Roles of Banda Sea upwelling on *Porphyra* sp. in Ambon Island, eastern Indonesia

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Abstract. This study provides evidence on the roles of Banda Sea upwelling in supporting favorable environmental conditions for *Porphyra* sp. in Ambon Island, eastern Indonesia. A cross-correlation analysis using historical sea surface temperature (SST) datasets between Banda Sea upwelling hotspot in eastern Banda Sea and waters nearby Ambon Island was employed to investigate the ocean teleconnection of Banda Sea upwelled water at Ambon Island. This ocean teleconnection was also investigated via weekly fieldwork samplings, measuring SST, sea surface salinity (SSS) and surface dissolved nutrients in the *Porphyra* habitats of Seri and Allang in Ambon Island during the peak of Banda Sea upwelling season (June-August 2023) to detect the presence of Banda Sea upwelled water in the habitats. The fieldwork also measured the growth of *Porphyra* sp. The principal component analysis (PCA) was further employed to identify the correlation between the environmental parameters and the growth of *Porphyra* sp. The cross-correlation analysis showed a very strong connection ($r \geq 0.90$) with very low time lag (<1 week) for the SST between Banda Sea upwelling hotspot in eastern Banda Sea and waters nearby Ambon Island. This indicated an immediate arrival of cool, salty, nutrient-rich upwelled Banda Sea water from the upwelling hotspot at Ambon Island during the peak upwelling season (June-August). Weekly observations in the *Porphyra* habitats in Ambon Island during the peak Banda Sea upwelling season confirmed the arrival of the upwelled water, showing cool SST (reaching up to 26°C), high SSS similar to typical deep-layer Banda Sea water (≥34.5 psu) and the elevated concentration of surface dissolved nitrate (reaching as much as 0.1 ppm) that were evident in the locations, coincident with the occurrence of *Porphyra* sp. From PCA analyses, the growth of *Porphyra* sp. correlated with SST cooling and the increases in SSS and nutrients. This environmental condition characterizes typical oceanic conditions in Ambon Island during Banda Sea upwelling season. The knowledge of the ecology of *Porphyra* sp. in Ambon Island presented here has application for being a reference in implementing successful cultivating process of the Ambon Island *Porphyra* sp.

Key Words: upwelling-teleconnection, Banda Sea, dissolved nitrate, southerly monsoon.

Introduction. *Porphyra* sp., a red-algae seaweed, is a major aquaculture crop in the world due to its high commercial value (FAO 2018; Levine & Sahoo 2010). Nori is the main product of *Porphyra* sp. commonly consumed in Japan can produce an annual retail value of USD 2 billion in the country alone. Meanwhile, the annual economic value from importing nori to western countries following the growing popularity of the product is also significant (e.g. more than USD 25 million to the US; Merrill 1993; Mumford Jr. & Miura 1988). The commercial importance of *Porphyra* sp. has attracted a great general interest to understand the ecology of the species. Knowledge on environmental factors influence on the ecology of this red-algae in natural habitats can be used in advancing efforts to cultivate the species (Conitz et al 2001; Frazer & Brown 1995; Pereira et al 2005; Pereira et al 2004; Stekoll & Lin 1999).

General insights on the ecology of *Porphyra* sp. indicate that the species is typically found in high latitude regions where cold-to-cool climate predominates and that rocky shorelines are the common habitat for *Porphyra* sp. (Brodie et al 1996; Yoshida 1997). Meanwhile, in the tropics, few studies have also reported the occurrence of *Porphyra* sp. such as in Thailand, Myanmar, Philippines, and Indonesia (Ame et al 2010;

Hatta 1990; Lewmanomont & Chittpoolkusol 1993; Pattiasina et al 2023; Ruangchuay & Notoya 2007). *Porphyra* sp. in the tropical habitats has a seasonal occurrence, linked to the coolest condition of the year (Ame et al 2010; Hatta 1990; Lewmanomont & Chittpoolkusol 1993; Pattiasina et al 2023; Ruangchuay & Notoya 2007).

Indonesia is the largest seaweed producer in the world (Saleh & Sebastian 2020). Yet, *Porphyra* sp., known for its high commercial value in the global seaweed market (FAO 2018; Merrill 1993), is not the main export commodity. The country is focusing on carrageenan seaweeds (Langford et al 2023). The natural habitats of *Porphyra* sp. in Indonesia are very rare in contrast to carrageenan seaweeds (van der Heijden et al 2022; Waters et al 2019). To our knowledge, the natural habitats of *Porphyra* sp. in the entire Indonesian archipelago have been only reported in Ambon Island, a small oceanic island in eastern Indonesia (Figure 1) and the species appears only in a certain seasonal condition (Hatta 1990; Pattiasina et al 2023; Pattipeilohy 2015). The scarcity of the natural habitats of *Porphyra* sp. in Indonesia hinders massive cultivations of the species in contrast to carrageenan seaweeds in the country (Langford et al 2023). In addition, there is a limited information on the ecology of the species particularly on what environmental factors support the occurrence and growth of *Porphyra* sp. in the island (Hatta 1990; Pattiasina et al 2023).

Previous studies on *Porphyra* sp. in Ambon Island (Hatta 1990; Pattiasina et al 2023; Pattipeilohy 2015), highlighted the occurrence of *Porphyra* sp. during the lowest seasonal temperature period between June and August (~ 26^{o}C), which was similar with studies in other tropical regions (Ame et al 2010; Hatta 1990; Lewmanomont & Chittpoolkusol 1993; Pattiasina et al 2023; Ruangchuay & Notoya 2007). Meanwhile, environmental factors such as salinity and nutrient levels responsible for the growth of blade and conchocelis of the species (Conitz et al 2001; Lin 1999; Stekoll & Lin 1999) are poorly investigated. The understanding of favorable salinity and nutrient levels for *Porphyra* sp. in Ambon Island would provide important insights for the cultivation of the species besides the initial information on the preferred temperature.

