Influence of environmental parameters on habitat preference of gelatinous zooplankton in various coastal ecosystems, the Straits of Malacca

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HIGHLIGHTS

- Managed mangroves had higher gelatinous zooplankton density, biomass and diversity.
- Turbidity and nutrients were main factors affecting the zooplankton community structure.
- Gelatinous zooplankton dominance, composition and distribution varied with habitats.
- Seasonal changes showed significant effects on the zooplankton community structure.

ARTICLE INFO

ABSTRACT

This study examined spatial distribution patterns of gelatinous zooplankton in three coastal areas, namely Matang mangrove area (managed mangrove area, MMA), Kuala Selangor coastal waters (reclaimed mangrove area, RMA) and Port Dickson coastal waters (a resort area, PDC). In each area, non-gelatinous and gelatinous zooplankton samples were collected by horizontal tows of a plankton net (140 μm mesh size) and a Bongo net (500 μm mesh size). Various environmental parameters were measured *in situ* (temperature, dissolved oxygen, pH, turbidity) as well as analyzed in the laboratory (nutrients, chlorophyll-a , zooplankton). Nineteen hydromedusae, two siphonophore and two ctenophore species were recorded from three different areas. Matang mangrove (MMA) had the highest number of species (19 species), followed by RMA (13 species) and PDC (9 species). Gelatinous zooplankton density and biomass were significantly higher ($p < 0.05$) in MMA than the other areas. Different gelatinous zooplankton groups dominated in different areas with ctenophores as the most important group (*Pukia* sp. formed 79.0% of total gelatinous zooplankton) in MMA. The hydromedusae (55.0% was *Eirene brevigona*) was the most dominant group in RMA that had high total suspended solids, and siphonophores (58.0% was *Lensia subtiloides*) dominated PDC characterized by high water transparency. Biotic-environmental (BIO-ENV) analysis showed significant roles of turbidity, salinity, nutrients, chlorophyll-a and non-gelatinous zooplankton ($p < 0.05$) in the distribution of gelatinous zooplankton in these tropical coastal ecosystems. Two-way ANOSIM (analysis of similarities) showed that there were significant differences in gelatinous zooplankton amongst the three habitats. In terms of monsoonal seasons, the gelatinous zooplankton density showed significant differences ($p < 0.05$) between the southwest and northeast monsoons. This study illustrated that gelatinous zooplankton diversity and density varied with the degrees of habitat disturbance and seasonal changes, implying the potential impacts of anthropogenic activities and climate change on its community structure.

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1. Introduction

Coastal ecosystems that are highly productive and rich in biodiversity have supported important fishery industries for centuries and contributed immensely to the economic development

of littoral states. However, anthropogenic activities such as industrial, agricultural, recreational and land-used activities along the coastlines have resulted in many habitat changes and water pollution (Smith et al., 1999; Rezai et al., 2009; Omar et al., 2018). In Malaysia, the increase of suspended particles and turbidity is one of the main forms of pollution due to unsustainable land-used practices associated with logging, agriculture and industrial developments. The increase of suspended particles such as organic matter, clay and silt from the anthropogenic activities that drain into the coastal waters resulted in increased nutrient and turbidity levels in the water. Changes in turbidity levels and nutrient concentrations would in turn modify the environmental conditions and eventually affect the structure and functions of coastal ecosystems including habitats of gelatinous zooplankton.

Gelatinous zooplankton play important roles in structuring coastal and estuarine ecosystems through predation on other zooplankton and ichthyoplankton, besides providing food for upper trophic levels, such as sea turtles, seabirds and various fish species (Suchman and Brodeur, 2005). Sweetman and Chapman (2015) reported that gelatinous zooplankton is recognized as an important component in nutrient cycling in the aquatic food web. Water pollution including increased nutrients and turbidity levels caused by anthropogenic activities provide competitive advantage to gelatinous zooplankton since they can survive in disturbed marine ecosystems due to their high adaptation capacity to pollution. High water column turbidity would enhance the population of gelatinous zooplankton as they are tactile predators in contrast to fish which are visual predators (Aknes, 2007; Pitt et al., 2008). Furthermore, they also have fast growth rates, broad diets and ability to tolerate hypoxia (Richardson et al., 2009). In addition, studies have reported that some species of gelatinous zooplankton have the ability to form resting cysts in harsh environments and rapidly reproduce in favorable environments (Arai, 2001; Boero et al., 2008).

The Straits of Malacca are located on the western side of Peninsular Malaysia with a total coastline of 1000 km (Rezai et al., 2003). The Straits are among the most important fishing grounds and international waterways since the 7th century. There are many highly productive ecosystems along the coast such as mangrove areas, sea-grass beds and coral reefs which contribute significantly to the fisheries industry in the Straits (Yusoff et al., 2006). In recent years these ecosystems are under threat due to rapid economic development including coastal land reclamation, aquaculture, port development and other land-used activities.

Studies on reproductive biology, taxonomic and molecular identification of Scyphozoa and Cubozoa have been accomplished in the coastal waters of Malaysia, Indonesia and the tropical Australia (Gershwin and Alderslade, 2005; Asrial et al., 2015; Nishikawa et al., 2015; Rizman-Idid et al., 2016; Maghsoudlou et al., 2017). Additionally, Graham et al. (2003) studied the invasion of Scyphozoa (*Phyllorhiza punctata*) in the northern Gulf of Mexico. Hydromedusae distribution has been reported by Santhakumari and Nair (1999) and Miglietta et al. (2008). The occurrence of hydromedusae blooms has been associated with increased in nutrients such as those from upwelling events (Miglietta et al., 2008).

Even though gelatinous zooplankton blooms are global issues, their effects at the local level are still unclear. Because of their potential population changes associated with many environmental parameters, such as pollution, and their interactions with other components of the food web, it is important to study gelatinous zooplankton community structure in different coastal ecosystems. It is hypothesized that the gelatinous zooplankton density will be higher in an ecosystem with high nutrient and turbidity levels compared to clear and nutrient poor waters. The goal of this study was to contribute to a better understanding of the diversity and distribution of gelatinous zooplankton in tropical coastal areas with different environmental characteristics.

2. Materials and methods

2.1. Study area

The study was carried out in three different areas in the Straits of Malacca from June 2010 to April 2011 during high tides with four sampling stations at each area (Fig. 1). These areas were the Matang mangrove estuary (managed mangrove area — MMA), Kuala Selangor coastal waters (reclaimed mangrove area — RMA) and Port Dickson coastal waters (a resort area — PDC). The Matang mangrove forest was the largest tract of a well-managed mangrove forest in Peninsular Malaysia. The water depths at Matang mangrove area did not exceed 8 m and the hydrology was dominated by semi-diel tidal circulation (Chew and Chong, 2011). In Kuala Selangor coastal waters, RMA, the mangrove area was cleared and an approximately 8 km stretch of the forest was turned into a 400-ha shrimp farm (particularly for the black tiger shrimp, *Penaeus monodon*) in early 2003 (Jahabar, 2005). The coastal zone was characterized by a semi-diel, macro-tidal regime with a mean spring tidal range of about 4.0 m (Theng and Mohamed, 2005). In the Port Dickson coastal area (PDC), more than 50% of its coastline was heavily developed to cater to the tourism industry. Generally, Port Dickson waters were relatively shallow (about 20 m depth) and well mixed (Praveena et al., 2011).

