Monsoonal and lunar variability in microzooplankton abundance and community structure in the Terusan mangrove creek (Malaysia)

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ABSTRACT
This study documents the monsoonal and lunar effects on species composition and abundance of microzooplankton in a tropical estuary. We investigated microzooplankton abundance in relation to the various environmental and biotic parameters, sampled in the Matang mangrove (Malaysia) from April 2013 to February 2014. A total of 39 microzooplankton taxa comprising four major groups, i.e. loricate ciliates (37.72%), aloricate ciliates (29.46%), dinoflagellates (24.33%) and meroplanktonic nauplii (8.49%) were identified. The loricate ciliates were the most diverse group with 31 taxa recorded. Four major species of loricate ciliates were identified, i.e. Tintinnopsis beroidea, Tintinnopsis rotundata, Stenosemella avellana and Tintinnidium primitivum, while Stombeidae and Strobilidiidae dominated the aloricate ciliates. Although small loricate ciliates were ubiquitous, redundancy analysis shows marked shifts in microzooplankton community structure, from one that was dominated by loricate ciliates during the drier SW monsoon, to aloricate ciliates at the onset of the wet NE monsoon, and then to dinoflagellates towards the end of the drier NE monsoon period. These shifts were associated with rainfall, dissolved inorganic nutrients, salinity, temperature and microbial food abundance. There was no clear lunar effect on abundance of microzooplankton except for Favella ehrenbergii and copepod nauplii, which were more abundant during neap than spring tides.

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Introduction
Microzooplankton are classified as heterotrophic and mixotrophic organisms that range from 20 to 200 µm in size. Planktonic ciliates such as the choreotrichids and oligotrichids (class Spirotrichea) usually dominate in terms of numbers and biomass (Godhantaraman & Uye 2003; Yang et al. 2008; Lynn 2010; Monti & Minocci 2013; Dolan et al. 2013; Stoecker et al. 2014). Choreotrichids are mainly the tintinnids and aloricate ciliates from the family Strobiliidae and Strombiidinopsidae, whereas oligotrichids are primarily from the Strombiidae and Tontoniidae in marine waters (Lynn 2010; Agatha 2011; Dolan et al. 2013a). Microzooplankton also include dinoflagellates, foraminifers and small metazoans such as copepod nauplii and copepodies and meroplanktonic larvae (Calbet 2008).

There has been a dramatic impetus in microzooplankton research ever since their discovery as trophic intermediaries, transferring materials and energy via the microbial loop to higher trophic levels (e.g. Azam et al. 1983; Robertson 1983; Stoecker & Capuzzo 1990; Putland & Iverson 2007). Microzooplankton biomass is always higher than mesozooplankton in estuaries (Buskey & Stoecker 1989) showing their greater importance in pelagic food webs. The small body size of microzooplankton makes them more efficient (than mesozooplankton) in consuming the even smaller nano- and picoplankton; in fact, they are also among the dominant grazers of phytoplankton (Burkill et al. 1993; Schmoker et al. 2013). Nonetheless, there is a general lack of knowledge about the microzooplankton in tropical estuarine and marine waters, thus hampering a deeper understanding of the functioning of the tropical microbial loop. The few studies in tropical waters were conducted mainly in India (Godhantaraman 2002; Jyothibabu et al. 2006, 2008a, 2008b; Asha Devi et al. 2010; Sarkar 2015) and South America (Pettigrosso 2003; Eskinazi-Sant’anna & Bjornberg 2006). Among these studies, the tintinnids...
were the most studied, while there is little information on the other microzooplankton, such as their close relatives, the aloricate ciliates.

In the tropical Matang mangrove estuary, mesozooplankton studies have focused mainly on copepods (Oka 2000; Ooi et al. 2005; Chew & Chong 2011; Chew et al. 2015), mysids (Ramarn et al. 2012) and small fish larvae (Ooi & Chong 2011) and their potential food sources, including phytoplankton (based on chlorophyll a) and bacterioplankton (Alongi et al. 2003; Lee & Bong 2008). The dense population of copepods dependent on phytoplankton or seston is a crucial component of the pelagic food web of mangroves as shown by stable isotope tracer studies (Chew et al. 2012). Bentho-pelagic mysids are plankto-detrivores and appear important in the coupling of the benthic and pelagic components of the mangrove food web (Ramarn et al. 2015). These studies, however, did not elucidate the role of the smaller microzooplankton, for example their intermediary role between basal sources and copepods. Tarutani et al. (2007) estimated that zooplankton (excluding microzooplankton) production in the Matang estuary accounted for only 19% of the phytoplankton productivity (340 mg C m$^{-2}$ d$^{-1}$) and suggested that the remainder was either degraded or consumed by non-planktonic filter feeders.

However, it is possible that a large portion of the primary production in Matang is being channelled to the microzooplankton (e.g. Lam-Hoai et al. 1997) and/or bacterioplankton (Lee & Bong 2008).

Thus, given the paucity of studies on microzooplankton and their potentially significant trophic contribution to estuarine food webs, the objective of this study was to identify Matang’s microzooplankton community structure and to elucidate their temporal distribution in relation to environmental factors. We tested the hypothesis that temporal variability of microzooplankton in a tropical mangrove estuary is the result of environmental parameters modulated by the lunar and monsoonal regime.