An oceanographic phenomenon in Banda Sea, the nearby deep-sea environment (Figures 1a and b), called seasonal Ekman upwelling is known to influence the coastal waters of Ambon Island and nearby waters including in the *Porphyra* habitats. The seasonal Ekman upwelling occurs at the eastern part of the Banda Sea basin (i.e. red box in Figure 1a based on Gordon & Susanto (2001)) between May and September due to the prevailing southeasterly monsoonal winds with the peak upwelling condition that exists in July and August (Iskandar 2010; Moore II et al 2003; Wyrtki 1961). The upwelling process uplifts cool, salty, nutrient-rich subsurface water from the thermocline layer (100-200 m depth) to the surface layers of the eastern Banda Sea Basin (Westeyn et al 1990; Wyrtki 1961; Zijlstra et al 1990). The upwelled water from the eastern Banda Sea basin has the potential to be transported northwestward by the prevailing southeasterly wind stress (Sprintall & Liu 2005) and this can allow the arrival of this cool, salty, nutrient-rich water to the surface layers of the coasts of Ambon Island, e.g. as reported in Ambon Bay (Figure 1c) by Tarigan & Wenno (1991), and in the nearby Piru Bay at the northern Ambon Island (Figure 1b; reported by Sapulete (1996)). The arrival of cool, salty, nutrient-rich upwelled water from Banda Sea in the coastal waters of Ambon Island might be the major factor for supporting the seasonal occurrence of *Porphyra* sp. in the island. The arrival of Banda Sea upwelled water in Ambon Island has been reported to cool the local sea surface temperature (SST) and local air temperature of the offshore parts of Ambon Bay (Salamena 2011; Salamena 2013; Tarigan 1989). The cooling process of the local SST and air temperature was observed to coincide with the occurrence of *Porphyra* sp. in Ambon Island (Hatta 1990; Pattiasina et al 2023). The nutrient-rich water carried by Banda Sea upwelled water reaching Ambon Island might also provide favorable conditions supporting the growth of *Porphyra* sp. in the island. This hypothesis is based on the positive relationships between high nutrient and growth rate of *Porphyra* sp. reported in other *Porphyra* studies (Conitz et al 2001; Lin 1999; Stekoll & Lin 1999). Despite this potentially supporting role of Banda Sea upwelled water to the occurrence and growth of *Porphyra* sp., there is no study investigating the cause-effect relationship between Banda Sea upwelling and *Porphyra* sp. in Ambon Island. In addition to the effort to unveil the potential roles of Banda Sea (an open ocean) on affecting the occurrence of *Porphyra* sp. (i.e. via oceanic-originated nutrients) in Ambon Island, this attempt is likely to add an important insight into the existing knowledge on the ecology of *Porphyra* sp. widely reported to be affected by terrestrial-originated nutrients during peak of wet seasons, including in the tropical habitats of *Porphyra* sp. (Ame et al 2010; Lewmanomont & Chittpoolkusol 1993; Pattiasina et al 2023; Pereira et al 2005; Ruangchuay & Notoya 2007).

This study primarily sought to unveil how significant the Banda Sea upwelling in regulating the occurrence and growth of *Porphyra* sp. in Ambon Island. It also attempted to reveal the favorable environmental conditions such as SST, sea surface salinity (SSS) and surface nutrient likely linked to Banda Sea upwelling in the *Porphyra* habitats in Ambon Island that support the growth of the species – this would be useful for the subsequent efforts in cultivating *Porphyra* sp. from Ambon Island.

Material and Method

Description of the study sites. Ambon Island is an oceanic island (red-colored island in Figure 1a being zoomed in Figure 1b) with volcanic-tectonic origin (Honthaas et al 1999; Lewerissa et al 2018; Pownall et al 2013) that is located in Banda Sea basin (average depth: 4,000 m), a deep-sea basin in eastern Indonesia. Seasonally, warm air temperature and SST in Ambon Island are found during the December-February period while the minimum period of temperature is during the June-August period (Tarigan 1989). The minimum temperature (both air temperature and SST) in Ambon Island has been thought to be linked to the effects of Banda Sea upwelling (Salamena 2013; Tarigan 1989). Seri and Allang in Ambon Island (Figure 1c) are typically rocky coasts that harbor the seasonal occurrence of *Porphyra* sp. particularly during the June-August period (Pattiasina et al 2023; Pattipeilohy 2015).

Visual observations and oceanographic parameter measurements. Seri and Allang in Ambon Island (Figure 1c) were two *Porphyra* habitats that were chosen in this study based on preliminary observations of Pattiasina et al (2023) and Pattipeilohy (2015). At both locations, visual observation on *Porphyra* sp. and the associated oceanographic measurements were conducted on a weekly basis between June and August 2023, during which the Banda Sea upwelling season reaches its peak (Gordon & Susanto 2001; Iskandar 2010; Wyrtki 1961; Zhu et al 2019). For the weekly visual observation, a 50 × 60 cm transect was employed and was consistently placed in the same position in the *Porphyra* habitats to photograph the images of *Porphyra* sp. The weekly images then were processed using Surfer 16 to estimate the gradual change in the area occupied by *Porphyra* sp. within the transect. During the weekly visual observation, the blade length of *Porphyra* sp. was also measured within the transect.

Oceanographic parameters measured at the *Porphyra* habitats of Seri and Allang in Ambon Island were SST, sea surface salinity (SSS) and surface dissolved nutrients such as nitrate (NO_3) and phosphate (PO_4) concentrations. The parameters were measured by firstly collecting surface water samples at the habitats using a bucket with a 10 m rope, while the magnitudes of SST and SSS were directly measured using the portable instruments WTW Multi 3430 (measuring water temperature and water salinity) and HI-98190 Hanna (measuring water temperature), the nitrate concentration was later estimated in the laboratory by applying the method of Strickland & Parsons (1972). In addition to oceanographic measurements, atmospheric datasets such as air temperature and daily rainfall were obtained from local weather station at Ambon Airport (airport location in Figure 1c).