The tidal levels ranged from 0.1 m to 2.5 m, 0.5 m to 4.9 m and 0.3 m to 3.0 m in MMA, RMA and PDC respectively (Fig. 2), indicating that the protected mangrove area (MMA) was of lower energy compared to the disturbed area in the coastal Kuala Selangor (RMA) and the clear-water Port Dickson (PDC). In general, the currents in the Straits of Malacca flow towards the northwest to the Andaman sea with magnitudes ranging from 10–70 cm s^{-1} at the surface and 10–30 cm s^{-1} at the 30–50 m layer (Syamsul et al., 2010). Coastal areas in Kuala Selangor and Port Dickson were directly exposed to these currents, but the protected area in the intact mangroves provided a better shelter for the development of zooplankton communities including gelatinous zooplankton.

The waters of the Straits are influenced by the inflow of freshwater from the numerous rivers on the western coast of Peninsular Malaysia and the eastern coast of Sumatra, causing drastic fluctuations of environmental characteristics in the coastal environment of the Straits. Rainfall distribution patterns are determined by the seasonal wind flow pattern and local topographic features. The climate is generally categorized into two monsoon seasons: southwest monsoon (May to September) which is normally dry and northeast monsoon (November to March) which is associated with heavy rainfall. The transition periods in between the monsoons are known as inter-monsoon seasons.

2.2. Sample collection and laboratory procedures

Gelatinous zooplankton and non-gelatinous zooplankton samples were collected bimonthly for an annual cycle during day time and high tide (Fig. 2). Samples were collected by horizontal tows of a Bongo net (mouth diameter: 0.3 m, mesh size: 500 μm) and a small-mesh plankton net (mouth diameter: 0.47 m, mesh size: 140 μm), both with calibrated flow meters (#5571-B; Rigo Co., Ltd., Tokyo, Japan) attached in the mouth of the net. The haul for investigating gelatinous zooplankton was carried out parallel to a haul for surveying the non-gelatinous zooplankton, and they were trawled simultaneously at a constant speed of 1.6–2.7 knots. Tow durations ranged between 5 and 10 min, depending on the incidence of net clogging. Collected samples were preserved in borax-buffered 5% formalin in seawater. All samples were transported to the laboratory for taxonomic identification, enumeration and biomass determination. The fixed samples
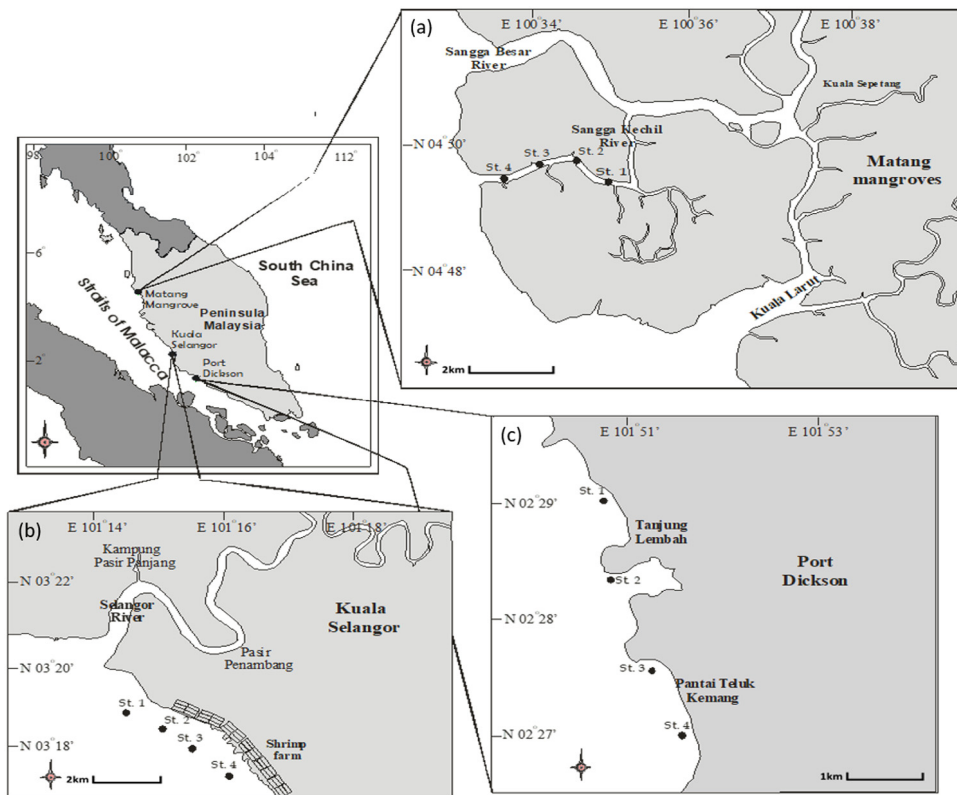
Fig. 1. Location of study areas (a) managed mangrove area (MMA), (b) reclaimed mangrove area (RMA), (c) resort area (PDC).
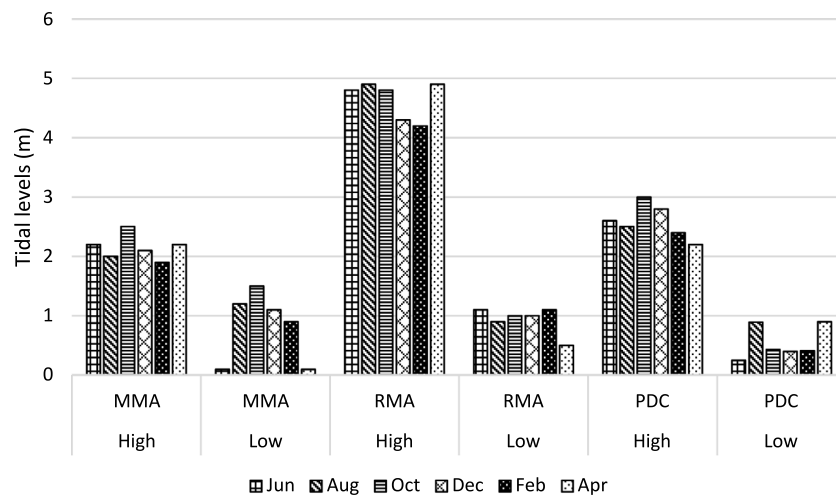

Fig. 2. Tidal levels (m) at managed mangrove area (MMA), reclaimed mangrove area (RMA) and resort area (PDC) during the period of study.

were further analyzed in the laboratory, where hydromedusae, siphonophores and ctenophores were sorted out, counted and identified to species or lowest taxon level, using a dissecting microscope (Nikon model SMZ645). The taxonomic identification followed identification keys pertinent to respective taxa, namely Kramp (1961), Bouillon and Boero (2000), and Bouillon et al. (2006) and from taxonomic articles available in related international journals. Species names were verified and updated through the World Register of Marine Organisms (WoRMS; www.marinespecies.org). The total gelatinous zooplankton biomass was estimated as wet weight (mgWW m^{-3}). The non-gelatinous zooplankton samples were grouped into easily distinguishable taxonomic categories (eg. Copepoda, Chaetognatha or Mollusca) and reported as densities (ind. m^{-3}).

