# Zooplankton in seagrass and adjacent non-seagrass habitats in Tun Mustapha Park, Sabah, Malaysia

## Lo Sing Lui<sup>1</sup>, Yap Tzuen Kiat<sup>1</sup>, Chen Cheng Ann<sup>1</sup>, Teruaki Yoshida<sup>1,2\*</sup>

<sup>1</sup> Borneo Marine Research Institute, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia <sup>2</sup> Unit for Harmful Algal Bloom Studies, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia

\*Corresponding author: teruaki.yoshida@gmail.com

## Abstract

A comparison of zooplankton abundance and community in the seagrass and non-seagrass areas of Limau-limauan and Bak-Bak waters within the newly established Tun Mustapha Marine Park was made during 15-17 May 2017. Samples were collected via horizontal tow of a 140  $\mu$ m plankton net. Environmental variables (temperature, salinity, DO, pH, turbidity) showed no significant differences among the study sites. However, zooplankton showed increasing abundance from non-seagrass, seagrass edge, to seagrass areas at Limau-limauan, while abundance values were comparable among the stations at Bak-bak. Overall zooplankton abundance was significantly higher at the seagrass areas relative to the non-seagrass station at Limau-limauan (p < 0.005), while no statistical difference was found at Bak-Bak (p < 0.21). Mean canopy height was 3-fold higher (p < 0.001) at Limau-limauan than Bak-Bak, suggesting the importance of seagrass bed structural complexity in habitat preference for zooplankton. Cluster analysis revealed the zooplankton community from the seagrass area at Limau-limauan was different from that at seagrass edge and non-seagrass areas, which may be attributed to the influence of seagrass meadows in forming characteristic zooplankton compositions. Marked differences in zooplankton composition and abundance even in close vicinity of sites suggest the importance of local small-scale variations in seagrass habitats in shaping the zooplankton community.

Keywords: Zooplankton, Seagrass, Habitats, Tun Mustapha Park, South China Sea

## Introduction

Seagrass beds provide structurally complex habitats that influence the distribution, density and species diversity of benthic organisms and fish fauna (Heck and Thoman, 1981, Boström et al., 2006). Their physical structure provides ecological functions that resemble mangroves, saltmarshes, and coral reefs (Sheridan 1997, Touchette 2007). Studies on seagrass-associated organisms often illustrate the importance of seagrass ecosystems to benthic and macrofaunal organisms. For example, animal abundance and biomass, such as decapod crustaceans (Gore et al., 1981), gastropods, mussels, and crabs (Lee et al., 2001), other epifaunal invertebrates (Stoner 1980, Attrill et al., 2000), and fish (Johnson and Jennings 1998, Wyda et al., 2002) are often positively associated with seagrass density. High structural complexity, primary and secondary production, and availability of vegetal detritus in seagrass beds are perceived as key reasons for the higher abundances and biomass of associated organisms, as these characteristics are likely to provide increased protection from predation and food availability (Nagelkerken 2009, Nanjo et al., 2014). Similarly, seagrass beds provide pelagic/planktonic zooplankton with biological and structural habitat interactions, forming direct or indirect ecological associations which may be important in the survival of these organisms. Experiments using artificial seagrass beds have reported positive colonization and increase in abundance of zooplankton that are comparable to natural seagrass beds (Chavanich et al., 2004). The increased complexity of structural characteristics in natural seagrass beds suggests higher abundance of faunal assemblages, including the zooplankton (Micheli et al., 2008). Distinct differences in zooplankton communities can also be observed in comparative studies between adjacent seagrass and non-seagrass habitats (Kimmerer and McKinnon 1985, Afiq et al., 2016, Metillo et al., 2018). As an important component in sustaining the trophodynamics of coastal marine ecosystems (Koch et al., 2006), continued seagrass bed loss will eventually lead to loss in important habitat functions, in addition to a significant decrease in secondary productivity of these ecosystems.

Sabah hosts mixed species of seagrass beds in coastal substrates ranging from sand, muddy-sand to coral rubble of the intertidal zone, with a total of 10 species out of the 16 species recorded throughout Malaysia (Japar Sidik et al., 2006, 2018). Six areas of intertidal seagrass ecosystems are found along the west coast at Bak-Bak (in this study), Tanjung Mengayau, Sepangar Bay and Gaya Island, while the four off-shore islands of Maganting, Tabawan, Bohey Dulang and Sipadan along the south-eastern coast that are home to subtidal seagrasses growing on coral rubble (Norhadi 1993, Japar Sidik et al., 2006, Josephine and De Silva 2007). These seagrasses are not only important feeding grounds for dugongs (status: vulnerable, VU A1cd) and green turtles (status: endangered, EN A1bd) but also for the livelihood of many local coastal communities, and yet their habitat

continues to be under the threat of human activities in Sabah (Jaaman 2000, Chan 2006, Rajamani and Marsh 2015).