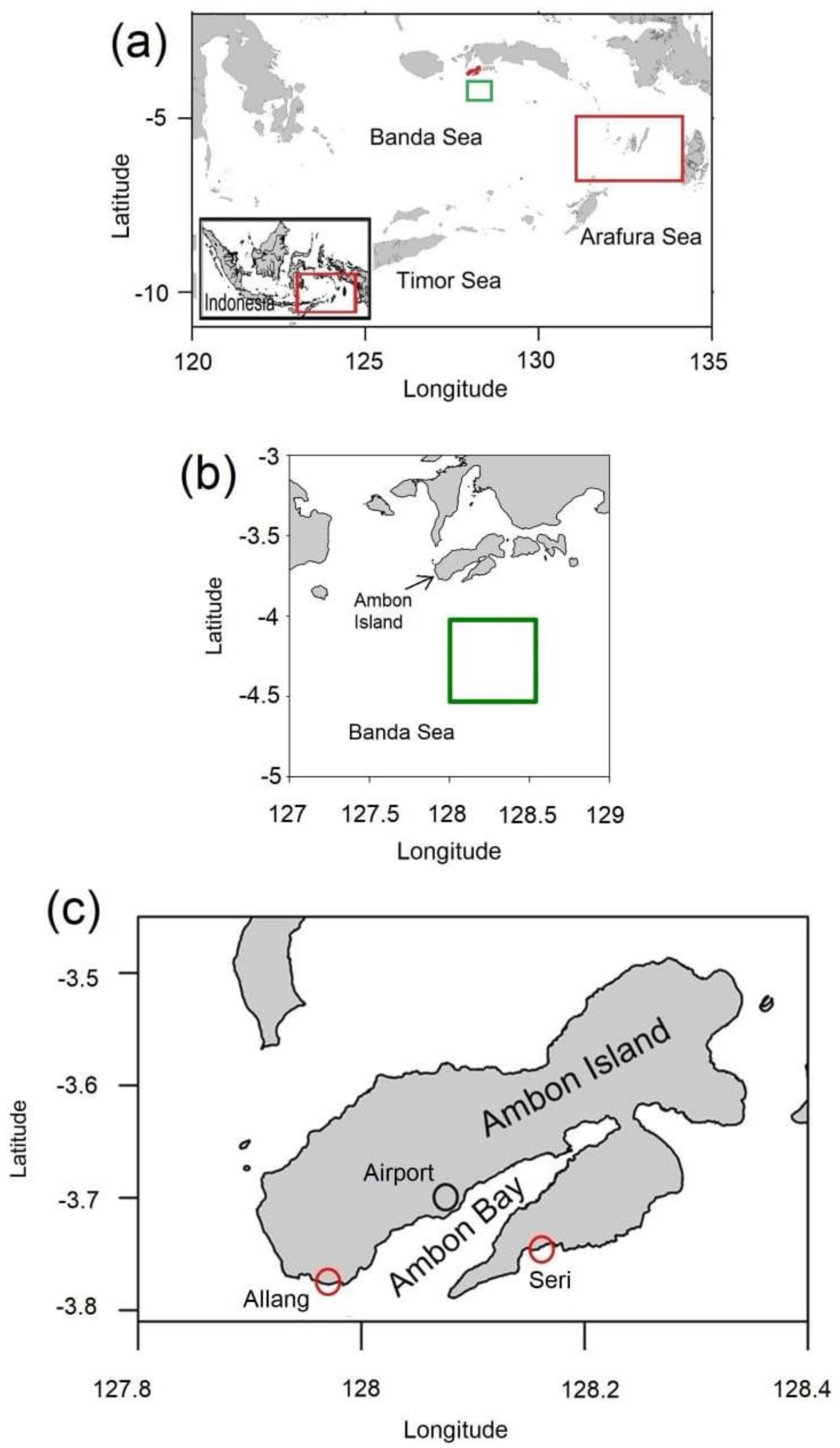

Figure 1. The location of study (a) The geography of Banda Sea in eastern Indonesia and the surrounding waters such as Arafura and Timor Seas; Ambon Island is colored red; red box indicates the Banda Sea upwelling hotspot in eastern Banda Sea based on Gordon & Susanto (2001), while green box indicates waters nearby Ambon Island. (b) The zoomed map from Figure 1a shows Ambon Island's nearby waters. (c) The geography of *Porphyra* habitats in Ambon Island, such as Seri and Allang with additional information on the locations of Ambon Bay and Ambon Airport.

High salinity as a proxy to identify Banda Sea upwelled water arriving at Ambon Island. Besides cool SST of 26°C commonly representing Banda Sea upwelled water (Iskandar 2010; Westeyn et al 1990; Zijlstra et al 1990), the upwelled water can be represented by SSS larger than 34 psu. Previous studies have reported that the typical vertical salinity profile in Banda Sea in the absence of Ekman upwelling is characterized by salinity ~34 psu occupying the surface layers and salinity ≥34.5 psu that is commonly found from the thermocline layer to the bottom (Hamzah 2023; Waworuntu et al 2000; Wyrtki 1961). The Ekman upwelling in eastern Banda Sea (red box in Figure 1a) upwardly transports water masses from the upper thermocline layer to the surface and this is likely to cause SSS ≥34.5 psu in Banda Sea (Gordon & Susanto 2001; Wyrtki 1961). As such, the observed SSS ≥34.5 psu in Ambon Island (including at the *Porphyra* habitats of Seri and Allang) during the Banda Sea upwelling season can prove the arrival of Banda Sea upwelled water at the location.

Statistical analyses*.* Teleconnection in the ocean or atmosphere is an phenomenon when two oceanic/atmospheric signals are related each other even though the locations of each signal are separated over a large distance (Rohli et al 2022). The teleconnection often involves time lags indicating the effects of one signal that might be delayed on the other (Cerrone et al 2017; Hopkins 2008; Lee & Julien 2016; Ni et al 2018). One effective method to detect the teleconnection is cross-correlation analysis that accounts for the correlation between two time series with regards to various time lags (Alan et al 2010; Cerrone et al 2017; Hopkins 2008; Ni et al 2018).

This study sought to reveal an ocean teleconnection between Banda Sea upwelling hotspot (i.e. red box in Figure 1a; Gordon & Susanto 2001) and waters nearby Ambon Island (green box in Figures 1a and b). The ocean teleconnection is likely to be in the form of the arrival of Banda Sea upwelled water (i.e. characterized by cool, salty, nutrient-rich water; Westeyn et al 1990; Zijlstra et al 1990) from the upwelling hotspot at waters nearby Ambon Island, via the prevailing southeasterly wind stress during the peak of upwelling season in the June-August period (Sprintall & Liu 2005). The use of cross-correlation analysis in this study primarily aimed to investigate the degree of similarity (hence, connection) between the variability of oceanic conditions, such as SST at Banda Sea upwelling hotspot and in the waters nearby Ambon Island. A high correlation regarding the SST variability between the two locations implies that low SST levels (hence, increases of salinity and nutrient) linked to seasonal upwelling in the upwelling hotspot will be experienced by waters nearby Ambon Island. The cross-correlation analysis in this study employed weekly SST data (i.e. 8-day average) being averaged over Banda Sea upwelling hotspot and waters nearby Ambon Island. The SST data was obtained from MODIS satellite observations spanning 2010-2022, downloaded from the NASA's Giovanni directory (https://giovanni.gsfc.nasa.gov).

All environmental data measured were pooled together with biological parameters from both locations to analyze the correlation among parameters. The biological parameter was represented by the length of *Porphyra* sp., while environmental data were obtained from water physicochemical parameters such as SST, SSS and dissolved concentrations of phosphate and nitrate. A multivariate analysis of Principal Component Analysis (PCA) was employed to conduct the statistical analyses; the biplot of score and loading plots of PCA were performed to reveal the correlations among parameters. Here, the biplot analyses of PCA revealed correlations of parameters between the two sampling sites (spatial) and, also among seasons (temporal). Strong correlations would be found among parameters that formed angles ≤45 degree, while no correlations were determined at angles that were close to 90 degrees. The angle that was close to 180 degrees between two parameters implied an inverse correlation. The PCA analyses were performed using XLSTAT 2021.

Results

Signatures of the teleconnection of Banda Sea upwelling in Ambon Island. There was an immediate teleconnection between Banda Sea upwelling signal and SST at waters nearby Ambon Island. Cross-correlation analysis of SST between Banda Sea upwelling hotspot (area within red box in Figure 1a) and waters in the proximity with Ambon Island (area within green box in Figure 1a) showed a very strong correlation ($r \geq 0.90$; Table 1). In addition, there was a very low time lag of the impact of the SST variability at the

Banda Sea upwelling hotspot on that in the nearby waters of Ambon Island (Table 1). This indicates that SST variation occurring at Banda Sea upwelling hotspot including SST cooling (typically around June to August; hence, high SSS) due to Ekman upwelling is immediately experienced by the waters nearby Ambon Island.

Table 1
Cross-correlation (*r*) of SST between Banda Sea upwelling hotspot offshore waters of Ambon Island

Time lag		*Year*												
		2010	*2011*	*2012*	*2013*	*2014*	*2015*	*2016*	*2017*	*2018*	*2019*	*2020*	*2021*	*2022*
r	0	0.90	0.92	0.92	0.91	0.97	0.95	0.92	0.91	0.93	0.96	0.96	0.94	0.95
	+ 1 w	0.85	0.89	0.91	0.85	0.93	0.92	0.83	0.85	0.90	0.89	0.90	0.88	0.92
	+ 2 w	0.83	0.86	0.85	0.76	0.87	0.81	0.71	0.70	0.81	0.82	0.81	0.77	0.84
	+ 3 w	0.78	0.81	0.80	0.64	0.80	0.68	0.58	0.60	0.67	0.70	0.70	0.65	0.73
	+ 1 m	0.67	0.68	0.71	0.55	0.69	0.52	0.47	0.46	0.51	0.57	0.55	0.50	0.56
	+ 2 m	0.06	0.06	0.14	0.06	0.14	0.17	0.08	-0.23	-0.18	-0.09	-0.08	-0.13	-0.14

w-week(s), m-month(s).