At each sampling station, environmental parameters such as dissolved oxygen, salinity, and temperature were measured *in situ* using a multi-parameter sonde (Model Hydrolab Surveyor 4). The water transparency was determined by a Secchi disk and turbidity was measured using a turbidimeter (Lovibond; Tintometer Gmbh, Dortmund, Germany). Triplicate samples for the determination of total suspended solids, chlorophyll-a and nutrient analyses (soluble reactive phosphorus, total ammonia nitrogen, nitrate and nitrite nitrogen, total nitrogen and total phosphorus) were collected using a Niskin water sampler. Analyses were carried out in the laboratory following standard methods for seawater analysis (Parsons et al., 1984).
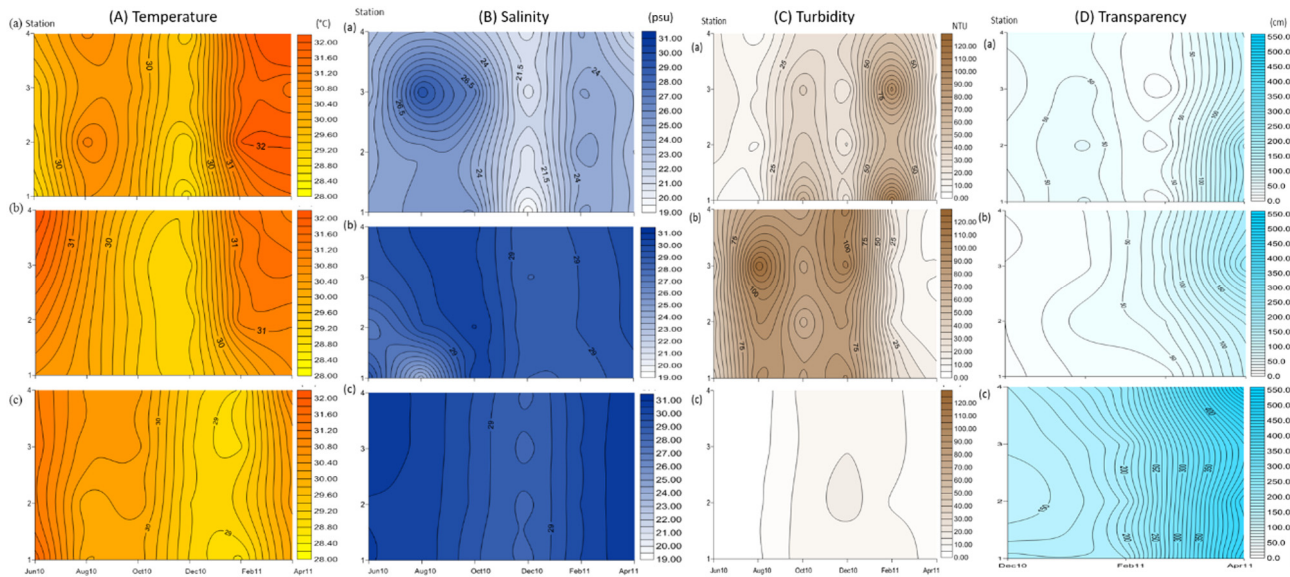
Fig. 3. Seasonal variations of (A) temperature, (B) salinity, (C) turbidity and (d) transparency at (a) managed mangrove area (MMA), (b) reclaim mangrove area (RMA) and (c) resort area (PDC) during the study period. Number 1, 2, 3 and 4 indicate the sampling stations in the study areas.

Fig. 4. Seasonal variations of (A) total suspended solids, (B) total phosphorus, (c) total nitrogen and (d) chlorophyll-a at (a) managed mangrove area (MMA), (b) reclaim mangrove area (RMA) and (c) resort area (PDC) during the study period. Number 1, 2, 3 and 4 indicate the sampling stations in the study areas.
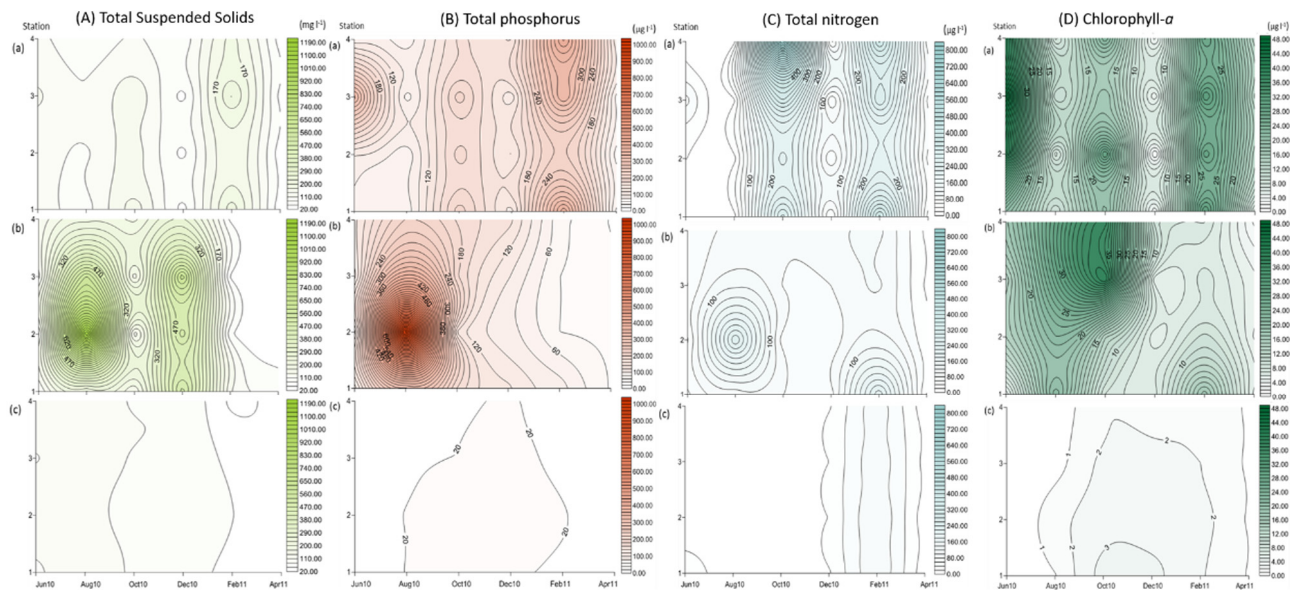
2.3. Data analyses

Temporal patterns in environmental parameters was illustrated using Surfer 10 (Golden Software). One-way analysis of variance (ANOVA) test was performed on the environmental data to determine if and where significant spatial differences existed across the study sites. Biodiversity was expressed as species richness (S) and Brillouin's diversity index (H_B) to emphasize the species composition (richness) rather than the density and distribution (evenness) due to large variations in abundance amongst sites and seasons. Non-parametric Kruskal–Wallis test was performed to determine if significant differences in density and biomass existed across the study sites. Species density data were square root transformed to balance the contributions from the very few abundant species with the many rare species (Clarke and Warwick, 1994). Bray–Curtis similarity was applied to examine variations in the gelatinous zooplankton density. The difference