**Materials and methods**

**Study area**

The chosen study site was at the Terusan channel, a 6 m-deep mangrove creek located in the Matang Mangrove Forest Reserve (MMFR) in the state of Perak, west coast of Peninsular Malaysia. The Terusan channel (4°526′N, 100°341′E) interconnects the Selinsing and Sangga Besar channels downstream of the Matang estuary (Figure 1). The MMFR is a silvicultured mangrove production forest.

![Figure 1. Map of Matang Mangrove Forest Reserve. Filled circle indicates location of Terusan channel. P1 indicates the fishing village of Kuala Sepetang.](https://example.com/figure1.png)
planted with mainly the favoured mangrove species, *Rhizophora apiculata* Blume. The large mangrove reserve of approximately 41,000 ha is composed of mangrove forests situated on the coast and several deltaic islands drained by the tributaries and interconnecting channels of three main rivers, the Sepe-tang, Larut and Terong. The tidal regime in the MMFR is semidiurnal, with MHWS, MHWN, MLWN and MLWS of 2.1, 1.5, 0.9 and 0.3 m above Chart Datum, respectively (National Hydrographic Centre, Malaysia). The deltaic estuary is relatively shallow with an average depth of 4.2 m, but depths ranged from 0.5 m to 14.4 m. A strong estuarine stratification in the upper estuary (upstream of P1) is evident during the NE monsoon season (November–March) during heavy rainfall, when a large quantity of fresh water is flushed into the estuaries. On the other hand, no significant stratification is observed during the SW monsoon season (May–September), when the rainfall is relatively lower (Chew et al. 2015). Nevertheless, freshwater inflows and weak vertical mixing during the SW monsoon particularly during neap tide may form a temporary salt wedge that could extend as far as 10 km upstream from the river mouth (Tanaka & Choo 2000). The water column is generally vertically well mixed during spring tides (Chew et al. 2015).

**Samplings and hydrographic measurements**

Bimonthly samplings (during spring and neap tide) were conducted at seven sampling stations in the deltaic estuary (Figure 1), from April to August 2013 (SW monsoon) and from October 2013 to February 2014 (NE monsoon), to collect microzooplankton and (HNP) were counted using a direct-count method. Both bacteria and heterotrophic nanoplankton (HNP) were counted using a direct-count method (Parson et al. 1984) using a Perkin Elmer LS55 spectrofluorometer. Samples were analysed as soon as possible (<7 days) so as to avoid further pigment degradation. Filtered seawater was analysed for dissolved inorganic nutrients (DIN, i.e. nitrite, nitrate, ammonium, silicate and phosphate) using standard methods (Parson et al. 1984) and a Hitachi U1900 spectrophotometer.

**Bacteria and heterotrophic nanoplankton abundance**

Water samples (30 ml) were fixed with filtered glutaraldehyde (0.2 µm pore size) to a final concentration of 4%. Both bacteria and heterotrophic nanoplankton (HNP) were counted using a direct-count method with a U-MWU filter cassette (excitor 330–385 nm, dichroic mirror 400 nm, barrier 420 nm) epifluorescent microscope under 1000× magnification (Olympus BX50, Tokyo, Japan). For bacteria, a 0.5 ml sample was filtered onto a black 0.2 µm pore size isopore filter. The filter was then stained with 4′,6-Diamidino-2-Phenylindole (DAPI, 1 µg ml⁻¹ final concentration) for seven minutes. A 5 ml sample of HNP was filtered onto a black 0.8 µm pore size isopore filter and then stained with 250 mg l⁻¹ primuline for 10 minutes (Caron 1983). Slides were kept frozen and their microscopy fields were photographed within 3 days. A minimum of 10 microscope fields or 300 cells were counted for bacteria, and at least 50 microscope fields or 30 cells were observed for HNP. To estimate the photoautotrophs, each microscope field was viewed under the U-MWG filter cassette (excitor 510–550 nm, dichroic mirror 570 nm, barrier 590 nm) for the autofluorescence of chlorophyll *a*. The abundance of photoautotrophs was subtracted from bacteria and HNP counts.
Phytoplankton and microzooplankton abundance

Two litres of the collected water sample were immediately fixed with 0.4% Lugol’s iodine after collection and allowed to stand for 48 hours at the laboratory before 1.5 l of the clear top liquid was siphoned off. The remaining 500 ml sample was gently tilted back and forth in its bottle to homogenize the mixture before pouring it into a sedimentation chamber (Utermöhl 1958). The plankton was allowed to settle down for at least 48 hours before 25 ml concentrate was collected from the cavity base. Lugol’s iodine (2 ml) was added to the plankton concentrates to obtain a final concentration of 10% iodine for long-term preservation (Stoecker 1994). Enumeration was done by transferring 1 ml of concentrated sample onto a Sedgwick-Rafter chamber and viewed under an inverted microscope (Leica DM IL LED) at 200×. The entire chamber was examined for each sample. Tintinnids were identified to species based on lorica size and shape, whereas the other microzooplankton were identified to the lowest taxa possible under magnification of 200× (Kofoid & Campbell 1929; Marshall 1934, 1969; Zhang et al. 2012). Phytoplankton which was enumerated at the same time, were identified to genus level (Tomas 1997).