Despite their perceived importance, zooplankton in seagrass habitats have rarely been assessed in tropical regions. Although there has been an increase in the frequency of such studies in recent years in SE Asia such as Thailand (Chavanich et al., 2004, Tantichaiwanit 2005), the Philippines (Metillo et al., 2019) and Peninsular Malaysia (Matias-Peralta and Yusoff, 2015, Azmi et al., 2016), there are knowledge gaps in our understanding the effects of seagrass on zooplankton biomass and distribution. The aim of this study was to examine the zooplankton composition and abundance in the seagrass areas of Tun Mustapha Marine Park and compare the zooplankton between seagrass and adjacent non-seagrass areas. This investigation probably reports the first record of zooplankton in seagrass habitat of Sabah.

## **Materials and Methods**

### Study site

Two seagrass habitats in the Tun Mustapha Marine Park were chosen as study sites (Figure 1a). The contours of seagrass patches at each study site were determined and areas mapped by estimates from Google Earth and in situ GPS recordings via snorkelling and SCUBA diving. Seagrass was identified to the lowest taxonomic level possible (McKenzie et al., 2003, Japar Sidik et al., 2006, 2018). The relative seagrass coverage and canopy height were determined from two transects (50 m long, 25 m apart) laid perpendicular to the coastline with eleven 50 × 50 cm quadrats placed at 5 m intervals along each transect within the seagrass habitat. Seagrass coverage estimates were obtained following the percent cover standards from Seagrass-Watch (McKenzie et al., 2003). Species-specific canopy heights (3-10 mature leaf blades quadrate<sup>-1</sup>) were measured in situ to obtain mean canopy heights for each study site.



Figure 1a. Location of seagrass study sites in the northern tip of Borneo (Kudat).

## Zooplankton collection

Samples were collected from a boat at i) seagrass ii) seagrass edge iii) adjacent non-seagrass areas (Figure 1b) via surface horizontal tow of a plankton net (140  $\mu m$  mesh; 0.5 m mouth diameter) attached with a flowmeter. The sampling areas

were approximately 50 m apart from each other and their depth ranged from 1.2-1.3 m the near coastal area to 1.8-1.9 m toward deepest end at both the study sites. Boat driven parallel to the coastline at a speed of 0.5 knot for a distance of 100 m based on pre-set GPS readings, with the net mouth completely submerged underwater (depth c.a. 0.1 m) throughout the towing period. The samples were immediately preserved in formalin 4% seawater solution (v/v) for subsequent examination in the laboratory. Zooplankton were identified to the lowest taxonomic level possible and enumerated under a stereomicroscope using appropriate references (Chihara and Murano 1997, Conway et al., 2003, Al-Yamani et al., 2011).



Figure 1b. Zooplankton sampling transects (100 m x 3; dashed lines) in the seagrass (S), seagrass edge (SE) and non-seagrass.

(NS) areas at each station.

#### Results

#### Environmental parameters

Environmental variables such as temperature, salinity, DO, pH, except for turbidity, showed no significant differences among the study areas (Table 1). Though not statistically significant, mean temperature was higher  $(31.0 \pm 0.1 \text{ vs } 30.3 \pm 0.1 \text{ °C})$  and salinity was lower  $(30.9 \pm 0.1 \text{ vs } 31.4 \pm 0.1 \text{ PSU})$  at Bak-bak compared with Limau-limauan. At both the stations, the mean dissolved oxygen (DO) and pH varied 6.48-6.70 mg L<sup>-1</sup> and 8.45-8.65, respectively. Turbidity readings were significantly higher (p < 0.01; One-way ANOVA) at the seagrass area at both the stations compared with seagrass edge and non-seagrass areas.

#### Seagrass composition, coverage and canopy height

Six species of seagrasses were observed at both the stations (Table 2). Composition of the seagrass community was characteristically different between the two stations; *Cymodocea rotundata* and *Halophila pinifolia* were dominant at Bak-bak, while *Enhalus acoroides* was abundant at Limaulimauan. *Halophila ovalis* and *H. uninervis* were also present at both the stations but were generally found in low numbers (<10 shoots/quadrate) and contributed <1% to the total seagrass coverage.

Environmental		Bak-bak		Limau-limauan			
variables	S	SE	NS	S	SE	NS	
Depth (m)	1.4	1.7	1.9	1.2	1.3	1.8	
Temperature (°C)	30.9 ± 0.1	$31.0 \pm 0.2$	$31.0 \pm 0.2$	$30.2 \pm 0.1$	$30.4 \pm 0.1$	$30.4 \pm 0.1$	
DO (mg L-1)	6.52 ± 0.01	$6.59 \pm 0.02$	$6.57 \pm 0.02$	$6.70 \pm 0.60$	6.55 ± 0.23	$6.48 \pm 0.27$	
Salinity (PSU)	30.8 ± 0.1	30.9 ± 0.1	$30.9 \pm 0.2$	$31.4 \pm 0.1$	$31.4 \pm 0.1$	$31.4 \pm 0.2$	
рН	8.65 ± 0.01	$8.45 \pm 0.04$	$8.50 \pm 0.03$	$8.49 \pm 0.04$	$8.58 \pm 0.01$	8.60 ± 0.02	
Turbidity (NTU)	0.9* ± 0.3	$0.5 \pm 0.1$	$0.3 \pm 0.2$	1.8* ± 0.1	$0.6 \pm 0.1$	$0.5 \pm 0.2$	
	N 06°56.39'	N 06°56.38'	N 06°56.37'	N 06°49.10'	N 06°49.09'	N 06°49.09'	
Coordinates	E 116°50.20'	E 116°50.21'	E 116°50.22'	E 116°51.43'	E 116°51.44'	E 116°51.46'	

**Table 1.** Environmental variables comparison among the seagrass (S), seagrass edge (SE), and non-seagrass (NS)areas at each station.

