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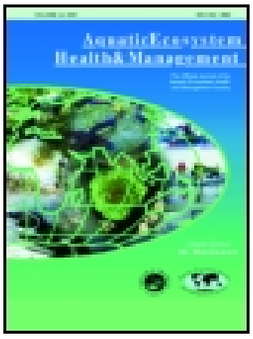

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# Diel patterns of Zooplankton community structure in nearshore waters of different substrates off Tinggi and Sibu Islands, Malaysia, with special reference to Copepods

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**Abstract**

The relationship between Zooplankton community structure and selected environmental conditions was investigated by simultaneous two-day consecutive sampling in the waters overlying Coral and sand sites off Sibu Island and a Seagrass site off Tinggi Island, Johor, Malaysia. A total of 129 taxa were identified, 60 non-copepod taxa and 69 copepod species in all samples. Uni- and multi-variate analyses reveal distinct Coral, sand, Seagrass copepod assemblages with indicator copepod species and attributes of their size fractions. Small fraction (100–335 µm) samples contained greatest number of individuals, few rare species and were densest at onshore depths, and the opposite for large fraction (>335 µm) samples but were densest at nighttime and most species rich in the Coral site at night. Higher species diversity at offshore stations is due likely to ecotonal effects of overlapping oceanic and nearshore communities. This study demonstrates the usefulness of uni- and multi-variate analyses in identifying patterns in Zooplankton community structure in representative shallow tropical habitats, and the need for accurate Zooplankton taxonomy, nighttime and daytime and onshore and offshore sampling, and size fractionation of samples.

***Keywords:*** community ecology, Copepod species, tropical, Coral reef, Seagrass



**Introduction**

Coral and Seagrass habitats represent important ecosystems in tropical coastal waters in terms of both biodiversity and biological production (Costanza et al., 1997; Reaka et al., 2008). In particular, those in Southeast Asia represent biodiversity pinnacles in the global ocean but are threatened by activities destructive to biodiversity (Roberts et al., 2002; Tittensor et al., 2010; Sanciangco et al., 2013) and by

global climate change (Burrows et al., 2011), necessitating knowledge on the current status of these ecosystems.

Zooplankton are ecological indicators (Soule, 1988; Richardson and Schoeman, 2004) and indispensable trophic links of Coral and Seagrass ecosystems (Heidelberg et al., 2004; Nakajima et al., 2014). However, the structure and function of Zooplankton communities in these habitats in Southeast Asia have been poorly investigated. Previous studies on Coral-reef Zooplankton revealed that species diversity peaks in Coral habitats (e.g., Heidelberg et al., 2004; Alldredge and King, 2009) but small invertebrates in tropical Seagrass habitats are often neglected (Blackmon and Valentine, 2013). Although tropical reef Zooplankton are known to display diel vertical migration and show affinities with specific substrates (Alldredge and King, 1977; Porter and Porter, 1977; Hamner and Carlton, 1979), and near reef and open water zones (Sale et al., 1976; Alvarez-Cadena, 1998; Carleton et al., 2001; Webber et al., 2005), knowledge on the relationships between environmental conditions and Zooplankton community structure at small spatial and temporal scales is limited (e.g., McKinnon et al., 2003; McKinnon et al., 2005; Carassou et al., 2010).

Located in the South China Sea, off the coast of Peninsular Malaysia, Tinggi and Sibu Islands encompass a unique combination of Coral and Seagrass habitats intervened by sandy beaches with minimal influence of river waters, thus providing an interesting setting to compare Zooplankton communities between these habitats. Both islands are part of the Pulau Tinggi group of islands declared as a Marine Park in 1994 under the Fisheries Act of 1985 and directly under the authority of the Department of Marine Parks, Malaysia (Ooi et al., 2011).

This study aims at analyzing small-scale Zooplankton community structure from Coral, sand and Seagrass habitats in Tinggi and Sibu Islands, Malaysia through a simultaneous and straight two-day collection. This study was specifically conducted to: (1) identify and quantify Zooplankton abundance, particularly focusing on copepod species, from small and large size fractions of samples that make up the assemblages from Coral, Seagrass and sand substrates; (2) analyze the relationship of selected environmental factors on

the structure of Zooplankton communities using univariate and multivariate ordination techniques; and (3) identify possible indicator copepod species and assemblages among different tropical nearshore substrates.

## Materials and Methods

### Study sites

This study was carried out at the neighboring Tinggi (2° 18.48' to 2° 18.49' N, 104° 5.62' to 104° 5.60' E) and Sibu Islands (2° 13.89' to 2° 13.49' N, 104° 03.64' to 104° 04.04' E), Malaysia, located 10.5-12.1 km off the east coast of the Malaysian Peninsula and southwest of the South China Sea (Fig. 1). Coral and sand sites were situated on the northeastern coast of Sibu Island while the Seagrass site was on the northwestern coast of Tinggi Island. Seven km apart, these islands form typical fringing Coral reefs dominated by *Acropora*, *Porites* and *Montipora* Corals with mean live coverage of 34.5% for Tinggi Island (Harborne et al. 2000), and 33.8% for Sibu Island (Toda et al., 2007). Inhabited by seven species with *Halophila ovalis* and *Halodule uninervis* as dominants, healthy and abundant Seagrass beds are found concentrated at the western nearshore waters off Tinggi Island (Ooi et al., 2011).