Data analyses

Prior to ANOVA, the abundance of bacteria, HNP, phytoplankton, and chlorophyll a data were log_{10} (x + 1)-transformed to meet parametric assumptions. Most microzooplankton taxonomy abundance did not meet parametric assumptions even after data transformation. Hence, non-parametric methods were used to test for significant difference. The Mann–Whitney test was performed to examine separately the monsoonal and lunar effect on the abundance of microzooplankton. A one-way Kruskal–Wallis test was then carried out to test the combined effects of monsoon and tide, namely, SW-spring, SW-neap, NE-spring and NE-neap. A Spearman rank order correlation was used to determine the significant relationship (if any) among environmental and microzooplankton variables. All statistical tests were performed using the Statistica Version 8 program (StatSoft Inc. 2007).

Redundancy analysis (RDA) is a constrained ordination technique used to construct ordination axes that are also linear combinations of the environmental variables (Ter Braak & Smilauer 2002). Here, the method was used to relate the microzooplankton abundance to the measured environmental parameters. The top 30 most abundant microzooplankton species and 14 environmental parameters (i.e. rainfall, salinity, dissolved oxygen, temperature, Secchi disc depth, dissolved inorganic ammonia, nitrate, nitrite, phosphate, and silicate, bacteria abundance, HNP abundance, chlorophyll a, and phytoplankton abundance) were selected for RDA. All biological data were log_{10} (x + 1)-transformed. RDA was performed using the CANOCO 4.5 program (Ter Braak & Smilauer 2002).

Results

Environmental parameters

Environmental parameters in the Matang estuary were strongly influenced by monsoon season. Rainfall, temperature, salinity, pH and chlorophyll a concentration showed significant differences between monsoons (P < 0.05, Table I). The SW monsoon started off with decreasing rainfall from April (308.2 mm) to July (93.8 mm; Figure 2a). During this period the Terusan channel was characterized by higher mean salinity (22.2 ± 0.7 ppt), warm water (30.1 ± 0.3°C), and higher chlorophyll a concentration (24.79 ± 3.77 µg l\(^{-1}\)) relative to other months. Towards the late SW monsoon (August) and with the onset of NE monsoon (October), the rainfall increased 2–3 fold (Figure 2a), ranging from 204.4 mm (August 2013) to 481.3 mm (November). During the peak NE monsoon (October 2013 to January 2014), the channel had become enriched with higher levels of dissolved inorganic nutrients (nitrate and phosphate; P < 0.05; Table I). Temperature, salinity and chlorophyll a concentrations became lower at 28.4 ± 0.2°C, 18.4 ± 0.1 ppt and 10.57 ± 1.47 µg l\(^{-1}\), respectively. The NE monsoon then ended with a dry spell in February. Rainfall decreased (74.9 mm) and water in the channel turned warmer (30.4 ± 0.3°C; with higher salinity 27.4 ± 0.3 ppt). Chlorophyll a concentration increased relative to the peak NE monsoon (16.71 ± 2.36 µg l\(^{-1}\)). Water transparency as measured by Secchi disc depth and dissolved oxygen concentration showed no difference between monsoons (Table I, Table SI, supplementary material).

Mean Secchi disc depth was significantly greater during neap than spring tide (P < 0.01, Table I). No lunar phase effects (P > 0.05) were observed for other water parameters. Although there was no significant difference in concentration between lunar phases for all DIN, the concentration of all DIN was comparatively higher during spring tide than neap tide (Table I, Figure 2b).

Bacteria, HNP and phytoplankton abundance

Bacteria abundance was fairly constant (P > 0.05) throughout the sampling period (2.42 × 10^9 to 1.14 ×
$10^{10}$ cell $l^{-1}$) despite a slight peak that occurred in November 2013 (Figure 2c). Compared with bacteria, the abundance of HNP was more variable among sampling months, with peaks recorded in June 2013 ($1.96 \times 10^8$ cell $l^{-1}$) and February 2014 ($7.48 \times 10^7$ cell $l^{-1}$) respectively (Figure 2c). The mean abundance of HNP ($1.98 \times 10^7 \pm 4.38 \times 10^7$ cell $l^{-1}$) was approximately three orders of magnitude lower than bacteria

**Figure 2.** Monthly mean of (a) physical parameters, (b) dissolved inorganic nutrients and (c) microzooplankton (MZP) potential food components. N denotes neap tide, S denotes spring tide. Error bars (S.E.) are indicated.
significantly more abundant during the SW monsoon than the NE monsoon ($P < 0.05$, Table I). Phytoplankton abundance and chlorophyll $a$ concentration ranged from $3.46 \times 10^4$ cell l$^{-1}$ to $3.69 \times 10^5$ cell l$^{-1}$ and $5.14$ µg l$^{-1}$ to $54.71$ µg l$^{-1}$, respectively. Both chlorophyll $a$ concentration and phytoplankton abundance showed significant difference between monsoons. The phytoplankton community was dominated by Skeletonema costatum (Greville) Cleve, composing 64% of phytoplankton abundance. There was no significant difference in abundance of bacteria, HNP and phytoplankton and chlorophyll $a$ concentration between lunar phases ($P > 0.05$; Table I).