\* values in bold indicate statistical difference (p < 0.01) among S, SE, and NS areas using one-way ANOVA.

Table 2. Species composition and coverage of seagrass at each station.

	Sta	tion		
Seagrass coverage (%)	Bak-bak Limau-limauan	Limau-limauan	р	
Enhalus acoroides	<1	17.9 ± 20.8	<0.001	
Cymodocea rotundata	26.7 ± 29.0	11.1 ± 14.7	0.031	
Thalassia hemprichii	$1.6 \pm 2.8$	6.5 ± 6.7	0.004	
Halophila pinifolia	25.9 ± 29.2	8.5 ± 9.7	0.015	
Halophila ovalis	<1	<1	-	
Halodule uninervis	<1	<1	-	
Total coverage (%)	48.2 ± 38.7	35.5 ± 21.6	0.135	
Canopy height (cm)	3.8 ± 2.8	11.5 ± 6.3	<0.001	
Seagrass area (×10 <sup>-2</sup> km ) <sup>2</sup>	1.3	4.5	-	

\* p values in bold indicate statistical difference using two-sample Student's t-test.

Table 3. Zooplankton abundances (inds. m-3) at seagrass (S), seagrass edge (SE), and non-seagrass (NS) areas of					
Limau-limauan and Bak-bak					

Таха		Bak-bak			Limau-limauan	NS
Taxa	S	SE	NS	S SE		
Acartia spp.	268.8	291.9	98.3	78.2	46.1	48.1
Acrocalanus spp.	8.0	9.0	2.0	0.0	0.0	16.0
Amphipoda	0.0	0.0	0.0	2.0	2.0	0.0
Appendicularia	68.2	69.2	56.2	10.0	24.1	180.5
Balanus spp.	24.1	20.1	24.1	4.0	20.1	28.1
Benthic Harpacticoida	124.4	76.2	0.0	1179.5	662.0	698.1
Bestolina sp.	0.0	4.0	6.0	0.0	0.0	0.0
Bivalvia	385.2	755.3	84.3	10.0	34.1	110.3
Brachyuran larvae	40.1	31.1	2.0	96.3	32.1	14.0
Calocalanus spp.	0.0	0.0	0.0	10.0	14.0	24.1
Candacia spp.	0.0	0.0	0.0	0.0	4.0	16.0
Canthocalanus spp.	292.9	397.2	108.3	42.1	52.2	367.1
Caridian larvae	22.1	14.0	0.0	56.2	22.1	0.0
Centropages spp.	0.0	1.0	4.0	0.0	0.0	0.0
Cephalopod egg	0.0	0.0	0.0	30.1	12.0	284.9
Cheatonagtha	6.0	83.2	22.1	8.0	2.0	30.1
Clytemnestra spp.	4.0	19.1	4.0	8.0	2.0	0.0
Copepod nauplii	3228.7	1377.1	1792.4	1374.1	1273.8	280.8
Corycaeus spp.	86.3	118.4	48.1	58.2	58.2	222.7
Creseis	54.2	222.7	100.3	6.0	34.1	114.3
Cyphonautes	0.0	0.0	0.0	0.0	0.0	200.6
Cyprid larvae	18.1	23.1	24.1	26.1	80.2	158.5
Decapod larvae	156.5	90.3	20.1	24.1	0.0	0.0
Doliolida	0.0	1.0	0.0	0.0	0.0	6.0
Euphausidae	0.0	0.0	0.0	0.0	0.0	28.1
Euterpina acutifrons	130.4	169.5	106.3	14.0	8.0	54.2
	14.0	9.0	0.0	4.0	0.0	6.0
Evadne spp.	20.1	62.2	8.0	38.1	110.3	250.8
Fish eggs Fish lewse	3.0	7.0	2.0	4.0	0.0	250.8 6.0
Fish larvae		1051.1			258.8	
Gastropoda Uslathuria larra	265.8		198.6	170.5		142.4
Holothuria larva	0.0	0.0	8.0	0.0	0.0	0.0
Hydromedusa	26.1	8.0	14.0	10.0	30.1	6.0
Isopoda	16.0	13.0	4.0	50.2	32.1	20.1
Labidocera spp.	0.0	0.0	0.0	0.0	0.0	4.0
Luciferidae	0.0	0.0	0.0	0.0	2.0	6.0
Macrosetella spp.	0.0	154.5	43.6	78.2	8.0	42.1
Megalopa	0.0	0.0	0.0	0.0	0.0	0.5
Metis sp.	32.1	20.1	14.0	16.0	10.0	6.0
Microsetella spp.	2.0	154.5	10.0	38.1	16.0	34.1
Oithona spp.	7819.4	4665.0	4521.5	858.6	1388.2	962.9
Oncaea spp.	50.2	30.1	18.6	66.2	40.1	92.3
Ostracoda	6.0	18.1	12.0	18.1	6.0	4.0
Paracalanus spp.	3062.7	3123.3	3125.3	244.7	93.3	834.5
Parvocalanus spp	3951.8	2376.1	2234.7	224.7	172.5	417.2
Penilia spp.	46.1	4.0	0.0	0.0	0.0	0.0
Podon spp.	6.0	0.0	0.0	4.0	2.0	6.0
Polychaeta	0.0	2.0	0.0	0.0	0.0	0.0
Polychaeta larvae	82.2	134.4	40.1	264.8	238.7	114.3
Salpida	0.0	0.0	0.0	0.0	0.0	0.0
Sapphirina sp.	0.0	0.0	0.0	2.0	2.0	2.0
Siphonorphora	2.0	0.0	0.0	2.0	8.0	48.1
Stomatopoda	0.0	4.0	0.0	0.0	0.0	0.0
Subeucalanus spp.	34.1	24.1	12.0	2.0	0.0	0.0
Tanaidacea	0.0	0.0	0.0	4.0	0.0	2.0
<i>Temora</i> spp.	38.1	18.1	16.0	0.0	2.0	34.1
Tintinida	124.4	51.2	25.1	36.1	2.0	4.0
Tortanus spp.	4.0	4.0	0.0	0.0	0.0	0.0