Variability of environmental parameters in the study locations. Regarding the SST (Figure 2a), in a regional scale such as in Banda Sea upwelling hotspot (dashed black line; the location is in Figure 1a) and in Banda Sea waters nearby Ambon Island (solid black line; the location is in Figure 1a), seasonally, there was a general declining trend of SST from March 2023 (30-31°C) reaching the minimum SST around June to August 2023 (25.5-27°C). The SST rebounded in September 2023 reaching the initial warm SST in March 2023 around November to December 2023. The local SST in Ambon Island (blue and red circles) observed between June and August 2023 was consistent with the regional SST seasonality, particularly in indicating an SST cooling around this particular period. In addition, local air temperature over Ambon Island (green solid line in Figure 2a) showed a similarity to the regional SST seasonality. The similarities of local temperature parameters (SST and air temperature) in Ambon Island to the regional SST seasonality in Banda Sea waters further support the immediate teleconnection. Regarding local SSS observed at Seri and Allang between June and August 2023 (Figure 2b), the parameter showed an increasing trend between June 2023 (34 psu) and August 2023 (on average, 34.5 psu). This was also true for surface nitrate concentration in both locations (from late June 2023 with values below 0.06 ppm to August 2023 with values >0.06 ppm; the maximum value: 0.1 ppm; Figure 2b). Note that surface phosphate concentration was not found to be correlated with the increase in the nitrate and rather was fluctuating.

Banda Sea upwelled water found at the study locations. The arrival of Banda Sea upwelled water was detected at the study locations of *Porphyra* sp. in Ambon Island. The salinity of Banda Sea is characterized by 34 psu occupying the surface layers and ≥34.5 psu that is typically found from the thermocline layer to the bottom (Waworuntu et al 2000). Between June and August, Ekman upwelling occurs in Banda Sea (particularly over the red box in Figure 1a; Gordon & Susanto 2001) and this mechanism upwells cool-salty water mass from the thermocline layer of Banda Sea to the surface. During the observations of SSS at Seri and Allang, the typical SSS of Banda Sea was found in the early June 2023 (34 psu, Figure 2b). However, as time progressed to the end of June 2023 and afterwards, the SSS in Seri and Allang increased up to the average of 34.5 psu, coinciding with the peak of Banda Sea upwelling period (Figure 2b). This salinity indicated that Banda Sea upwelled water had reached the study locations of *Porphyra* sp. in Ambon Island.

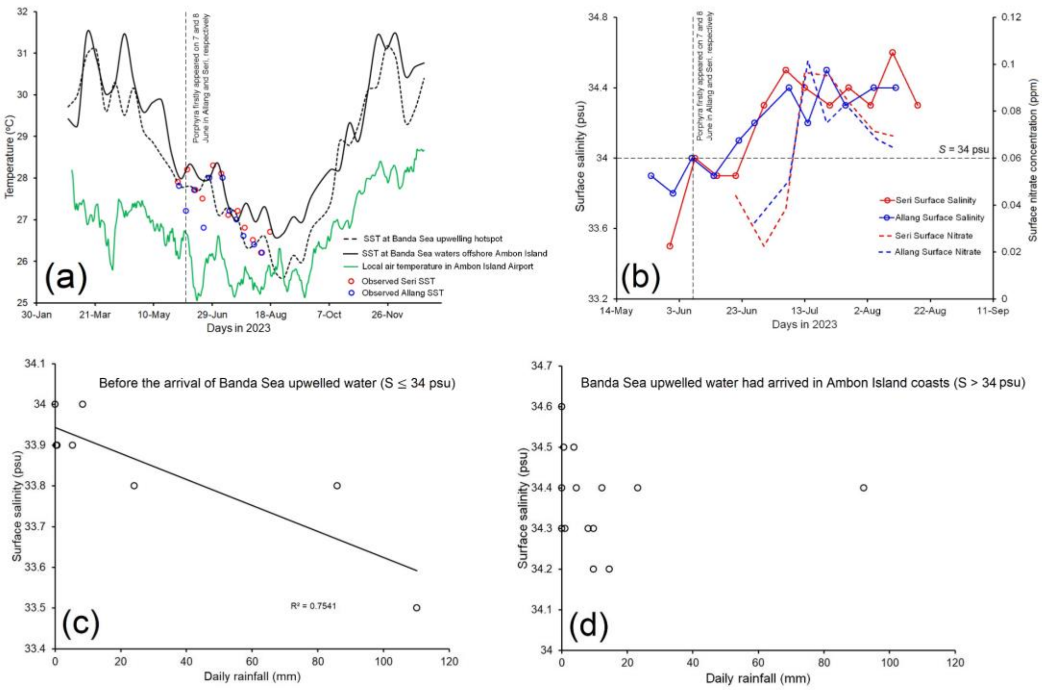

Figure 2. (a) Temporal changes of observed SSTs at Seri (red circles), Allang (blue circles), offshore waters of Ambon Island shown by green box in Figure 1a (solid black lines) and Banda Sea upwelling hotspot shown by red box in Figure 1a (dashed black line) coupled with observed air temperature over Ambon Island (green line); vertical dashed line indicates the onset of *Porphyra* sp*.* (b) Similar to Figure 2a regarding the observations at Seri and Allang but for SSS and surface dissolved nitrate. The scatter plots of SSS versus daily rainfall over Ambon Island (a) prior to and (b) after the arrival of Banda Sea upwelled water at Ambon Island.

The arrival of the Banda Sea upwelled water at Ambon Island, such as at the study locations of *Porphyra* sp., disturbed the controlling role of the local rainfall on SSS. Prior to the arrival of Banda Sea upwelled water at Seri and Allang, in general, SSS was regulated by the daily local rainfall (r^2=0.754) with a high precipitations quantity (e.g. >100 mm) resulting in low SSS (i.e. 33.5 psu, Figure 2c). The arrival of Banda Sea upwelled water with high SSS (>34 psu) at these locations overshadowed the effect of the daily rainfall on the SSS; i.e., variations of the daily local rainfalls ranging 0-90 mm did not affect the high SSS (Figure 2d), as previously found in the absence of Banda Sea upwelled water (Figure 2c).