in gelatinous zooplankton densities between sampling sites and seasons were tested by two-way crossed ANOSIM (analysis of similarities). SIMPER analysis (similarity percentage) was performed to determine the contribution of each gelatinous zooplankton species to the average similarity within the defined site. Biotic-environmental (BIO-ENV) analysis was applied to determine the environmental parameters that best explained the gelatinous zooplankton distribution pattern. Environmental and biotic data were then ordinated using a correlation-based principal component analysis (PCA) to identify variations and patterns in datasets. Data were transformed (Log X + 1) and normalized before the PCA was carried out. All analyses were done using PRIMER-PERMANOVA V7 (Primer-E Ltd, Plymouth, UK) (Clarke and Warwick, 1994) and IBM SPSS Statistics 22. In this study, hydrozoans were divided into hydromedusae (medusa form of Hydrozoa) and siphonophores.
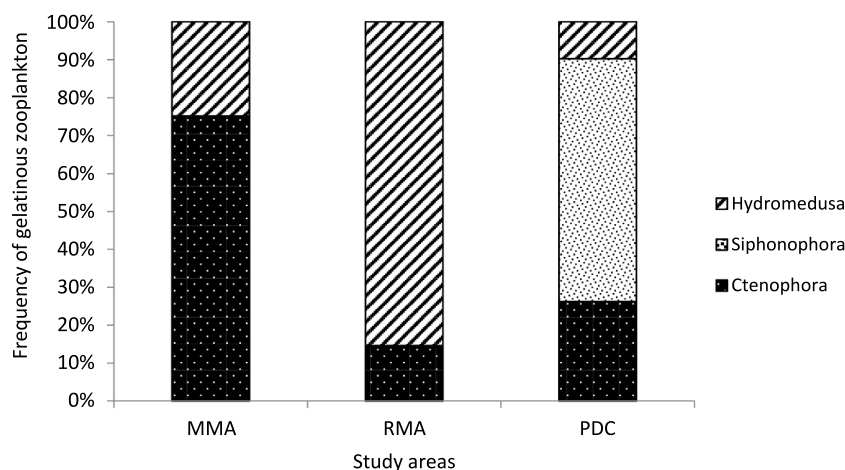
Fig. 5. Comparison of gelatinous zooplankton groups frequency (%) at managed mangrove area (MMA), reclaimed mangrove area (RMA) and resort area (PDC).
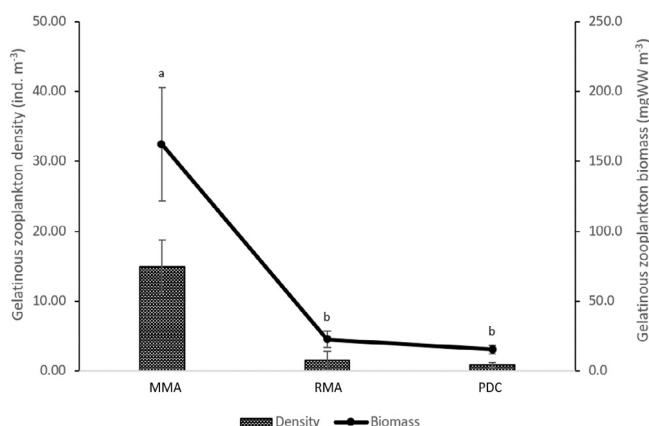

Fig. 6. Gelatinous zooplankton density (ind. m^{-3}) and biomass (mgWW m^{-3}) at managed mangrove area (MMA), reclaimed mangrove area (RMA) and resort area (PDC). Vertical bars indicate standard errors. Different superscripts indicate significantly different means ($p < 0.05$).

3. Results

3.1. Spatial and temporal variations of environmental parameters in study areas

Except for the temperature (Fig. 3A), other environmental parameters among study sites showed significant differences, especially those related to turbidity and nutrients ($p < 0.05$). In the managed mangrove area (MMA), salinity fluctuated from a minimum of 20.31 psu to a maximum of 27.11 psu, while no significant salinity variations were observed in RMA and PDC (Fig. 3B). Unlike the other sampling sites, MMA showed a seasonal pattern, with the highest salinity observed during the southwest monsoon and the lowest salinity during the northeast monsoon. Turbidity values in MMA were higher during the northeast monsoon (162.22 ± 31.85 NTU) compared to the southwest monsoon (10.65 ± 1.75 NTU) (Fig. 3C). Meanwhile, turbidity values in RMA were high during the southwest monsoon (105.00 ± 13.22 NTU) and decreased towards the northeast monsoon. The water transparency in the resort area ranged from 145.0 cm to 530.0 cm, which was higher compared to the other sites (Fig. 3D). Water transparency in MMA ranged from 12.5 cm to 192.5 cm, while in RMA, the values ranged from 15.0 cm to 220.0 cm. Total suspended solids in RMA was significantly higher ($p < 0.05$) than other locations, ranging from 54.48 to 1116.00 mg l^{-1}

with the highest value recorded during the southwest monsoon (Fig. 4A). The concentrations of total phosphorus were lowest in PDC compared to the other sampling sites (Fig. 4B). The concentrations of total phosphorus in MMA were highest (353.13 ± 45.48 µg l^{-1}) during the northeast monsoon and lowest (68.39 ± 1.04 µg l^{-1}) during the southwest monsoon. The highest concentration of total nitrogen (425.15 ± 133.03 µg l^{-1}) was recorded in MMA during the post-southwest monsoon (October 2010) (Fig. 4C). Chlorophyll-a concentration was significantly higher ($p < 0.05$) in MMA and RMA compared to PDC (Fig. 4D). The highest chlorophyll-a concentration (37.47 ± 5.69 mg m^{-3}) in MMA was recorded during the southwest monsoon and lowest (3.07 ± 0.52 mg m^{-3}) during the northeast monsoon (Fig. 4D). In RMA, the highest chlorophyll-a concentration (25.18 ± 1.94 mg m^{-3}) was recorded during the southwest monsoon, while the lowest (3.65 ± 0.65 mg m^{-3}) during pre-southwest monsoon (Fig. 4D).

3.2. Spatial and temporal patterns of gelatinous zooplankton composition and densities

A total of 23 species of gelatinous zooplankton from 16 genera and 14 families were identified in the study areas along the Straits of Malacca (Table 1). There were 19 species belonging to 12 genera of hydromedusae, two species belonging to two genera of siphonophores and two species belonging to two genera of ctenophores at the three sampling sites (Table 1). There were significant differences ($p < 0.05$) in the species diversity (S and H_B) between the study areas. The managed mangrove area (MMA) had the highest number of species (19 species from 14 genera and 13 families) followed by RMA and PDC with 13 and 9 species, respectively (Table 1). The order Leptomedusae had the highest number of species at MMA (13 species), followed by RMA (10 species) and PDC (five species) (Table 1). Brillouin's diversity index (H_B) in MMA ($H_B = 0.44$) was significantly higher ($p < 0.05$) compared to RMA ($H_B = 0.25$) and PDC ($H_B = 0.23$) (Table 1).

Different gelatinous zooplankton groups dominated at each study area. Ctenophores represented 75.1% of the total gelatinous zooplankton density at MMA (Fig. 5). At RMA and PDC, gelatinous zooplankton communities were dominated by hydromedusae (85.4% of the total gelatinous zooplankton density) and siphonophores (64.0%), respectively (Fig. 5). Gelatinous zooplankton density was significantly higher ($p < 0.05$) at MMA (14.9 ± 3.8 ind. m^{-3}) than at RMA (1.5 ± 1.3 ind. m^{-3}) or PDC (0.9 ± 0.3 ind. m^{-3}) (Fig. 6). Similarly, the gelatinous zooplankton biomass was highest ($p < 0.05$) at MMA (162.1 ± 40.6

Table 1
Mean densities (ind. m^{-3}) and frequency (%) of gelatinous zooplankton in different tropical coastal ecosystems.