Total seagrass coverage was comparatively lower at Bak-bak (35.5  $\pm$  21.6%) but was not statistically different from that at Limau-limauan (48.2  $\pm$  38.7%; p = 0.135, two-sample Student's t-test). Mean canopy height was 3-fold higher at Limau-limauan than Bak-bak (p < 0.001, two-sample Student's t-test). In addition, Limau-limauan was the larger seagrass habitat(approximately 3 times larger) at 4.5 × 10<sup>-2</sup> km<sup>2</sup> compared with 1.3 × 10<sup>-2</sup> km<sup>2</sup> for Bak-bak.

#### Zooplankton composition and abundance

A total of 57 taxa of zooplankton, including 22 copepod taxa were identified (Table 3). Overall total zooplankton abundance at Limau-limauan was 2.2-4.0 times higher than Bak-bak (p < 0.0083, 2-independent sample t-test; Figure 2a). Zooplankton abundance showed a decreasing trend from seagrass (S) to non-seagrass (NS) area at Limau-limauan, while it was similar among the S, SE, and NS areas at Bak-bak. Zooplankton abundance were significantly higher at the seagrass areas (S and SE) relative to the non-seagrass station at Limau-limauan (p < 0.0051, Mann Whitney U-test), while no difference was found at Bak-bak (p < 0.21). Copepods were dominant at both the stations (Figure 2a, 2b) and comprised 54-81% of total zooplankton, followed by copepod nauplii (5-27%), gastropods (2-5%), polychaete larvae (1-5%), bivalves (1-5%) and brachyuran larvae (0.5-2.0%).





Apart from copepods, the other major component of the zooplankton consisted of meroplankton such as bivalves, gastropods, and brachyuran larvae. While the composition of Bivalvia to the total zooplankton was higher at Limaulimauan, polychaete larvae showed a higher abundance at Bak-bak. Copepod nauplii were dominant at the S and SE areas at Bak-bak, and the contribution of other zooplankton such as cirripede larvae, siphonophores, cyphonautes, and fish eggs increased at the NS area. The copepod community composition at Limau-limauan was characteristically different from that at Bak-bak (Figure 2b). Abundance of *Oithona* spp. were comparable at the two stations. However, *Parvocalanus* spp. and *Paracalanus* spp. showed higher abundance at Limau-limauan, while benthic Harpacticoid copepods displayed higher occurrence in place of the *Paracalanidae* at Bak-bak. Cluster analysis (single linkage, Euclidean distance measure) performed on the zooplankton communities from all the sampling areas revealed two distinct groups of zooplankton with respect to the two stations (Figure 3). Similarity levels were closer for the zooplankton community at the SE and NS area than the S area for Limau-limauan, while those in Bak-bak showed comparable similarity across the S, SE and NS areas.









#### Discussion

Environmental variables (temperature, salinity, DO, pH) were almost similar in the study areas (S, SE, NS) at both the stations (Table 1), except for turbidity. Turbidity values were significantly higher (p < 0.01; One-way ANOVA) at the seagrass area at both the stations compared with seagrass edge and non-seagrass areas. Close proximity to the coast may have resulted in higher turbidity values in the seagrass area, where the influence of terrestrial sediment input is stronger (Robert et al., 2006).

