is characterized by high density dominated by diatoms and high species biodiversity (Nursuhayati et al 2013). Diatom dominance among phytoplankton groups has been reported by Shah et al (2008), Ananthan et al (2008), Muylaert et al (2009), Setyadji & Priatna (2011), and Nassar et al (2014).

Phytoplankton growth rate and distribution are tremendously influenced by environmental factors. The affecting parameters differ for each species (Adenan et al 2013). The variety of planktonic diatom species existing in temperate waters is essential. Horizontal distribution influence factors are temperature, salinity, and current. *Rhizosolenia* as the great of number species found dispersed along tropical seawater (circumtropical) and has being adapted with warm temperature (Morrisey & Sumich 2012; Cokrowati et al 2014). Water temperature is very vital for metabolic processes, growth and reproductive ability among aquatic organisms. Power plants can affect temperature fluctuations in the water and can influence the composition of phytoplankton communities. The effect is primarily for phytoplankton existence such as declining of community composition, abundance, and their productivity in water column (Chuang et al 2009; Choi et al 2012).

In addition, species from the Chlorophyta and Cyanophyta divisions in the waters have relatively low species diversity, although *Oscillatoria limosa* exhibits a fairly high abundance in the three distinct seasons. *Oscillatoria* dominance will be in line with the high value of BOD. The dominance of the *Oscillatoria* can be an indication of the decline of water quality or pollution by organic waste disposal (Kumari et al 2008; Rangpan 2008; Panich-pat et al 2009).

Phytoplankton abundance and phisyco-chemical parameters correlation. The relationship between the abundance of phytoplankton and environmental parameters is shown in Table 4. The parameters which have positive correlation with phytoplankton abundance are pH ($r = 0.15$; $p > 0.05$), NO_3 ($r = 0.06$; $p > 0.05$), NH_3 ($r = 0.04$; $p > 0.05$), PO_4 ($r = 0.65$; $p < 0.05$), and chlorophyll-*a* ($r = 0.83$; $p < 0.05$), while it was inversely correlated with temperature ($r = 0.51$; $p > 0.05$), salinity ($r = 0.47$; $p > 0.05$), and dissolved oxygen ($r = 0.83$; $p < 0.05$).

Table 4

Correlation matrix between the physico-chemical parameters and the total counts of phytoplankton in the Gorontalo Bay

	Phyto.	*Temp.*	*pH*	*Salinity*	*DO*	*NO_3*	*NH_3*	*PO_4*	*Chl-a*
Phyto.	1.00								
Temp.	-0.78	1.00							
pH	0.54	-0.95	1.00						
Salinity	-0.77	1.00	-0.96	1.00					
DO	-0.98	0.64	-0.37	0.63	1.00				
NO_3	0.50	-0.93	1.00	-0.94	-0.33	1.00			
NH_3	0.96	-0.56	0.28	-0.55	-0.99	0.23	1.00		
PO_4	0.74	-0.15	-0.17	-0.13	-0.85	-0.21	0.90	1.00	
Chl-*a*	0.96	-0.57	0.28	-0.55	-1.00	0.24	1.00	0.90	1.00

Conclusions. The most productive season in Gorontalo Bay, Indonesia was shown in east monsoon season with the abundance of phytoplankton in average of 673026 cell L^{-1}, followed by the transition and west monsoon season with the mean counts of phytoplankton of 352704 cell L^{-1} and 3839 cell L^{-1} consecutively. The highest variety of phytoplankton species found in waters is from the Chrysophyta group. Spatially, the highest abundance of phytoplankton founded in the Station 3 with an average of 9891 cell L^{-1} followed by Station 4 with an average of 8770 cell L^{-1}, Station 1 with an average of 7493 cell L^{-1}, Station 2 with an average of 6343 cell L^{-1}, and Station 5 with the average of 2651 cell L^{-1}.

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