Table II, Figure 3). Both $H'$ and $J'$ were not significantly different between the lunar phases ($P > 0.05$, Table II).

The overall mean microzooplankton abundance was $8.74 \pm 9.65 \times 10^5$ ind l$^{-1}$. The mean total abundance of microzooplankton was significantly higher during the NE monsoon as compared with the SW monsoon ($P < 0.05$; Table I, Figure 2c); peak microzooplankton abundance occurred in October 2013 and lowest abundance in August 2013 (Figure 3). The microzooplankton were dominated by loricate ciliates during the SW monsoon (50.92 ± 5.82%), while the aloricate ciliates were predominant during the NE monsoon (38.99 ± 8.83%; Figure 3). Copepod nauplii were always the least abundant component between both monsoons and lunar effects, ranging from 60 ind l$^{-1}$ to 1275 ind l$^{-1}$ across months.

Out of the 39 identified microzooplankton taxa, 29 taxa belonged to the loricate ciliates. Four major species of loricate ciliates (> 95% occurrence, see Table II) were identified, namely, Tintinnopsis beroidea Stein, 1867, Tintinnopsis rotundata Kofoid & Campbell, 1929, Stenosemella avellana (Meunier, 1919) and Tintinidium primitivum (Kofoid & Campbell, 1929), Stein, 1867, Tintinnopsis rotundata Kofoid & Campbell, 1929, Stenosemella avellana (Meunier, 1919) and Tintinidium primitivum (Kofoid & Campbell, 1929) and T. acuminata, most of the loricate ciliates were commonly more abundant during the SW monsoon. All...
three *Leprotintinnus* species were present almost the year round (Table II) and only showed significantly higher abundance during SW monsoon (Table III). Most of the loricate ciliates did not exhibit a significant difference in abundance between lunar phases except for *Favella ehrenbergii* (Claparède & Lachmann, 1858) Jörgensen, 1924 and *Tintinnopsis nana* Lohmann, 1908. The large *F. ehrenbergii* was only observed during neap tide while *T. nana* occurred in significantly greater abundance during spring tide (Tables II and III). There were eight rare species with relatively low abundance of less than 1%, namely, *Tintinnopsis mortenseni* Schmidt, 1902, *T. vasculum* Meunier, 1919, *T. acuminata* Daday, 1887, *T. buetschlii* Daday, 1887, *Tintinnidium incertum* Brandt, 1906, *Rhizodomus tagatzi* Streklow & Wirketis, 1950, *Eutintinnus* sp., and *Amphorellopsis* spp. (Table II). Interestingly, these rare species were all collected only once during the SW monsoon, except for *Eutintinnus* sp. which were collected twice during the spring tide, one each during the SW monsoon and the NE monsoon.

The aloricate ciliates were represented by five major families: Mesodiniidae, Strombidiidae, Strobilidiidae, Pleuronematidae and Vorticellidae. Aloricate ciliates were more abundant during the NE monsoon, with Strombidiidae, Strobilidiidae and Mesodiniidae showing significant difference between monsoon periods. In particular, the monotypic Mesodiniidae in
the Cyclotrichida was only present during the rainy months of the NE monsoon (October to January, Table II). An exceptional peak abundance of cyclotrichs was recorded in October 2013, reaching 36,250 ind l$^{-1}$.

The lunar effect on the aloricate ciliate community was not significant.

Five genera of dinoflagellates (i.e. Peridinium, Ceratium, Dinophysis, Noctiluca and Prorocentrum) were
identified. *Peridinium*, *Prorocentrum* and *Ceratium* showed the same distribution; their numbers were significantly higher during the NE monsoon, reaching maximum abundance towards the end of the NE monsoon as the dry spell began. Of all the dinoflagellate genera, *Ceratium* spp. recorded an exceptional peak (11,313 ind l\(^{-1}\)), about five-fold its average abundance during the end of the NE monsoon when the local climate was at its driest (74.9 mm, Table II). No significant lunar phase effect was observed in the dinoflagellate community.

Copepod nauplii were present in all samplings. As opposed to most microzooplankton, which did not exhibit lunar phase difference, copepod nauplii recorded significantly higher (\(P < 0.001\)) mean abundance during neap tide.

**Species-environment relationship**

The relationship between environmental parameters and 30 microzooplankton species (those with >30% of occurrence) is depicted as an ordination triplot in Figure 4, derived from redundancy analysis (RDA). The first two canonical axes explained 44.8% of the total variance in the species data and 55.3% of the species-environment relation. Monthly total rainfall, which was relatively higher during the NE monsoon (compared with SW monsoon), was correlated to most DIN concentrations, positively with NO\(_3\)\(^-\), PO\(_4\)\(^{3-}\), SiO\(_2\), NO\(_3\) (upper-right quadrant), dissolved oxygen and negatively with salinity (diagonally opposite quadrant). Temperature and chlorophyll \(a\) concentration were correlated and relatively higher during the SW monsoon. Pearson’s correlation test further verified the significant correlations between dissolved inorganic nitrate, phosphate and silicate with rainfall (0.38 ≤ \(r\) ≤ 0.52) and salinity (−0.52 ≤ \(r\) ≤ −0.41). Among all the dissolved inorganic nitrogen, nitrate appeared to affect the community to a greater extent compared with ammonium and nitrite (Table II).