Resuspension/sedimentation processes of particulate organic matter (POM) inherent in the seagrass beds (Cabaço et al., 2008) may also explain the higher turbidity values. Turbidity is inversely correlated with light penetration at the seabed. The elevated turbidity is commonly considered a stressor of seagrass (Petrou et al., 2013, Chartrand et al., 2016). However, the turbidity in this study ranged at lower levels compared with those found in other tropical seagrass habitats in the region (2-28 NTU assuming  $\alpha = 0.076$  m<sup>-1</sup>/NTU, Vermaat et al 1997; 1-12 NTU, Ahmad-Kamil et al 2013; 9-24 NTU, Matias-Peralta & Yusoff 2014), suggesting the light condition is not a stressor or limiting to the seagrass primary production at both Bak-bak and Limau-limauan.

Total zooplankton abundance was 2.2 - 4.0 fold higher at Limau-limauan than at Bak-bak (Figure 2a) for all S, SE, and NS areas, and the zooplankton community was characteristically different between the two stations (Figure 3). This could be attributed to the difference in physical habitat structure and spatial scale of the seagrass areas between the two stations, which accounts for variations in habitat suitability, food availability and protection from the predators for the zooplankton. Limau-limauan presents a habitat with significantly higher structural complexity than Bak-bak (Enhalus vs Halophila dominant community, ×3 mean canopy height; Table 2). This potentially provides protection from predators as well as hydrodynamic forces. Zooplankton are reported to reside in or near the substrate presumably to avoid visual predators in the coral reefs (Alldredge and King 1985, Carleton et al., 2001, Nakajima et al., 2008) and seagrass beds (Gan et al., 2010, Metillo et al., 2018), suggesting the importance of substrate structural complexity in habitat preference for zooplankton (Hacker and Steneck 1990, Micheli et al., 2008). In addition, the presence of seagrass modifies currents, effectively weakening water fluxes (Fonseca and Fisher, 1986, Fonseca et al., 2007) and offers greater protection from hydrodynamic forces for the zooplankton. Reduced current fluxes also promote sediment deposition (Fonseca and Fisher, 1986) that serves as the detrital food source for the zooplankton. This is consistent with the reports that have suggested that zooplankton may obtain a large proportion of their nutrition by feeding on detritus in seagrass beds (Roman et al., 1983, Thresher et al., 1992). Indeed, many copepod species previously thought to be strict herbivores have been observed to exercise shifts in feeding behaviour to consume a wide variety of food items, including detritus, depending on the available food composition in the environment (Roman 1984, Turner and Tester 1989, Kleppel and Hazzard 2000, Yoshida et al., 2012). The significantly higher zooplankton abundance observed in the seagrass area (i.e. S and SE) compared with NS area at Limau-limauan could also indicate the effect of adaptive behavior by the zooplankton for protection from predators and hydrodynamic forces.

Phytoplankton diversity and abundance are reported to be higher in seagrass habitats where structural complexity is high (Mabrouk et al., 2011, Ambo-Rappe 2016). This is especially evident in diatoms Bacillariophyceae, apparently due to enhanced nutrient acquisition or retention capacity in vegetated versus non-vegetated sediments (Barrín et al., 2006) and adequate mixing of the water column by the combined effects of epifaunal processes (i.e. biomixing) and water motion (Mabrouk et al., 2011). Although information on the phytoplankton is not available in this study, the higher abundance of zooplankton at Limau-limauan may be due to higher food availability (phytoplankton) compared to that at Bak-bak. Finer spatial distribution patterns observed among the S, SE, and NS areas at Limau-limauan also indicate that food availability (i.e. phytoplankton and detritus) can vary dramatically over a few meters within the vicinity of the seagrass meadow, resulting in the concurrent variation in the zooplankton distribution.

Besides phytoplankton, the leaves and stems of seagrasses support numerous epiphytes which are fed upon by zooplankton and epifaunal organisms such as amphipods and gastropods (Jernakoff and Nielsen 1998, Borowitzka et 2006). Meroplankton such as brachyuran larvae, al., gastropods and polychaete larvae formed the dominant zooplankton component after copepods in the S and SE areas at both the stations, indicating that the adult stages are possibly more abundant in seagrass areas compared with non-seagrass areas where conditions for refuge and food availability are favourable for both adult and larval stages of epifaunal organisms. This is in agreement with previous reports where abundance and diversity of epifaunal organisms such as decapod crustaceans, gastropods, mussels, crabs, and other invertebrates increase with increasing seagrass density (Lee et al., 2001, Stoner 1980, Attrill et al., 2000), although recent studies suggest the distribution within seagrass patches may be quite variable (Whippo et al., 2018) and may be related to "edge effects" (Macreadie et al., 2010). Accordingly, the positive edge effect on some zooplankton species may explain the high contribution of meroplankton in the SE area at both stations.