The habitats of Porphyra* sp*. at Seri and Allang of Ambon Island. The habitat of *Porphyra.sp* at Seri is characterized by rocky capes (top panel of Figure 3) with steep topographies (>60^o steepness) of the rock formation towards the ocean (middle panels of Figure 3). Here, *Porphyra* sp*.* was found to mostly occupy the sloping sides of the rocky capes with only small patches on the top of the capes (middle right and bottom panels of Figure 3). In contrast to Seri, the habitat of *Porphyra* sp. at Allang is attributed by rocky capes (top panel of Figure 4) without steep topography towards the ocean (middle left panel of Figure 4). Here, *Porphyra* sp. mostly occupied areas over the capes (middle right panel of Figure 4). Due to the main difference in physical characteristics of the *Porphyra* habitats between Seri and Allang, Seri was significantly less accessible for collecting the samples of *Porphyra* sp. than Allang. There was a major difference regarding the community structure of *Porphyra* sp. between Seri and Allang. At Seri, *Porphyra* sp. was found to occupy the rocky capes without the presence of any possible competitor such as *Gymnogongrus* sp. (middle right panel and bottom panel of Figure 3). In contrast, at Allang, *Gymnogongrus* sp. was found to inhabit the same space with *Porphyra* sp. (bottom panel of Figure 4).

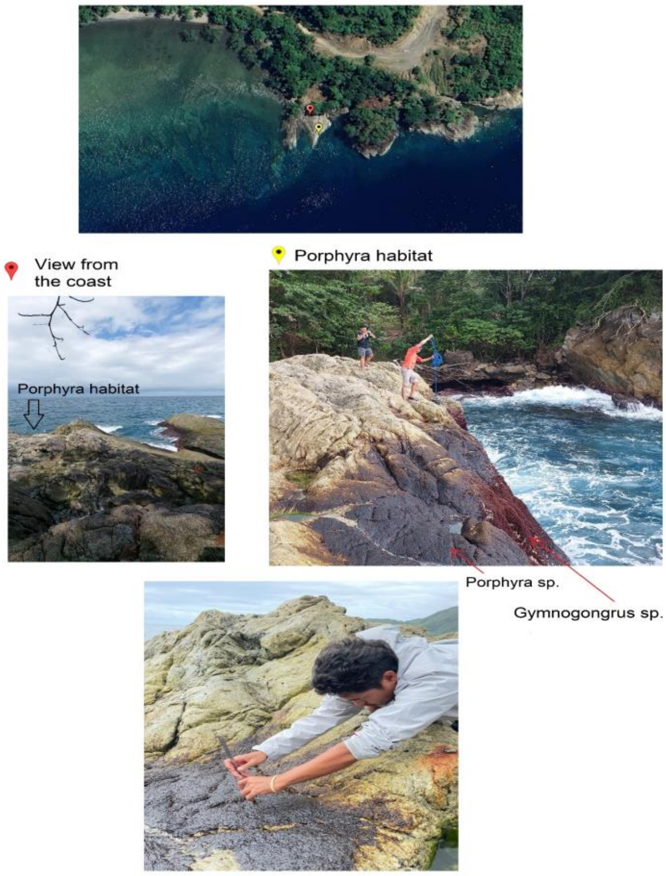

Figure 3. The physical description of the habitat of *Porphyra* sp. at Seri of Ambon Island.

Figure 4. The habitat of *Porphyra* sp. at Allang of Ambon Island.

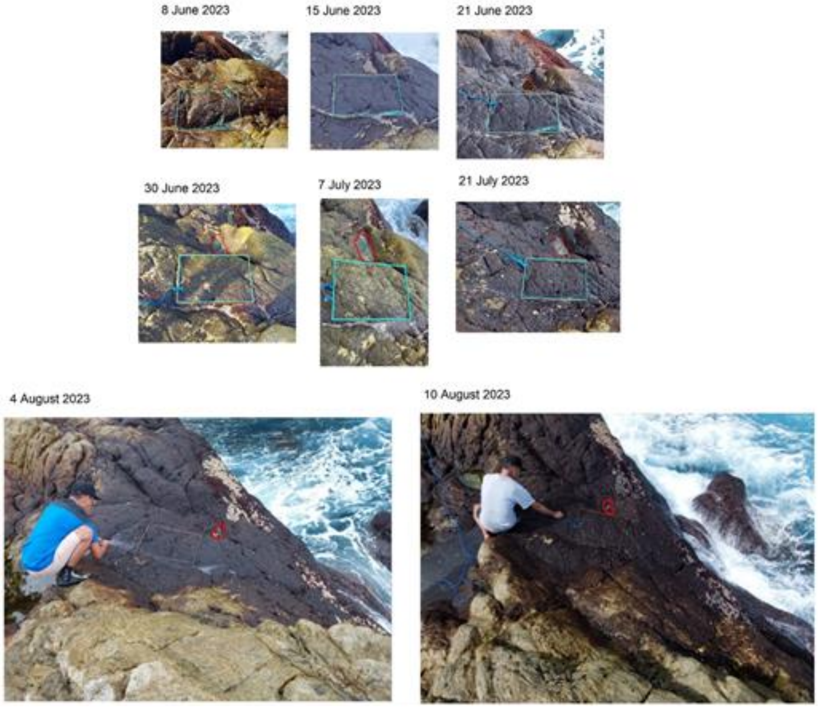

Figure 5. The visual observation of *Porphyra* sp. using the 50 × 60 cm^2 transect with regards to weekly observations from June to August 2023 at Seri, Ambon Island.

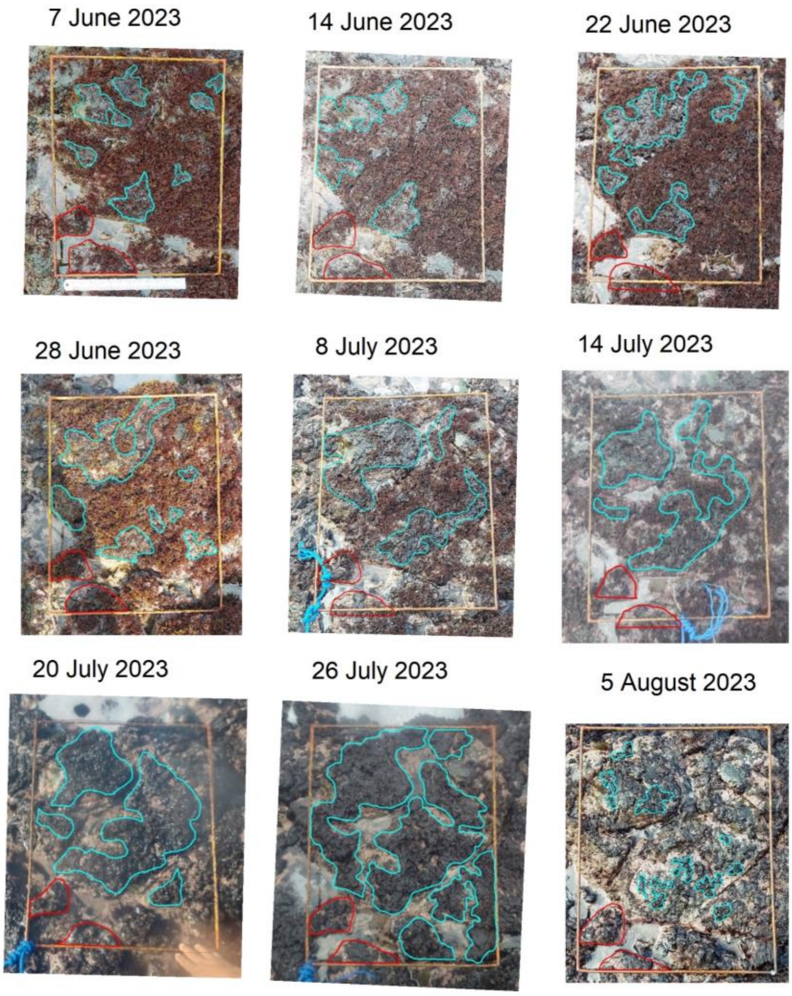

Figure 6. The habitat of *Porphyra* sp. at Allang of Ambon Island.