For potential food sources of microzooplankton, HNP, which had higher abundance during the SW monsoon, was positively and highly correlated with salinity (and negatively correlated with rainfall), and to a lesser extent with temperature, chlorophyll \(a\) concentration and dissolved oxygen (see also Table IV). Bacteria abundance as indicated by the short arrow was not obviously related to the physical and chemical parameters and showed no significant changes throughout the sampling. Both bacteria and phytoplankton were not closely related to any particular monsoon period. Except for bacteria, both HNP and chlorophyll \(a\) exhibited negative correlation with dissolved inorganic nutrients (Table IV), i.e. their arrow heads pointed in opposite directions (Figure 4). Among all potential food sources, phytoplankton as represented by chlorophyll \(a\) concentration showed the most significant relationship with microzooplankton (Table IV).

Based on the (monthly) sample distribution and the rainfall arrow on the triplot, axis 1 on the right (positive) was interpreted to indicate the trend of increasing rainfall and the dominant effect of the NE monsoon, whereas axis 1 on the left (negative) indicates higher temperature and the dominant effect of the SW monsoon. On the other hand, axis 2 on the top
Table IV. Spearman rank order correlation matrix among environmental parameters, microzooplankton potential food components and key taxa of microzooplankton in Terusan channel.

|          | Bact  | HNP  | Phyto | Chl a | H'   | J'   | Rain | Temp | Sal | DO  | Secc | NH₄⁺ | NO₂⁻ | NO₃⁻ | PO₄³⁻ | SiO₂⁻ |
|----------|-------|------|-------|-------|------|------|------|------|-----|-----|------|------|------|------|------|------|
| Bact     |       |      |       |       |      |      |      |      |     |     |      |      |      |      |      |      |
| HNP      | 0.34  | −0.77| 0.64  | 0.69  | −0.75| −0.66| −0.38|      |     |     |      |      |      |      |      |      |
| Phyto    | 0.35  |      |       |       |      |      |      |      |     |     |      |      |      |      |      |      |
| Chl a    | 0.34  | 0.35 |       |       |      |      |      |      |     |     |      |      |      |      |      |      |
| H'       | 0.91  |      |       |       |      |      |      |      |     |     |      |      |      |      |      |      |
| J'       | 0.91  |      |       |       |      |      |      |      |     |     |      |      |      |      |      |      |
| Tintinnopsis rotundata Kofoid & Campbell, 1929 | 0.39  | 0.37 |      |       | 0.37 |      |      |      |     |     |      |      |      |      |      |      |
| Tintinnidium primitivum Busch, 1923 | 0.45  | 0.42 |      |       | −0.39| 0.49 | 0.41 |      |     |     |      |      |      |      |      |      |
| Tintinnopsis tubulosa Levander, 1900 | −0.33 |      |       |       |      |      |      |      |     |     |      |      |      |      |      |      |
| Tintinnopsis nana Lohmann, 1908 |       |      |       |       |      |      |      |      |     |     |      |      |      |      |      | 0.37 |
| Leprotintinnus elongatus Skryabin & Al-Yamani, 2007 | 0.38  |      |       |       |      |      |      |      |     |     |      |      |      |      |      |      |
| Tintinnopsis meunieri Kofoid & Campbell, 1929 | 0.33  | 0.47 | 0.37  | 0.36  | 0.41 |      |      |      |     |     |      |      |      |      |      |      |
| Leprotintinnus nordqvisti (Brandt, 1906) Kofoid & Campbell, 1929 | 0.67  | 0.33 | 0.64  | 0.31  |      |      |      |      |     |     |      |      |      |      |      |      |
| Tintinnopsis tocantinensis Kofoid & Campbell, 1929 | 0.68  | 0.61 | 0.36  |      | −0.65| 0.71 | 0.63 | −0.36|    |     |      |      |      |      |      |      |
| Leprotintinnus bottnicus Jörgensen, 1900 | 0.49  | 0.34 | 0.37  |      | −0.48| 0.62 | 0.51 |      |    |     |      |      |      |      |      |      |
| Codonellopsis spp. | 0.61  | 0.49 |      |      | −0.51| 0.56 | 0.51 | −0.49|    |     |      |      |      |      |      |      |
| Tintinnidium incerta incertum Brandt, 1906 | −0.46 | −0.41| 0.55  | −0.47| −0.44|      |      |      |    |     |      |      |      |      |      |      |
| Tintinnopsis ehrenbergii (Claparède & Lachmann, 1858) Jörgensen, 1924 | −0.39 |      |      |      |      |      |      |      |    |     |      |      |      |      |      |      |
| Strobilidiids | −0.48 |      |      |      |      |      |      |      |    |     |      |      |      |      |      |      |
| S. suecicus | −0.32 | −0.71|      |      |      |      |      |      |    |     |      |      |      |      |      |      |
| Pleuronematina | 0.32 |      |      |      |      |      |      |      |    |     |      |      |      |      |      |      |
| Cyclotrich | −0.53 | −0.54| −0.35 | −0.33| 0.51 | −0.55| −0.63|      |    |     |      |      |      |      |      |      |
| Vorticella | 0.38  | 0.31 |      |      | −0.41| 0.38 | 0.39 |      |    |     |      |      |      |      |      |      |
| Peridinium spp. |       |      |      |      |      | −0.32|      |      |    |     |      |      |      |      |      |      |
| Ceratium spp. |       |      |      |      |      |       | −0.45|      |    |     |      |      |      |      |      |      |
| Dinophysis spp. |       |      |      |      |      |       | −0.36|      |    |     |      |      |      |      |      |      |
| Proorocentrum spp. | −0.46| −0.34| −0.37| −0.49| 0.37 |      |      |      |    |     |      |      |      |      |      |      |
| Noctiluca spp. | 0.42  | 0.56 |      |      | −0.32| 0.37 |      |      |    |     |      |      |      |      |      |      |
| Nauplius <200 µm | −0.4  | 0.6  |      |      | −0.47| −0.47| −0.41|      |    |     |      |      |      |      |      |      |