The results of this study suggest the variability of zooplankton assemblage was associated with the density and species composition of seagrass, which determines the habitat structural complexity. Marked differences in zooplankton composition and abundance between immediately adjacent study sites serve to highlight the importance of local small-scale variations of seagrass habitats in shaping the zooplankton community. The newly established Tun Mustapha Park should enhance future

conservation and rehabilitation efforts to prevent the decline of seagrasses in the north Bornean coastal region which is essential for ecological functioning in the marine ecosystem.

#### Acknowledgement

We thank Cheong Kai Ching for his help in the field and laboratory. This study was partially funded by the grant of the Marine Scientific Expedition to Tun Mustapha Park ESM 2017 (SDK0006-2017) and the JSPS Core-to-Core Program, B. Asia-Africa Science Platforms (CCORE-Rensea).

#### References

Ahmad-Kamil E. I, Ramli, R., Jaaman, S. A *et al.* (2013). The effects of water parameters on monthly seagrass percentage cover in Lawas, East Malaysia. **The Scientific World Journal** ID 892746, DOI: 10.1155/2013/892746.

Alldredge, AL and King, JM. (1985). The distance demersal zooplankton migrate above the benthos: Implications for predation. **Marine Biology** 84, 253–60.

Ambo-Rappe R, (2016). Differences in richness and abundance of species assemblages in tropical seagrass beds of different structural complexity. **Journal of Environmental Science and Technology** 9, 246-256.

Al-Yamani, F.Y., Skryabin V., Gubanova A. *et al.* (2011). Marine zooplankton practical guide for the Northwestern Arabian Gulf, Kuwait. Institute for Scientific Research, Kuwait.

Attrill MJ, Strong JA, Rowden AA (2000) Are macroinvertebrate communities influenced by seagrass structural complexity? **Ecography** 23,114–121

Azmi, A. A., Yoshida, T., Toda, T., *et al.* (2016) Comparison of zooplankton abundance and community in seagrass and non-seagrass areas of Merambong shoal. **AIP Conference Proceedings, Volume 1784**, Issue 1, DOI: 10.1063/1.4966840

Barrín, C., Middelburg, J. J., & Duarte, C. M. (2006). Phytoplankton trapped within seagrass (*Posidonia oceanica*) sedimentsare a nitrogen source: An in situ isotope labeling experiment. **Limnology and Oceanography** 51(4), 1648-1653. DOI:10.4319/lo.2006.51.4.1648

Borowitzka, M. A., Lavery, P.S., & van Keulen, M. (2006). Epiphytes of seagrasses. In: **Seagrasses: Biology, Ecology and Conservation** (Larkum, A.W.D., Orth, R.J. and Duarte, C. M., eds.).Springer, Netherlands, ISBN: 978-1-4020-2942-4, 441-461.

Boström, C., Jackson, E. L., & Simenstad, C. A. (2006). Seagrass landscapes and their effects on associated fauna: A review. **Estuarine**, **Coastal and Shelf Science**, 68(3-4), 383-403. DOI: 10.1016/j.ecss.2006.01.026

Bulmer, R.H., Townsend, M., Drylie, T., *et al.* (2018). Elevated turbidity and the nutrient removal capacity of seagrass. **Frontiers in Marine Science** 5, 462. DOI: 10.3389/fmars.2018.00462

Cabaço, S., Santos, R., & Duarte, C. (2008). The impact of sediment burial and erosion on seagrasses: A review. **Estuarine, Coastal and Shelf Science** 79, 354-366. DOI: 10.1016/J.ECSS.2008.04.021

Canion, C. R., Heck, K. L. (2009). Effect of habitat complexity on predation success: re-evaluating the current paradigm in seagrass beds. **Marine Ecology Progress Series** 393, 37-46. DOI: 10.3354/meps08272

Chan, E. H. (2006). Marine turtles in Malaysia: On the verge of extinction? Aquatic Ecosystem Health & Management 9, 175-184. DOI: 10.1080/14634980600701559

Carleton, J. H., Brinkman, R., & Doherty, P. J. (2001). Zooplankton community structure and water flow in the lee of Helix Reef (Great Barrier Reef, Australia). **Marine Biology** 139, 705–17.

Chartrand, K. M., Bryant, C. V., Carter, A. B. *et al.* (2016). Light thresholds to prevent dredging impacts on the Great Barrier Reef seagrass, *Zostera muelleri* ssp. capricorni. **Frontiers in Marine Science** 3,106. DOI:10.3389/fmars.2016.00106

Chavanich, S., Phiu-On, W, Viyakarn, V. (2004) Colonization of marine zooplankton and epifauna on artificial seagrass beds with different morphology. **The Natural History Journal of Chulalongkorn University** 4,101-103

Chihara, M., & Murano, M. (1997). An illustrated guide to marine plankton in Japan. Tokyo. Tokai University Press. 1574 p.

Conway, D. V. P., White, R. G., Hugues-Dit-Clies, J., *et al.* (2003). **Guide to the coastal and surface zooplankton of the South-Western Indian Ocean.** Occasional Publication of the Marine Biological Association of the United Kingdom, No 15, Plymouth, UK.