Visual observations in the habitats of *Porphyra* sp. to detect the onset of the plant were conducted since the late May 2023. However, *Porphyra* sp. started to be found in early June 2023 (dashed lines in Figures 2a and b) on 7th of June 2023 in Allang and on 8th of June 2023 in Seri (Figures 5 and 6). This sub-section presents the growth of *Porphyra* sp. within a 50 × 60 cm^2 transect between June and August 2023 with focuses on (i) the area of expansion and (ii) the length of *Porphyra* sp. In particular to §4.4.2.1, the 50 × 60 cm^2 transect was consistently placed in the same position (despite slight change in the angle of photographs each week due to safety measures) and this was indicated by the key notifications labelled by red polygons at Seri (i.e. a water hole see Figure 5) and at Allang (i.e. stones within the transect particularly at the bottom left); meanwhile, green polygon in Figures 5 and 6 indicated the area occupied by *Porphyra* sp. It should be noted that for the observations of areas occupied by *Porphyra* sp. within the transect, safety dictated that the photographs in Seri on 13th and 27th of July 2023 were not able to be conducted due to frequent ocean wave run-up at the sloping habitat of the *Prophyra* sp. However, the lengths of *Porphyra* sp. on the particularly observational dates were successfully obtained.

Table 2

Total area occupied by *Porphyra* sp. within the 50 × 60 cm^2 transect at Allang

Observational dates	*Total area of Porphyra sp. inside the 50 × 60 cm^2 transect (unit: cm^2)*	*% area from the total transect area*
7th of June 2023	349	11.6
14th of June 2023	449	15.0
22nd of June 2023	637	21.2
28th of June 2023	655	21.8
8th of July 2023	695	23.2
14th of July 2023	743	24.8
20th of July 2023	954	31.8
26th of July 2023	1557	51.9
5th of August 2023 (massive harvest by locals)	150	5

Temporal evolution of the area of Porphyra sp. At Seri (Figure 5), in general, *Porphyra* sp. had occupied mostly the area within the 50 × 60 cm^2 transect throughout the observational period. In contrast, at Allang where *Gymnogongrus* sp. shared the same niches with *Porphyra* sp., there was a gradual increase in the total area occupied by *Porphyra* sp. (Figure 6) between 7th of June 2023 and 26th of July 2023 as in detail presented in Table 2. On the 5th of August 2023 however the area of *Porphyra* sp. dramatically reduced due to full harvest by locals (Table 2, Figure 6). In addition to the Allang observation, the mixed niche occupation of *Porphyra* sp. and *Gymnogongrus* sp. (bottom panel of Figure 4 and Figure 6) allows the analysis of the effects of *Gymnogongrus* sp. in affecting the expansion of the area of *Porphyra* sp. Between 7th of June 2023 and 8th of July 2023, *Gymnogongrus* sp. was found to share the space with *Porphyra* sp. within the 50 × 60 cm^2 transect (Figure 6), leading to low, albeit gradual increase of *Porphyra* sp. which was ≤25% of the transect area (Figure 6 and Table 2). After 8th of July 2023 when *Gymnogongrus* sp. was almost absent (harvested by locals), the expansion of *Porphyra* sp. within the 50 × 60 cm^2 transect was significant, that is, almost a half of the transect area on 26th of July 2023 (Figure 6 and Table 2).

Changes of blade of Porphyra sp. At Seri (Figure 7a), the blade length of *Porphyra sp.* was found to steadily increase between 15th of June 2023 (length: 4 cm) and 7th of July 2023 (length: 10 cm). As the length of *Porphyra* sp. reached 10 cm on 6th of July 2023, generally it modestly varied within the figure afterwards with the maximum length to be 13 cm (Figure 7a). The moderate variation in the length of *Porphyra* sp. at 10 cm showed the mature length of the organism at Seri. At Allang (Figure 7b), the blade length of

Porphyra sp. was found to steadily increase between 14th of June 2023 (length: 2 cm) and 8th of July 2023 (length: 13 cm). After 8th of July 2023, the length of *Porphyra* sp. dropped to 7 cm and 6 cm (Figure 7b). From our visual observations, the dramatical reduction of the *Porphyra* length was found to be linked to the harvest by locals. From the observations of the blade length of *Porphyra* sp., the growth trend of the species regarding the timing in both Seri and Allang was consistent despite their separated locations in Ambon Island (Figure 1c). For instance, the growth trend of *Porphyra* sp. at Seri was between 15th of June 2023 and 7th of July 2023 (Figure 7a), very similar to that at Allang (14th of June-8th of July 2023; Figure 7b). However, the mean growth rate of the species was found to be faster at Allang (0.41 cm day^{-1}) than at Seri (0.24 cm day^{-1}) within this growth period.

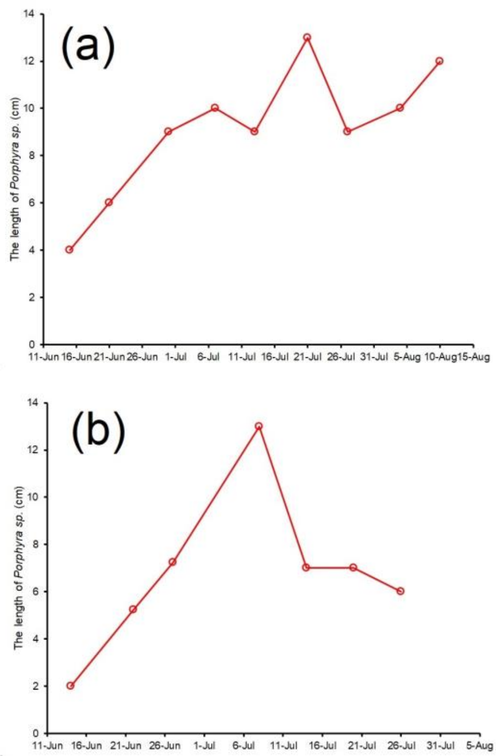

Figure 7. Temporal changes in the length of the thallus of *Porphyra* sp. at (a) Seri and (b) Allang.

Environmental ranges during monitoring of Porphyra sp. in Ambon Island. In general, *Porphyra* sp. at Seri and Allang in Ambon Island observed during the June-August 2023 period flourished on the SST range of 26-28°C (circles in Figure 2a). The ranges of SSS and dissolved nitrate concentration, that supports the life of *Porphyra* sp. in Ambon Island, were found to be, on average, 34.5 psu and 0.02-0.1 ppm, respectively (Figure 2b).