			Managed mangrove area (MMA)	Frequency (%)	Reclaimed mangrove area (RMA)	Frequency (%)	Port Dickson coastal area (PDC)	Frequency (%)
Hydrozoa (Hydromedusa)	Anthoathecata	*Nemopsis* sp.	0.01	0.06	–	0.00	–	0.00
	Leptothecata	*Aequorea parva*	0.02	0.14	–	0.00	–	0.00
		Blackfordia virginica	2.70	18.08	<0.01	0.23	–	0.00
		Clytia sp.	0.04	0.24	<0.01	0.23	0.05	5.06
		Eirene averuciformis	0.16	1.08	0.02	1.40	–	0.00
		Eirene brevigona	0.01	0.06	0.06	4.20	–	0.00
		Eirene brevistylis	–	0.00	0.01	0.50	<0.01	0.19
		Eirene brevistyloides	0.08	0.53	–	0.00	–	0.00
		Eirene chiaochowensis	0.22	1.50	–	0.00	–	0.00
		Eirene hexanemalis	<0.01	0.03	0.02	1.38	0.01	0.77
		Eirene kambara	–	0.00	<0.01	0.23	–	0.00
		Eirene menoni	0.01	0.09	0.03	1.90	<0.01	0.19
		Lovenella sp.	0.01	0.04	–	0.00	–	0.00
		Malagazzia sp.	0.35	2.36	0.07	4.40	–	0.00
		Obelia longissima	0.07	0.43	–	0.00	0.01	1.16
		Phialella sp.	0.01	0.07	–	0.00	–	0.00
		Pseudoclytia pentata	–	0.00	0.01	0.50	–	0.00
	Limnomeduase	*Gonionemus* sp.	<0.01	0.02	–	0.00	–	0.00
	Trachymedusae	*Liriope tetraphylla*	0.01	0.08	1.08	70.40	0.02	2.30
Hydrozoa (Siphonophora)	Siphonophorae	*Lensia subtiloides*	<0.01	0.02	<0.01	0.23	0.36	39.32
		Diphyes chamissonis	–	0.00	–	0.00	0.22	24.72
Ctenophora	Beroida	*Beroe* sp.	0.14	0.96	–	0.00	–	0.00
	Cydippida	*Pukia* sp.	11.09	74.19	0.22	14.40	0.24	26.28
		Total number of species	19		13		9	
		Total number of genera	14		8		7	
		Total number of family	13		7		6	
		Brillouin's diversity index	0.44		0.25		0.23	
		Total % abundance		100.00		100.00		100.00

mgWW m^{-3}) followed by RMA (22.7 ± 5.9 mgWW m^{-3}) and PDC (15.3 ± 3.0 mgWW m^{-3}) (Fig. 6).

The density of non-gelatinous zooplankton populations was highest in RMA, (8243.1 ± 2014.9 ind. m^{-3}), followed by MMA (5486.3 ± 1520.5 ind. m^{-3}) and PDC (1389.1 ± 486.3 ind. m^{-3}). The non-gelatinous zooplankton populations were mostly dominated by copepods at all study areas (Fig. 7). In MMA, copepods contributed 79.0% of the total zooplankton population, followed by Cirripedia (10.1%), Appendicularia (3.6%) and Chaetognatha (2.6%) (Fig. 7). The rest of the zooplankton groups contributed less than 2.0% of the total zooplankton. Similarly, in RMA, the non-gelatinous zooplankton populations were dominated by copepods contributing 73.8% of the total density, followed by Cirripedia (16.2%) and Malacostraca (5.5%), while the rest of the zooplankton groups contributed less than 2.0% of the total zooplankton (Fig. 7). Meanwhile, in PDC, the copepods contributed 79.4%, followed by Appendicularia (12.4%), Malacostraca (2.8%) and Cirripedia (2.0%). The rest of the zooplankton groups contributed less than 2.0% of the total zooplankton.

SIMPER analyses, based on community estimates in different coastal ecosystems, identified the discriminator species, which primarily accounted for the assemblage differences between different ecosystems. In MMA, within-group similarities based on density data indicated that *Pukia* sp. (Ctenophora) contributed about 78.9% to the total similarity (Table 2). Meanwhile, at RMA and PDC, *Eirene brevigona* (Hydromedusa) and *Lensia subtiloides* (Siphonophora) contributed about 55.0% and 58.0% to the total similarity, respectively (Table 2).

There was no gelatinous zooplankton in June 2010 except at MMA (Fig. 8). The gelatinous zooplankton density in MMA increased towards the time of the inter-monsoon. The highest gelatinous zooplankton density in MMA was recorded during post-southwest monsoon in October 2010 (27.5 ± 8.8 ind. m^{-3}) and lowest during the northeast monsoon in December 2010

(5.0 ± 4.0 ind. m^{-3}). Meanwhile, in RMA, the peak gelatinous zooplankton density was observed in during the northeast monsoon in February 2011 (4.7 ± 1.8 ind. m^{-3}). However, the gelatinous zooplankton in RMA was totally absent in April 2011. The gelatinous zooplankton density in PDC increased during the northeast monsoon and peaked during pre-southwest monsoon in April 2011 (2.0 ± 1.0 ind. m^{-3}) (Fig. 8).