Fonseca, M. S., & Fisher, J. S. (1986). A comparison of canopy friction and sediment movement between four species of seagrass with reference to their ecology and restoration. **Marine Ecology Progress Series** 29, 15-22.

Fonseca, M. S., Koehl, M. A. R. & Kopp, B. S. (2007). Biomechanical factors contributing to self-organization in seagrass landscapes. **Journal of Experimental Marine Biology & Ecology** 340,227-246.

Gan, S.Y., Azman, B. A. R., Yoshida, T., *et al.* (2010). Comparison of day and night mysid assemblages in a seagrass bed by using emergence traps, with key to species occurring at Pulau Tinggi, Malaysia. **Coastal Marine Science** 34, 74-81.

Gore, R. H., Gallaher, E. E., Scotto, L. E., *et al.* (1981). Studies on decapod Crustacea from the Indian River region of Florida. II. Community composition, structure, biomass and species-areal relationships of seagrass and drift algae-associated macrocrustaceans. **Estuarine and Coastal Shelf Science** 12,485–508

Heck, K. L., & Thoman, T. A. (1981). Experiments on predator-prey interactions in vegetated aquatic habitats. **Journal of Experimental Marine Biology and Ecology** 53,125–134.

Hacker, S. D., & Steneck, R. S. (1990). Habitat architecture and the abundance and body-size dependent habitat selection of a phytal amphipod. **Ecology** 71, 2269-2285.

Jaaman, S. A. (2000). Malaysia's endangered species (Marine mammals and whale shark). Paper presented in **Maritime Awareness Programme Forum Series 2000**, 2000 April 8. Maritime Institute of Malaysia, Kuala Lumpur, Malaysia

Japar, S. B., Muta, H. Z, & Arshad, A. (2006). Distribution and significance of seagrass ecosystems in Malaysia. Aquatic Ecosystem Health Management 9, 1–12

Japar, S. B., Muta, H. Z., & Short, F. T. (2018). Seagrass in Malaysia: Issues and challenges ahead. In **The Wetland Book** (Finlayson, C., Milton, G., Prentice, R., & Davidson, N., eds.). Springer, Dordrecht. DOI: 10.1007/978-94-007-4001-3\_268

Jernakoff, P., & Nielsen, L. (1998). Plant-animal associations in two species of seagrasses in Western Australia. Aquatic Botany 60, 359-376.

Johnson, B. L., & Jennings, C. A. (1998). Habitat associations of small fishes around islands in the upper Mississippi River. **North America Journal of Fisheries Management** 18, 327–336

Josephine, N., & De Silva, R. N. (2007). Issues and challenges of seagrass with special reference to Sabah, Malaysia. Universiti Malaysia Sabah Publication. ISBN 978Â-983-2369Â-61-5

Kimmerer, W. J., & McKinnon, A. D. (1985). A comparative study of the zooplankton in two adjacent embayments, Port Phillip and Westernport Bays, Australia. **Estuarine, Coastal and Shelf Science** 21, 145-159.

Kleppel, G. S., & Hazzard, S. E. (2000). Diet and egg production of the copepod Acartia tonsa in Florida Bay. II. Role of the nutritional environment. **Marine Biology** 137, 111–121. DOI: 10.1007/s002270000319

Koch, E. W., Ackerman, J., van Keulen, M., *et al.* (2006). Fluid dynamics in seagrass ecology: from molecules to ecosystems. In **Seagrasses: Biology, ecology and conservation**. (Larkum, A. W. D., Orth, R. J. & Duarte, C. M., eds.). Springer Verlag, 193-225.

Lee, S. Y., Fong, C. W., & Wu, R. S. S. (2001). The effects of seagrass (*Zostera japonica*) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds. **Journal of Experimental Marine Biology and Ecology** 259, 23–50.

Mabrouk, L., Hamza, A., Brahim, M. B. *et al.* (2011). Temporal and depth distribution of microepiphytes on *Posidonia oceanica* (L.) Delile leaves in a meadow off Tunisia. **Marine Ecology** 32, 148-161.

Macreadie, P. I., Hindell, J. S., Keough, M. J., *et al.* (2010). Resource distribution influences positive edge effects in a seagrass fish. **Ecology** 91(7), 2013-21.

Matias-Peralta, H. M. & Yusoff, F. M. (2014). Seasonal environmental quality variations in a tropical seagrass ecosystem in the Straits of Malacca. **Malayan Nature Journal** 66, 59-74.

#### McKenzie, L. J., Campbell, S. J., & Roder, C. A. (2003). Seagrass-Watch: Manual for mapping & monitoring seagrass resources by community (citizen) volunteers. 2nd Edition. (QFS, NFC, Cairns) 100pp.