Abbreviations used: bacteria (Bact), heterotrophic nanoplanктон (HNP), phytoplankton (Phyto), Chlorophyll a (Chl a), salinity (Sal), rainfall (Rain), temperature (Temp), Secchi depth (Secc), dissolved oxygen (DO). Species arranged with percentage occurrence, from highest to lowest in each category. Only significant correlations are shown; pairwise n = 40.
(positive) indicates higher DO and at the bottom (negative) indicates higher salinity. Thus, there is a clear separation in community structure of microzooplankton between the SW and NE monsoons.

The microzooplankton community was represented by large-bodied loricate ciliates with an affinity for higher salinity and temperature during the SW monsoon (negative axis of RDA1). The large-bodied loricate tintinnid species (c. 150 µm in total length) included *Leprotintinnus nordqvisti* (Brandt, 1906) Kofoid & Campbell, 1929 (Lnor), *L. elongatus* Skrjabin & Al-Yamani, 2007 (Lelo), *L. bottnicus* Jörgensen, 1900 (Lbot), *Tintinnopsis meunieri* Kofoid & Campbell, 1929 (Tmeu), *T. tocantinensis* Kofoid & Campbell, 1929 (Ttoc), *T. chinglanensis* Nie & Ch'eng, 1947 (Tchng) and *Codonellopsis* spp. (Cod). These species also show strong positive correlations with chlorophyll a concentration (0.38 ≤ R ≤ 0.64) and HNP (0.38 ≤ R ≤ 0.68; Table IV).

The relatively small loricate tintinnid species (c. 80 µm) *Stenosemella avellana* (Meunier, 1919) (Save), *Tintinnopsis nana* (Tnan), *T. rotundata* (Trot) and *T. beroidea* (Tber) were sampled throughout the sampling months. With the exception of *Stenosemella avellana*, which showed significant correlation with phytoplankton, no species showed any association with changes in their food abundance (Table IV). Although loricate ciliates were more abundant during the SW monsoon, *Tintinnopsis tubulosa* (Ttub), *T. acuminata* (Tauc) and *Tintinnidium primitivum* (Tnper) were among the tintinnids that were more abundant during the NE monsoon. The aloricate ciliates, strobilidiids (Strob), strombidiids (Strom) and Pleuroonematine (Pleu) were sampled throughout the sampling period, but they peaked in abundance during the NE monsoon (positive axis 1). These aloricate families were also probably influenced by DIN concentrations. Only *Vorticella* among the aloricate ciliates showed negative correlation with rainfall (R = −0.41, P < 0.05). The dinoflagellates *Ceratium* spp. (Cer), *Dinophysis* spp. (Dphys) and *Proorocentrum* (Prot) were also found to be more abundant during the NE monsoon as compared with the SW monsoon. The former two genera bloomed during the latter part of the NE monsoon when total rainfall decreased. *Noctiluca* was the only dinoflagellate that showed greater abundance during the SW monsoon.

Copepod nauplii, the only metazoan group in the microzooplankton, was positioned on the negative side of axis 2; it was neither associated with any potential food nor rainfall. The abundance of copepod nauplii, however, showed significant correlation with dissolved oxygen and Secchi disc depth (Table IV).