3.3. Spatial and temporal gelatinous zooplankton community relationships

The distinct distribution of gelatinous zooplankton densities in different study sites is shown by a dendrogram and non-metric multidimensional scaling (NMDS), where the dissimilarity between groups were 75% (Fig. 9). Two-way ANOSIM of the overall combination of gelatinous zooplankton densities in all study sites across all seasons revealed that gelatinous zooplankton communities in MMA, RMA and PDC were significantly different ($p < 0.05$) with a high range value of R (= 0.55) for the global test (Table 3). High range values of R (= 0.61 and 0.67) for the MMA v RMA and MMA v PDC comparisons, contrasted with a much lower value ($R = 0.36$) for RMA v PDC, indicating that Matang mangrove area (MMA) was significantly different ($p < 0.05$) from both the reclaimed mangrove (RMA) and resort (PDC) areas. Similarly, two-way ANOSIM of the overall combination of gelatinous zooplankton density in all monsoon seasons across all sites showed that the gelatinous zooplankton density was significantly different ($p < 0.05$) with a mid-range of R (= 0.23) for the global test (Table 3). In addition, the gelatinous zooplankton density during the northeast monsoon was significantly different from that in the southwest monsoon ($p < 0.05$)
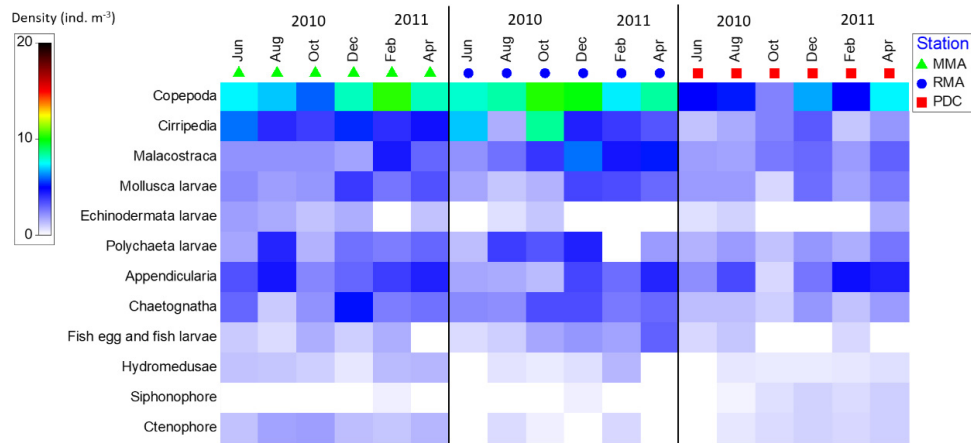
Fig. 7. Shade plot of monthly variations of non-gelatinous zooplankton density (ind. m^{-3}) at managed mangrove area (MMA), reclaimed mangrove area (RMA) and resort area (PDC). White space denotes absence of that species at that station and month; depth of color scale is linearly proportional to a fourth-root transformation of density. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
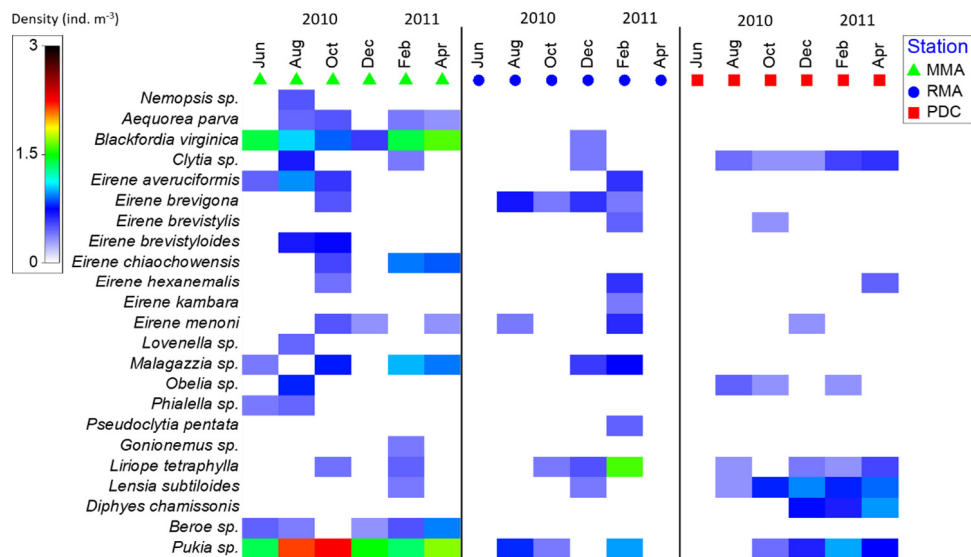

Fig. 8. Shade plot of monthly variations of gelatinous zooplankton density (ind. m^{-3}) at managed mangrove area (MMA), reclaimed mangrove area (RMA) and resort area (PDC). White space denotes absence of that species at that station and month; depth of color scale is linearly proportional to a fourth-root transformation of density.

Table 2
Major gelatinous zooplankton species contribution (% abundance) for managed mangrove area (MMA), reclaimed mangrove area (RMA) and resort area (PDC) based on SIMPER analysis.

Species	Managed mangrove area (MMA)	Reclaimed mangrove area (RMA)	Port Dickson coastal area (PDC)
Pukia sp.	78.93	23.85	14.28
Blackfordia virginica	17.96		
Eirene brevigona		55.01	
Liriope tetraphylla		16.02	
Lensia subtiloides			58.04
Diphyes chamissonis			15.98

3.4. Linking gelatinous zooplankton and environmental parameters

The correlation of gelatinous zooplankton and environmental parameters was analyzed using biotic-environmental (BIO-ENV) analysis. The Global Test from BIO-ENV showed that gelatinous zooplankton density was significantly ($p < 0.05$) correlated with environmental parameters (Table 4). From the BIO-ENV analysis, transparency, total suspended solids, salinity, chlorophyll-a and non-gelatinous zooplankton were best correlated to gelatinous zooplankton with $\rho = 0.43$. The correlation between the gelatinous zooplankton and environmental parameters in each area

is shown by PCA where axis 1 and axis 2 together explained 59.2% of the cumulative variance (Fig. 10). Principal Component 1, explaining 41.1% of total variance, had high positive loading on transparency and high negative loading of total phosphorus, total nitrogen, turbidity, chlorophyll-a and copepod (Fig. 10). The positive parameters in PC1 clearly described the clear water in Port Dickson resort area (PDC). High loading of total phosphorus, total nitrogen, turbidity and chlorophyll-a showed that MMA was clearly distinguished by greater amounts of nutrients and chlorophyll-a, probably due to outwelling from the mangrove area and surface runoff from the reclaimed mangrove forest.
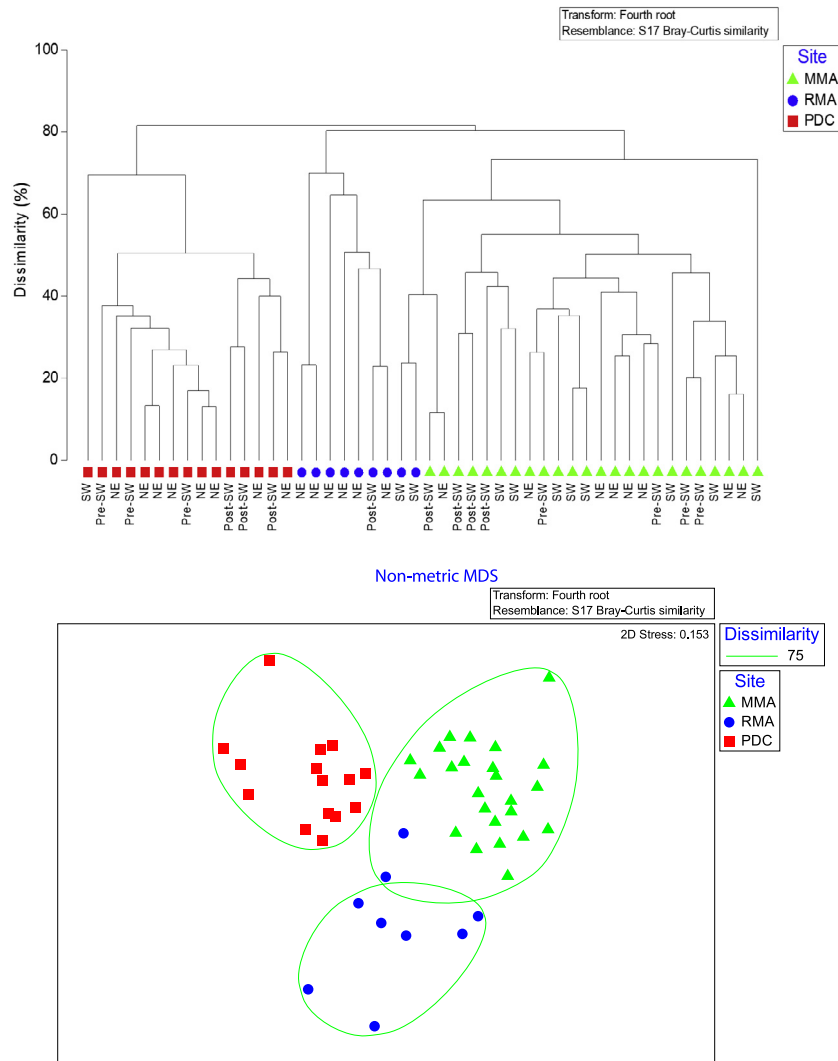
Fig. 9. Dendrogram and non-metric multidimensional scaling (NMDS) of gelatinous zooplankton density at managed mangrove area (MMA), reclaimed mangrove area (RMA) and resort area (PDC) in different seasons. SW = Southwest, NE = Northeast.
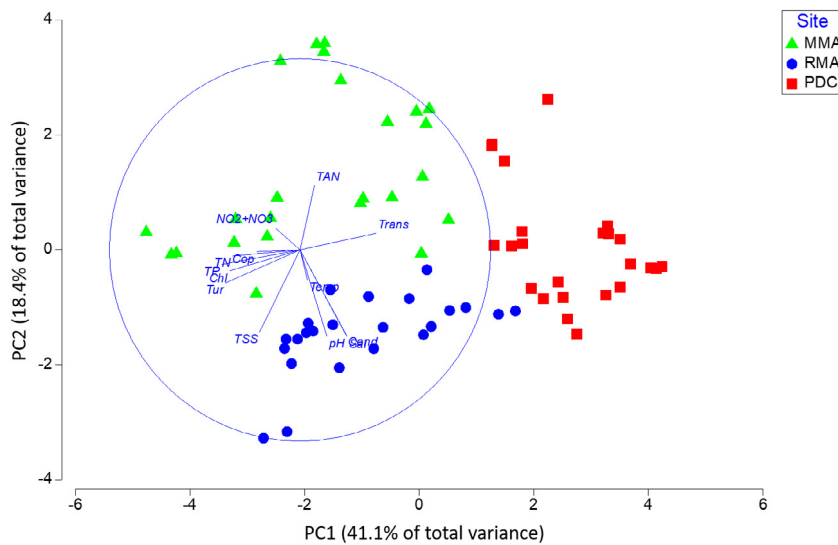