Metillo, E. B., Nishikawa, J., Othman, B. H. *et al.* (2018). Diel patterns of zooplankton community structure in nearshore waters of different substrates off Tinggi and Sibu Islands, Malaysia, with special reference to copepods. **Aquatic Ecosystem Health & Management** 1-29. DOI: 10.1080/14634988.2018.1505139

Metillo, E. B., Villanueva, R., Hayashizaki, K., *et al.* (2019). Stable C and N isotope analysis elucidated the importance of zooplankton in a tropical seagrass bed of Santiago Island, Northwestern Philippines. **Chemistry and Ecology** 35(2), 143-163, DOI: 10.1080/02757540.2018.1533957

Micheli, F., Bishop, M. J., Peterson, C. H., *et al.* (2008). Alteration of seagrass species composition and function over two decades. **Ecological Monographs** 78, 225-244.

Nagelkerken, I. (2009). Evaluation of nursery function of mangroves and seagrass beds for tropical decapods and reef fishes: patterns and underlying mechanisms. *In* **Ecological Connectivity among Tropical Coastal Ecosystems**, 357-399. Dordrecht, Heidelberg, London, New York: Springer Verlag. ISBN: 9789048124053

Nakajima, R., Yoshida, T., Othman, B. H. R., *et al.* (2008). Diel variation in abundance, biomass and size composition of zooplankton community over a coral-reef in Redang Island, Malaysia. **Plankton and Benthos Research** 3, 216-226.

Nanjo, K., Kohno, H., Nakamura, Y., *et al.* (2014). Differences in fish assemblage structure between vegetated and unvegetated microhabitats in relation to food abundance patterns in a mangrove creek. **Fisheries Science** 80, 21–41

Norhadi, I. (1993). Preliminary study of seagrass flora of Sabah, Malaysia. **Pertanika Journal of Tropical Agriculture Science** 16(2), 111-118.

Petrou, K., Jimenez-Denness, I., Chartrand, K., *et al.* (2013). Seasonal heterogeneity in the photophysiological response to air exposure in two tropical intertidal seagrass species. **Marine Ecology Progress Series** 482, 93–106. DOI: 10.3354/meps10229

Rajamani, L., and Marsh, H. (2015). Mapping seagrass cost-effectively in the Coral Triangle: Sabah, Malaysia as a case study. **Pacific Conservation Biology** 21, 113

Orth, R. J., Carruthers, T. J., Dennison, W. C., *et al.* (2006) A Global Crisis for Seagrass Ecosystems, **BioScience** 56(12), 987–996, DOI: 10.1641/0006-3568(2006)56[987:AGCFSE]2.0.C0;2 Roman, M. R. (1984). Utilization of detritus by the copepod *Acartia tonsa*. **Limnology and Oceanography** 29, 949–959. DOI: 10.4319/lo.1984.29.5.0949

Roman, M. R., Reeve, M. R., & Froggatt, J. L. (1983). Carbon production and export from Biscayne Bay, Florida. Vol. I: Temporal patterns in primary production, seston and zooplankton. **Estuarine, Coastal and Shelf Science** 17, 45-59.

Sheridan, P. (1997). Benthos of adjacent mangrove, seagrass and nonvegetated habitats in Rookery Bay, Florida, USA. **Estuarine, Coastal and Shelf Science** 44, 455-469.

Stoner, A. W. (1980). The role of seagrass biomass in the organization of benthic macrofaunal assemblages. **Bulletin of Marine Science** 30, 537–551

Tantichaiwanit, W. (2005). Zooplankton dynamics in Kung Krabaeng Bay Chantaburi Province. MSc Thesis, Chulalongkorn University, pp.210

Thresher, R. E., Nichols, P. D., Gunn, J. S., *et al.* (1992). Seagrass detritus as the basis of a coastal planktonic food chain. **Limnology and Oceanography** 37(8), 1754-1758.

Touchette, B. W. (2007). The biology and ecology of seagrasses. Journal of Experimental Marine Biology and Ecology 350, 1–2

Turner, J. T, & Tester, P. A. (1989). Zooplankton feeding ecology: nonselective grazing by the copepods *Acartia tonsa* Dana, *Centropages velificatus* De Oliveira, and *Eucalanus pileatus* Giesbrecht in the plume of the Mississippi river. **Journal of Experimental Marine Biology & Ecology** 126, 21–43. DOI: 10.1016/0022-0981(89)90122-6

Vermaat, J. E., Agawin, N. S. R., Fortes, M. D., *et al.* (1997). The capacity of seagrasses to survive increased turbidity and siltation: The significance of growth form and light use. **Ambio** 26(8), 499-504.

Whippo, R., Knight, N. S., Prentice, C., *et al.* (2018). Epifaunal diversity patterns within and among seagrass meadows suggest landscape-scale biodiversity processes. **Ecosphere** DOI: 9(11):e02490.10.1002/ecs2.2490

Wyda, J. C., Deegan, L. A., Hughes, J. E., *et al.* (2002). The response of fishes to submerged aquatic vegetation complexity in two ecoregions of the mid-Atlantic bight: Buzzards Bay and Chesapeake Bay. **Estuaries** 25, 86–100

Yoshida, T., Eio, E. J., Toda, T., *et al.* (2012) Food size dependent feeding and egg production of *Acartia pacifica* from a tropical strait. **Bulletin of Marine Science** 88, 251-266.