**Discussion**

This is the first study in Malaysia and one of a few studies in tropical waters to investigate the temporal dynamics of microzooplankton in a mangrove estuary. In agreement with other studies in tropical (Godhantaraman 2002; Sarkar 2015), temperate (Petersen et al. 2007; Asha Devi et al. 2010; Stoecker et al. 2014), polar (Dolan et al. 2013b; Dolan & Pierce 2014) and freshwater (Kalinowska 2004; Hambright et al. 2007) environments, the microzooplankton in the Matang estuary are dominated by both aloricate and loricate ciliates. Most of the tintinnid ciliate genera (e.g. *Tintinnopsis*, *Leprotintinnus*, *Favella* and *Codonellopsis*) found in the present study are, however, known to be cosmopolitan groups (Pierce & Codonellopsis 1993). Tintinnid and aloricate ciliate concentrations are comparable with those of other tropical estuarine and coastal waters (Jyothibabu et al. 2008a, 2008b; Agatha 2011; Rakshit et al. 2014; Sarkar 2015). Thus, the microzooplankton in tropical estuarine waters as in Matang are rich in diversity, although community structure and species abundance are highly variable temporally. The temporal variations of microzooplankton abundance in the Matang estuary appear to be closely linked to rainfall, salinity, temperature and their likely microbial prey. In temperate waters, the abundance of ciliates normally peaks in spring and summer, primarily due to high phytoplankton food abundance and temperature (Kamiyama 1994; Bojanić et al. 2004; Barria de Cao et al. 2005). Unlike temperate waters, tropical mangrove waters like in Matang are conditioned by the monsoonal climate rather than temperature (Godhantaraman 2002; Jyothibabu et al. 2008a; Asha Devi et al. 2010). In Matang, the causal link of the temporal variations of microzooplankton is species-dependent. High salinity, temperature and phytoplankton abundance during the SW monsoon are favourable for the growth of the large-bodied tintinnids (i.e. *Leprotintinnus bottnicens*, *L. nordqvisti*, *L. elongatus*, *Tintinnopsis tocantinensis*). Ciliate biomass is correlated with chlorophyll a concentration as phytoplankton serves as one of their major food sources (Jiang et al. 2013; Yu et al. 2013; Wang et al. 2014; Sarkar 2015). The positive correlation of loricate ciliates with phytoplankton or chlorophyll a shows a nutritional dependence (Kimor & Golandsky 1977). Degrading phytoplankton cells and materials are also advantageous to large-bodied tintinnids, which are more conspicuous and vulnerable to predators, since they need these materials to build their protective lorica (Capriulo 1982).

In contrast, the small-bodied tintinnids such as *Stenosemella avellana*, *Tintinnopsis beroidea*, *T. nana* and...
T. rotundata are ubiquitous, being present throughout the sampling period. This suggests that salinity, temperature and phytoplankton, which are variable factors, are not the prime factors controlling their temporal abundance (Dolan & Gallegos 2001; Sarkar 2015). Apart from being eurythermal and euryhaline (Rakshit et al. 2014), small-bodied tintinnids, with a seeming lack of temporal variability in their abundance, may depend on the unlimited bacterial food present throughout the year. There are, however, two exceptions; two low-salinity tintinnid species, Tintinnopsis tubulosa and Tintinnidium primitivum, were more abundant in the low-salinity environment during the NE monsoon. Rakshit et al. (2014) demonstrated a weak negative correlation between T. primitivum abundance and salinity, while T. tubulosa predominated in summer with higher rainfall and runoffs (Kamiyama & Tsujino 1996).

The freshwater input into the estuary significantly increases the amount of ammonium, nitrate and silicate, resulting in higher concentrations of these nutrients during the rainy NE monsoon. The higher rainfall during the NE monsoon apparently triggers the proliferation of aloricate ciliates but not the large-bodied tintinnids in the Matang estuary. In particular, cyclotrich ciliates bloom during the early part of the NE monsoon, when increased riverine discharges dilute estuarine waters, bringing down the salinity but increasing the DIN. Microzooplankton samplings conducted from upstream to downstream in the Sepetang, Selinsing and Sangga Besar channels revealed that cyclotrich ciliates were low in numbers at the upper and mid sections of Selinsing and absent in the lower section of the Sepetang, including all other areas, during the SW monsoon (Yong et al. unpublished data). The salinity tolerance of the cyclotrich ciliates ranges from 5 ppt (Crawford & Lindholm 1997) to 35 ppt (Proença 2004). Thus, the blooms of cyclotrich ciliates in the estuary are unlikely to be ciliates that originated from upstream or those that were flushed downstream during the NE monsoon. Cloern et al. (1994) showed that with heavy precipitation and runoffs, cyclotrichs are very likely to bloom. It has been reported that the endosymbiotic chloroplasts found in the cyclotrich ciliates can take up the dissolved ambient, inorganic nitrogen to bloom (Wilkinson & Grunseich 1990; Liu et al. 2012). Therefore, the cyclotrich blooms during the NE monsoon are probably triggered by high DIN in the estuary. Given that the cyclotrich ciliates are the main prey for dinoflagellates (Nagai et al. 2008), the gradual disappearance of the cyclotrich ciliates towards the end of the NE monsoon is likely due to such predation and their declining reproductivity as dissolved inorganic nitrogen became limiting for cell replication.