Fig. 10. Principle component analysis (PCA) ordination relating environmental parameters to gelatinous zooplankton community at managed mangrove area (MMA), reclaimed mangrove area (RMA) and resort area (PDC). Temp = temperature, Trans = transparency, Tur = turbidity, TSS = total suspended solids, Con = conductivity, Sal = salinity, TAN = total ammonium nitrogen, TN = total nitrogen, TP = total phosphorus, Chl = chlorophyll-a, Cop = copepod.

Table 4
Summary of the environmental variables that best explain the gelatinous zooplankton community in the study area, showing spearman rank correlation (ρ) obtained by BIO-ENV analysis.

Global Rho (ρ) = 0.423; p = 0.1%		
No. Variables	Correlation (ρ)	Selections
1	0.330	Transparency
2	0.398	Transparency, salinity
3	0.413	Transparency, salinity, chlorophyll-a
4	0.421	Transparency, salinity, chlorophyll-a, copepod
5	0.423	Transparency, total suspended solids, salinity, chlorophyll-a , copepoda
5	0.419	Transparency, turbidity, salinity, chlorophyll-a , copepod
5	0.418	Transparency, salinity, total phosphorus, chlorophyll-a, copepod

Table 3
Pairwise R-statistic values and significance levels (p) for two-way ANOSIM test on the data for the gelatinous zooplankton density recorded in managed mangrove area (MMA), reclaimed mangrove area (RMA) and resort area (PDC) seasonally from June 2010 to April 2011. SW = Southwest, NE = Northeast.

(Global R = 0.55; p = 0.1%)			(Global R = 0.23; p = 0.1%)		
Groups (Site)	R	p(%)	Groups (Season)	R	p (%)
MMA, RMA	0.61	0.1	SW, Post-SW	0.01	39.8
MMA, PDC	0.67	0.1	SW, NE	0.28	0.1
RMA, PDC	0.36	0.1	SW, Pre-SW	0.05	21.6
			Post-SW, NE	0.35	0.1
			Post-SW, Pre-SW,	0.13	8.3
			NE, Pre-SW	0.25	0.8

Meanwhile, PC2 had positive loading of total ammonium nitrogen (TAN) and negative loading of total suspended solids, salinity, conductivity and pH explained 18.4% of total variation (Fig. 10).

4. Discussion

Twenty-three species of gelatinous zooplankton (Hydrozoa and Ctenophora) were identified in this study. The number of species identified in this study was comparable to that described by Gusmao et al. (2015), who found 21 species in the tropical southwestern Atlantic, where the climate was warm (27.2 °C to 29.1 °C) and the coastal area was influenced by runoff from rivers. The gelatinous zooplankton in this study area also showed low mean densities ranging from 0.8 to 15.0 ind. m^{-3}. Similarly, Gusmao et al. (2015) also observed low gelatinous zooplankton density (1.4 ind. m^{-3}) in the tropical southwestern Atlantic. Vansteenbrugge et al. (2015), who studied gelatinous zooplankton population dynamics in the North Sea and an adjacent estuary, reported that the gelatinous zooplankton density remained below 3.0 ind. m^{-3} in the estuary, compared to higher densities of gelatinous zooplankton (up to 18.0 ind. m^{-3}) in the near coastal and open seas. However, the present study showed that higher densities of gelatinous zooplankton could occur in sheltered areas of mangroves than other exposed coastal areas.

In general, densities and biomass of gelatinous zooplankton at the mangrove area, MMA, were significantly higher ($p < 0.05$) compared to reclaimed area (RMA) and resort area (PDC), suggesting more favorable conditions for gelatinous zooplankton in MMA, especially *Pukia* sp. *Pukia* sp. has been reported previously only in Australia and Japan by Gershwin et al. (2010) and Lindsay (2017), respectively. The PCA analysis showed that the density and species composition of gelatinous zooplankton at MMA seemed to be controlled by turbidity and associated parameters (water transparency and total suspended solids), salinity, nutrients, chlorophyll-a and non-gelatinous zooplankton density, suggesting the roles of anthropogenic activities and climatic condition on gelatinous zooplankton population growth. The positive relationship of gelatinous zooplankton densities to nutrients and chlorophyll-a further supported the influence of primary productivity on gelatinous zooplankton density. However, the relationship might be indirect since the primary food items of gelatinous

zooplankton were other zooplankton, the production and biomass of which were largely dependent on phytoplankton production. The presence of high densities of micro- and mesozooplankton in response to the highly productive mangrove system (as evidenced by high chlorophyll-a concentrations) observed at MMA (Balqis et al., 2016) could support high populations of gelatinous zooplankton. Furthermore, PCA analysis also showed gelatinous zooplankton in MMA were significantly correlated with copepods. Ctenophores are well-known as voracious predators on copepods that can depress the latter's density (Shiganova, 1998; Purcell and Decker, 2005; Oghenekaro et al., 2018). A decline in copepod's abundance was noted in August and October 2010 when the density of ctenophores (*Pukia* sp.) was relatively high during this period. In addition, most of ctenophores are hermaphroditic, capable of self-fertilizing and producing viable offspring (Lucas and Dawson, 2014). Such characteristic of reproduction probably favored mass occurrence of ctenophores in this sheltered mangrove area compared to open coastal waters of RMA and PDC.