Relationships between Banda Sea upwelling and the growth of Porphyra sp. The PCA analysis to seek the relationship between *Porphyra* sp. and environmental drivers at Seri and Allang focused on spatial and temporal analyses. For the spatial analysis, the loading plot showed a high variance value between the first and second components with a total variability of 80.91% (Figure 8a). The squared cosine of the first component (F1) was constructed by SST, SSS, dissolved nitrate and *Porphyra* sp. blade's length. Meanwhile, the second component (F2) was represented by the dissolved phosphate concentration. The loading plot analysis of the PCA revealed a strong positive correlation between the blade's length and SSS, while nitrate showed a weak influence on the length of blades (Figure 8a). In addition, based on the scatter plot analysis of the observed locations, there was no significant difference between both the sampling stations.

However, the SSS levels regulated *Porphyra* sp. blades' length at Seri, and nitrate showed correlations at both locations (Figure 8a).

For the temporal analysis (Figure 8b), a high variability between the first and second components composed the total of 86.78% variance. Similar to the spatial analysis, the temporal PCA analysis showed that SST, SSS, nitrate and blade's length composed the first component (F1), and phosphate was found as the parameter at the second component (F2). The loading plot for the temporal observation revealed a strong positive correlation between the blade's length and environmental drivers such as SSS and dissolved nitrate. Influences of the SSS levels and dissolved nitrate concentrations were evident between July and August (Figure 8b), during which upwelling of the Banda Sea reached the onshore of Ambon Island. Negative correlations between the SST and SSS levels were found at both sampling locations.

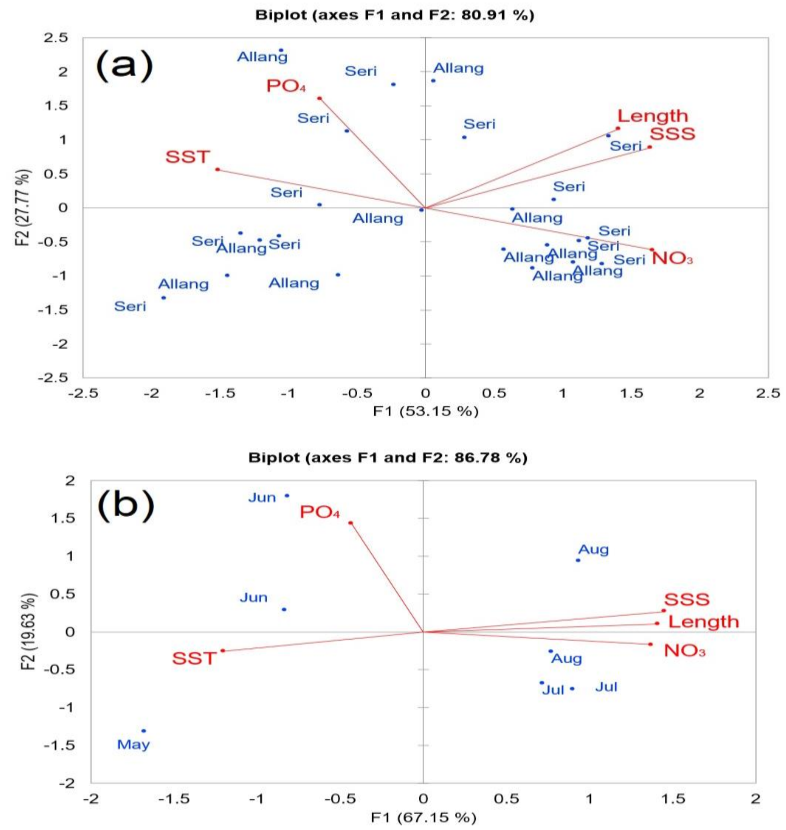

Figure 8. PCA analysis of loading and scatter plots between *Porphyra* sp. blade's length and environmental drivers regarding (a) spatial and (b) temporal observations.

Discussion

Characteristics of environmental conditions supporting Porphyra sp. in Ambon Island. The cool temperature between June and August 2023 in Ambon Island appears to provide favorable conditions for the occurrence of *Porphyra* sp*.* in the location. *Porphyra* sp*.* has been widely known to be a species living in high latitudes where cool climate predominates (Brodie et al 1996; Yoshida 1997). Meanwhile, the occurrence of *Porphyra* sp*.* in the tropics with warm climate was also reported with its seasonal occurrence particularly during the coolest period of the year such as during winter or rainy season (Ame et al 2010; Lewmanomont & Chittpoolkusol 1993; Ruangchuay & Notoya, 2007). Regarding the Ambon Island, located at 3°S, close to the equator, the seasonal cool-temperature condition supporting the occurrence of *Porphyra* sp*.* was also prevalent. The occurrence of *Porphyra* sp. with its onset on early June 2023 (dashed line in Figure 2a) was coincident with the cooling of local and regional SSTs and of local air temperature (Figure 2a), approaching the peak of seasonal low temperature of the year in Ambon Island, typically between June and August (Tarigan 1989). The PCA analysis (Figure 8) further supports this by demonstrating that the increase in the blade length of *Porphyra* sp*.* in Ambon Island corresponded to the SST cooling. In addition, the elevated magnitudes of SSS and nitrate appear to support the growth of *Porphyra* sp. in Ambon Island. This current study, that is fieldwork-based, showed that the elevated magnitudes of SSS and nitrate were coincident with the growing period of the blade of *Porphyra* sp. as highlighted by the PCA analysis (Figure 8)*.* This condition is consistent with some studies regarding the *Porphyra* cultivation experiments, showing that high salinity (30-40 psu) and high nitrate are favorable for the growths of the blade and conchocelis of *Porphyra* sp. (Conitz et al 2001; Lin 1999; Stekoll & Lin 1999).

Banda Sea upwelling providing favorable conditions for Porphyra sp. Banda Sea upwelling appears to regulate favorable environmental conditions for the life of *Porphyra sp.* in Ambon Island. The SST cooling coupled with high SSS (hence, high surface nutrient) in Banda Sea is linked to Ekman upwelling at eastern Banda Sea during southeasterly monsoon (May to September) with the upwelling peak between July and August (Gordon & Susanto 2001; Iskandar 2010; Wyrtki 1961; Zhu et al 2019). The upwelling process transports cool, salty, nutrient-rich subsurface water from the upper thermocline layer (i.e. temperature: 26^{o}C; salinity: 34.5 psu) to the surface layer (Gordon & Susanto 2001; Iskandar 2010; Waworuntu et al 2000; Westeyn et al 1990; Wyrtki 1961; Zhu et al 2019; Zijlstra et al 1990). The upwelled water at the surface layer of the Banda Sea upwelling hotspot (red box in Figure 1a) is expected to be transported northwestward by the prevailing southeasterly monsoon wind stress (Sprintall & Liu 2005) that can reach waters nearby Ambon Island immediately, with a low time lag (i.e. less than a week). The Banda Sea upwelled water, ultimately, reached the Ambon Island coasts, as observed in the mid-July 2023. The arrival of cool, salty, nutrient-rich upwelled water from Banda Sea at Ambon Island coasts provided favorable conditions for *Porphyra* sp*.* Previous laboratory culture studies had shown that *Porphyra* sp. growth rates were higher in low temperature, high saline water and high nutrient levels (Ame et al 2010; Conitz et al 2001; Lin 1999; Ruangchuay & Notoya 2007; Stekoll & Lin 1999). Here, our field study found similar results considering cool SST, high salinity, and high nutrient concentrations (given by nitrate) as the impact of Banda Sea upwelled water triggered the rapid growth of *Porphyra* sp. The other periods beside the peak of the Banda Sea upwelling season in June-August is less likely to provide favorable conditions for *Porphyra* sp. in Ambon Island. Regarding the temperature conditions, beside the Banda Sea upwelling season, the other seasons have the traits of a warm climate (both SST and air temperature are typically 29 to 32^{o}C) in Ambon Island (Figure 2a). These environmental conditions coincided with the absence of *Porphyra* sp. in the island (Hatta 1990). The disappearance of the species associated with the seasonal warming condition in Ambon Island is consistent with a study of other tropical *Porphyra* habitats in Thailand (i.e. the occurrence during cool seasonal conditions in December with SST=27^{o}C and the disappearance during the warmest conditions in March with SST=31^{o}C) (Ruangchuay & Notoya 2007). Regarding salinity and nutrients, the absence of Banda Sea upwelling (providing both high SSS and high nutrient levels; Figure 2b) in other seasonal conditions means that the coastal waters at the habitats of *Porphyra* sp. in Ambon Island are likely to be low saline and oligotrophic. This does not seem to provide favorable conditions for the growth of *Porphyra* sp. in Ambon Island, which is consistent with the absence of the species in the seasons beside Banda Sea upwelling season.