Although most of the microzooplankton abundance appeared not to be influenced by lunar phase, the predatory tintinnid Favella ehrenbergii was sampled in considerable numbers during neap tide (17 ind l⁻¹) but was not present during spring tide. Similarly, the abundance of copepod nauplii was significantly higher during neap than spring tide in both SW and NE monsoons. In terms of body size, these two groups were the largest among the microzooplankton. Both of them are known to feed on other ciliates (Robertson 1983; Buskey & Stoecker 1989), placing them in the upper trophic level of the microzooplankton. These organisms were also the few microzooplankton (2 taxa) that were significantly correlated with water transparency (Secchi reading); all others were not, indicating the generally high water turbidity in Terusan channel (Table IV). Nevertheless, it is not clear why less turbid or clearer water favoured F. ehrenbergii and copepod nauplii; it may be due to the higher light intensity that also attracts their prey. Nonetheless, it may explain why F. ehrenbergii and copepod nauplii were more abundant during neap tide (clearer water) than spring tide. However, the lunar difference in abundance may also be explained by their reproductive timing and swimming ability so as to prevent population loss by strong tidal advection during spring tide. Compared to mesozooplankton, planktonic ciliates are less capable of swimming against currents and tides (Fenchel 1987; Dolan et al. 2013b). They rely more on water diffusion and either swimming at the water boundaries or drift with the flow (Zhu et al. 2013). However, larger ciliates such as F. ehrenbergii are capable of directional swimming towards food and against gravity (Jonsson 1989; Harvey & Manden-Deuer 2011). Interestingly and in contrast, the adult copepods of Acartia (Odontacartia) spinicauda Giesbrecht, 1889 were more abundant during spring than neap tide at the same sampling site (Kong et al. 2015). Apparently, the need for upstream penetration and population retention necessitates such a behaviour mediated through tidally induced vertical migration (Schmitt et al. 2011; Chew et al. 2015). However, since larval copepods are weak swimmers, the timing of copepod spawnings during neap tide is clearly an adaptive strategy to avoid more serious advective losses of their young stages during spring tide.

Many studies have been conducted to investigate the correlation between microzooplankton and environmental parameters. Some suggest bottom-up control, for example by temperature, salinity and
current (Verity 1986; Sanders 1987; Cordeiro et al. 1997; Eskinazi-Sant’anna & Bjornberg 2006), whereas others suggest a top-down control, such as by predators (Dolan & Gallegos 2001; Urrutxurtu et al. 2003). However, both bottom-up and top-down controls such as temperature, light, tidal effect, oxygen concentration, nutrients, prey and predator abundance can affect the formation of ciliate cysts (Jonsson 1994; Kamiyama 1994; Lynn 2010; Dolan et al. 2013a). With the great environmental fluctuations in the estuary, both encystment and excystment of ciliates could well explain the ‘disappearance’ and ‘bloom’ of certain species.

The present study used both cell density and chlorophyll a concentration of phytoplankton as measures of the potential autotrophic food source for microzooplankton. Although both variables were highly correlated, only DIN was significantly correlated (albeit negatively) with chlorophyll a concentration but not phytoplankton density. This is likely due to the poorer preservation of the smaller-size or soft-bodied phytoplankton other than diatoms by Lugol’s iodine. Fresh field samples compared with iodine-preserved samples conserve more of the actual phytoplankton community (Rodríguez-Ramos et al. 2014). Thus, ‘phytoplankton’ in our study contained more diatoms and much less of the smaller size fraction which included the phytoflagellates and coccoliths; therefore, cell density of the preserved phytoplankton was likely underestimated when viewed under the light microscope. On the other hand, chlorophyll a concentration from filtered fresh phytoplankton cells comprising both diatoms and the smaller-size phytoplankton appeared accountable for its negative correlation with DIN, probably due to rapid uptake and depletion of the nutrients.

The r/K selection theory was applied to tintinnid and aloricate ciliates by Margalef (1982) to explain their adaptation strategies, but he did not provide experimental or field data to show that tintinnids grow more slowly than aloricate ciliates. However, the growth rates of ciliates tend to decrease with larger body size, but increase with higher temperature and a favourable environment (Müller & Geller 1993). If we assumed that the drier SW monsoon offers less favourable conditions for ciliate growth such as lower DIN, the larger loricate tintinnids would represent K-adapted species since they accumulate their biomass (or abundance) slowly but persistently at low nutrient concentrations, while expending substantial energy on lorica building (Dolan et al. 2013b). On the other hand, the aloricate ciliates represent the r-adapted species since they are smaller, and reproduce and grow rapidly when the environment is favourable, such as in the NE monsoon (Figure 4). Nonetheless, our study could not provide direct evidence of the higher growth rates of aloricate ciliates except by proxy, i.e. their high abundance. Thus, more studies on how size and environment affect ciliate reproduction and growth are required to verify the hypothesized r/K adaptive strategies in small and large ciliates.

**Conclusion**

Microzooplankton were diverse and numerically very abundant in the Matang estuary compared with similar studies in tropical estuaries (Godhantaraman 2002; Jyothibabu et al. 2008a, 2008b; Sarkar 2015). Shifts in microzooplankton community structure between monsoons are apparently associated with rainfall, salinity, temperature, DIN and microbial food concentrations. Lower rainfall and higher chlorophyll a concentration during the SW monsoon favoured the loricate ciliates. With the increase in rainfall and dissolved inorganic nutrients during the NE monsoon, aloricate ciliates then dominate. Except for a few taxa, a lunar phase which affects the strength of tidal current (neap and spring tide) has no effect on microzooplankton abundance. Given their high abundance, it is likely that Matang’s microzooplankton channels substantial trophic energy to higher trophic levels.

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