Within hydromedusae, *Blackfordia virginica* was the only dominant species at MMA. Many studies have shown that this species is usually found in estuaries and considered to be a euryhaline species (Moore, 1987; Mills and Sommer, 1995; Marques et al., 2015). High densities of copepods, copepod nauplii and barnacle nauplii in MMA probably enhanced the growth of *B. virginica* in this area, as this species has been reported to prey on copepods, copepod nauplii and barnacle nauplii (Mills and Sommer, 1995). *B. virginica* is an invasive species that is considered native to the Black Sea (Mills and Sommer, 1995; Freire et al., 2014; Marques et al., 2015). It might be transported and introduced via ship ballast water, since all localities where this species has been found are near large international harbors or in international shipping routes such as the Straits of Malacca (Chicharo et al., 2009; Freire et al., 2014; Gusmao et al., 2015). The Straits of Malacca is the world's second busiest shipping route and the likelihood of species being introduced via ballast water is high. However, the origin of *B. virginica* at MMA is still unclear because there are no published reports on the gelatinous zooplankton communities of the Straits of Malacca.

High nutrient concentrations also might have contributed to the growth of gelatinous zooplankton populations at MMA. According to Legovic (1987), high nutrient enrichment can cause an increase in the gelatinous zooplankton population, since they are able to utilize indirectly the nutrient pool. At MMA, nutrient supply in the mangrove estuary could have been positively affected by the outwelling from sediments of the mangrove swamp and creek (Tanaka and Choo, 2000). Gelatinous zooplankton might benefit from enriched waters because they can take up nutrients and dissolved organic matter (DOM) (Skikne et al., 2009; Purcell, 2012). In fact, gelatinous zooplankton are able to survive in eutrophic environments since organic solutes can be absorbed across the body surface with a sufficient amount of DOM.

Dawson and Martin (2001) observed that differences in the gelatinous zooplankton community composition and population

densities could be influenced by different latitudinal and geographical locations of study areas. In the present study, MMA, which received river inputs, had higher densities of gelatinous zooplankton compared to RMA and PDC located along the coast without estuaries. Pitt and Kingsford (2000) also observed that sampling stations closer to riverine inputs showed greater number of individuals compared to other sites away from estuaries. Furthermore, MMA had lower ranges of tidal levels compared to RMA and PDC indicating that the protected mangrove area was of lower energy compared to exposed areas in RMA and PDC. Waryani et al. (2014) showed that more sheltered estuarine areas allowed the retention of gelatinous zooplankton populations as these areas were relatively calmer, enabling gelatinous zooplankton to swim and maintain their position in the upper reaches of the estuary, in contrast to regions with stronger water movement.

At RMA, the gelatinous zooplankton population was dominated by *E. brevigona,* which is commonly found in the Indo-Pacific region (Kramp, 1968). Navas-Pereira and Vannucci (1991) also reported *E. brevigona* from the Malayan coast. The PCA analysis showed that densities and species composition of gelatinous zooplankton at RMA seemed to be influenced by high total suspended solids and temperature. High concentrations of total suspended solids can also cause an increase in surface water temperature, because the suspended particles absorb heat from sunlight. Studies have shown that temperature plays an important role in asexual budding of gelatinous zooplankton (Matsakis, 1993; Fitt and Costley, 1998; Kawamura and Kubota, 2008; Liu et al., 2009). *E. brevigona* polyp colonies produce medusae by asexual budding. High concentrations of total suspended solids may have induced an appropriate water temperature for rapid budding of *E. brevigona*. However, no significant difference in water temperature was found amongst the study areas, suggesting that other environmental parameters could also influence the asexual budding of gelatinous zooplankton. Kawamura and Kubota (2008), for example, reported that food availability is also an important environmental parameter accelerating medusa budding. High density of non-gelatinous zooplankton at RMA probably played an important role as food for the hydromedusae polyp. Furthermore, some species of hydromedusae have the capability to survive in harsh environments by producing more polyps and ephyrae, or by forming dormant cysts which then can quickly grow into adult medusa under favorable conditions (Arai, 2009). Therefore, large fluctuations in density of gelatinous zooplankton on the temporal scale was observed in RMA.

Different from *E. brevigona, Liriope tetraphylla* has a direct development that lacks the hydroid stage (Bouillon et al., 2006). *L. tetraphylla* contributed 70% to the density of gelatinous zooplankton in RMA and recorded a high density in February 2011. This species is known as an oceanic species and affected by low salinity (de Souza et al., 1996). Therefore, high density of this species has been observed in coastal waters compared to a coastal area near a river mouth (Buecher et al., 1997; Pavez et al., 2010). On the other hand, Yilmaz (2015) claimed that low salinity was not a limiting parameter for this species as it could survive and bloom at various salinity levels ranging from 21.7 to 28.7 psu in the Sea of Marmara. In the present study, occurrence of *L. tetraphylla* has been observed in all study areas with high densities in coastal waters of RMA and PDC which have higher salinity compared to MMA which was situated in a mangrove-fringed estuary with lower salinity.

The siphonophores *L. subtiloides* and *Diphyes chamissonis* were commonly found at PDC. The PCA analysis showed the density and species composition of gelatinous zooplankton at PDC seemed to be influenced by salinity and transparency. Mills (1984) reported that the density of siphonophores was usually influenced by the salinity, with most siphonophores preferring high-salinity oceanic waters. Similarly, Grossmann et al. (2015) found

L. subtiloides was dominant at the Sulu Sea with near-constant salinity (34 psu) at the surface (top 50 m). In this study, the salinity at PDC was more stable, ranging from 28 to 30 psu, compared to MMA (20–27 psu) and RMA (23–30 psu). Therefore, the higher density of siphonophores at PDC compared to mangrove areas was probably due to the greater influence of oceanic water with less river runoff at this site. Furthermore, significantly higher water transparency ($p < 0.05$) at PDC compared to the other sites was probably due to the lower riverine input and could be a reason for the occurrence of these neritic siphonophore species (Lo et al., 2014). Other species of gelatinous zooplankton rarely occurred and were only observed in certain months, such as *Nemopsis* sp., *Aequorea parva* and *Phialella* sp. which were found during the southwest monsoon. Similarly, Petrova et al. (2011) reported that some species of gelatinous zooplankton only occurred in certain months of the year.

5. Conclusion

A total of 23 species of gelatinous zooplankton from 16 genera were identified. There was significantly higher species diversity in the sheltered mangrove area (MMA) compared to other exposed coastal environment of the reclaimed mangrove (RMA) and the resort (PDC) areas. In addition, most of the gelatinous zooplankton, particularly Ctenophora, occurred in high density in the mangrove area compared to the coastal waters. Environmental parameters related to turbidity (including total suspended solids and water transparency), salinity, nutrients and biotic factors (chlorophyll-a and non-gelatinous zooplankton) were the main drivers influencing the distribution of the gelatinous zooplankton. There were significant differences in the gelatinous zooplankton distribution amongst sites with different levels of disturbance. The highly productive area with high nutrients and chlorophyll-a (the managed mangrove area) was dominated by *Pukia* sp. (Ctenophora), while the area with the highest concentrations of total suspended solids (reclaimed mangrove area) was dominated by *E. brevigona* (Hydromedusa). Meanwhile, *L. subtiloides* (Siphonophora) was dominant in relatively clear waters with high transparency and salinity (in the resort area that did not have any river inflow). In addition to habitats, gelatinous zooplankton distribution was also influenced by seasonal changes, especially in areas with freshwater inputs such as the Matang mangrove area.

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