Comparing environmental conditions of Porphyra sp. in Ambon Island to other locations. The temperature range for *Porphyra* sp. in the Ambon Island habitat is mostly comparable with that in other tropical habitats. *Porphyra* sp. in Ambon Island grows within the temperatures range of 26-28^{o}C (§4.5), very similar to the optimal values for the species in Thailand (25-27^{o}C) (Ruangchuay & Notoya, 2003), slightly cooler than those for the species in Myanmar (30^{o}C) (Aye-Mon-Sein et al 2003) and relatively warmer than those for the species in Philippines (20-24^{o}C) (Ame et al 2010; Evelyn et al 2010). The optimum range of temperatures for *Porphyra* sp. in Ambon Island is also comparable with that for the species in India, a temperate region (25°C) (Pereira et al 2005). Meanwhile, this range of the Ambon Island habitat is significantly warmer than that for *Porphyra* sp. living in other temperate regions such as Australia and New Zealand (14°C), Portugal (15°C), British Isles (18°C) and New England of the US (10-15°C) (Ackland et al 2006; Kim et al 2007; Knoop et al 2020; Pereira et al 2004); and for the sub-polar region such as Canada (10-15°C) (Blouin et al 2007) and Alaska (11°C) (Lin 1999; Stekoll & Lin 1999). Regarding salinity linked to nutrient for supporting *Porphyra* sp., there is a key difference between the Ambon Island habitat and the other tropical habitats. In the tropical *Porphyra* habitats in Thailand, Myanmar and Philippines, the occurrence of the species was coincident with high nutrient concentration and low salinity (25 psu in Thailand; 10-25 psu in Myanmar; 29-31 psu in Philippines), which was linked to high rainfall (Ame et al 2010; Aye-Mon-Sein et al 2003; Lewmanomont & Chittpoolkusol 1993; Ruangchuay & Notoya 2007). The high nutrient corresponding to low salinity means that nutrients supporting *Porphyra* sp. in Thailand, Myanmar and Philippines likely originate from the terrestrial sources, being transported by river runoff (with low salinity) during high rainfall condition. In contrast, in the Ambon Island habitat, the occurrence of *Porphyra* sp. in the presence of high nutrient is concurrent with high salinity from Banda Sea (~34.5 psu; Figure 2b), indicating the important role of the open ocean Banda Sea (via upwelling) for the *Porphyra* sp. in Ambon Island.

Lessons for cultivating Porphyra sp. originating from the Ambon Island habitats. Environmental parameters supporting *Porphyra sp.* reported in this study determine the culture conditions for *Porphyra* sp. originating from Ambon Island. Many cultivation experiments of *Porphyra* sp. have highlighted the importance of considering environmental factors such temperature, salinity and nutrients that support the growth of *Porphyra* sp. for the successful culture of the species (Aye-Mon-Sein et al 2003; Conitz et al 2001; Hafting 1999; Kim et al 2007; Kim & Notoya 2004; Knoop et al 2020; Lin 1999; Pereira et al 2004; Redmond et al 2014; Stekoll & Lin 1999). To our knowledge, there have been limited efforts to cultivate *Porphyra* sp. from the Ambon Island habitat due to inadequate information on the favorable temperature, salinity and nutrients supporting the species (Pattiasina et al 2023). The favorable temperature (26-28°C), salinity (~34.5 psu) and nitrate (above 0.06 ppm) (Figures 2a and 2b) for *Porphyra* sp. in Ambon Island reported in this present study can provide reference for successfully implementing the cultivation of the species.

Conclusions. This study provides an important insight on the role of Banda Sea upwelling in supporting the occurrence of *Porphyra* sp. in Ambon Island, eastern Indonesia. There was a very strong correlation ($r \geq 0.90$) with very short time lag (<1 week) for SST between Banda Sea upwelling hotspot in eastern Banda Sea and waters nearby Ambon Island, the *Porphyra* habitat. This indicates that during the peak upwelling season (June-August), cool, salty, nutrient-rich upwelled Banda Sea water from the upwelling hotspot can immediately arrive at Ambon Island. Weekly environmental parameter observations during Banda Sea upwelling season between June and August 2023 in the *Porphyra* habitats of Seri and Allang in Ambon Island found SST cooling (reaching 26°C), high SSS similar to typical deep-layer Banda Sea water (≥34.5 psu) and the elevated concentration of surface dissolved nitrate (reaching as much as 0.1 ppm). This coincided with the occurrence and subsequent growth of *Porphyra* sp. in the locations. The growth rates of *Porphyra* sp. were found to be 0.24 cm day^{-1} and 0.41 cm day^{-1} in Seri and Allang, respectively. From PCA analyses, the blade length was found to be significantly linked to SST cooling and the increases in SSS and nutrients, characterizing typical oceanic conditions in Ambon Island during Banda Sea upwelling season. The current study adds an important insight into the existing knowledge of the ecology of *Porphyra* in the tropical habitats, regarding the source of nutrients for supporting the presence and growth of the species. In the reported tropical habitats of *Porphyra* sp. (e.g. Thailand, Myanmar and Philippines), the nutrient supporting the species likely originates from the terrestrial environment since the occurrence of *Porphyra* sp. is coincident with high nutrient coupled with low salinity. In contrast, this current study reported that the nutrient source for the tropical *Porphyra* habitat of Ambon Island originates from deep-sea environment (i.e. subsurface Banda Sea water being upwelled) due to high nutrient concentration found in the presence of high salinity that was observed during the occurrence of *Porphyra* sp. in Ambon Island. It should be pointed out that there was a possible competition that was observed during the fieldwork campaigns at Allang, as *Porphyra* sp. and *Gymnogongrus* sp. shared the same niche. Yet, in this present study, we excluded this complex biological process from our discussions as the competition aspect was beyond the scope of this current study (i.e. seeking the link between Banda Sea upwelling and the occurrence of *Porphyra* sp. in Ambon Island). Thus, future studies are required to investigate this competition aspect and the adaptive and survival strategies of *Porphyra* sp. in Allang.

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

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