### Sampling

Environmental parameters and Zooplankton were sampled on 15-16 October 2008. At each site, one onshore station 50 m away from and perpendicular to the shore and another offshore station aligned with the onshore station were sampled for two consecutive days three times both day (1000, 1200, 1400 hrs) and night (1900, 2100, 2300 hrs). In order to keep a uniform depth of about 8 m, the Seagrass, Coral and sand offshore stations were respectively located 100 m, 200 m and 200 m away from the onshore station (Fig. 1). All sites were sampled simultaneously using three boats to remove bias due to sampling time. A conical plankton net (mouth diameter, 30 cm; mesh aperture, 100 µm (Turner, 2004; McKinnon et al.,

2013) was hand-towed vertically from 1 m above the bottom to the surface. Total volume ($m^3$) filtered by the plankton net for all samples were comparable for Coral, Seagrass and sand sites with mean (± SD) values of 1.01± 0.58, 0.84 ± 0.36, and 1.09 ± 0.41, respectively. At each sampling occasion three to five tows were made and all captured Zooplankton were combined to comprise a composite sample which was fractionated into small (100-335 □m) and large (>335 □m) fractions using a 335 □m-mesh sieve. Each of these fractions was then split equally into two sub-samples by repeated mixing and pouring of the original sample into two vials to obtain the same volume. Only one of these sub-samples was examined for the present analysis. All these samples were preserved in 5% formalin seawater buffered with sodium tetraborate. The volume of water filtered through the net was determined using a non-reversing flow meter (Rigo-sha Co. Ltd.). At the first and last sampling occasions of both day and night, temperature, salinity, and dissolved oxygen (DO) were measured at 1-m interval from the surface to the bottom using portable underwater sensors (YSI model EXO1). Current patterns around Tinggi and Sibu Islands were determined using a downward-facing 1MHz AWAC (Acoustic Wave and Current Meter) from Nortek (USA). The AWAC was deployed on 15-16 October 2008 along four equidistant transect lines perpendicular to the shore (Appendix A in the online supplemental information). A 2-L water sample was taken for chlorophyll *a* from subsurface and 4-m depth and measured following Strickland and Parsons (1968). In the laboratory, aliqouts were taken from each of the 1/2 sub-samples with a Stempel pipette, and metazoan Zooplankton were enumerated for higher taxonomic groups to reach a total count of 500 individuals, except for samples that contained few specimens wherein the entire sample was enumerated. Adult copepods were identified to species, while immature copepodids were identified only to the genus or higher levels.



**Data analyses**

The analysis at the higher taxonomic levels was performed for all metazoan Zooplankton, while those at the species level were done only on the adult copepods. Copepod species community parameters,

Shannon-Wiener diversity index (*H'*), Pielou's evenness index (*J'*), and number of species, were calculated in a given sample using PRIMER version 5 (Clarke and Warwick, 2001). To ensure normality and homogeneity of data, all values were square-root-transformed and subjected to Levene's test, respectively (Clarke and Warwick, 2001). If these tests failed, instead of the parametric ANOVA (*F* test), the nonparametric analysis of variance (Kruskal-Wallis *H* test) and comparison of means (Mann-Whitney *U* test) were used to analyze statistical variations of parameters between site, station, day, time, and depth using the software SPSS ver. 11 (SPSS, 2002).

*Indicator copepod species and assemblage*

The indicator value method was used to identify copepod indicator species and species assemblages characterizing groups of samples and/or sites (Dufrene and Legendre, 1997). It combines a species relative abundance (expressed here as individuals $m^{-3}$) with its relative frequency of occurrence in the various groups of sites. The indicator value index (% $IndVal_{ij}$) is maximum when all individuals of a species are found in a single group of sites and when the species occurs in all sites of that group. The procedure and formula to calculate the indicator value index are provided by Dufrene and Legendre (1997). A threshold value of 25% was set for a species to be considered an indicator (Dufrene and Legendre, 1997). This value supposes that a characteristic species is present in at least 50% of one site group and that its relative abundance in that group reaches at least 50%.

*Multivariate analysis*

The relationships among Zooplankton taxa distribution and abundance (individuals $m^{-3}$) and environmental variables (time, depth, temperature, salinity, dissolved oxygen, chlorophyll *a*) were investigated using the canonical correspondence analysis (CCA) with built-in Pearson correlation analysis available in the software Canonical Community Ordination (CANOCO) vers. 4.5 (Ter Braak and Šmilauer, 2002). Constraints of environmental variables were removed which ensured that confounding effects of noise did not affect the analysis (McCune, 1997). Zooplankton and environmental data were log

(x+1)-transformed. The correlation between Zooplankton and environmental variables was evaluated using Monte Carlo permutation available in the same CANOCO software.

## Results

### Environmental parameters

Currents (0.1-0.5 $ms^{-1}$), primarily tidal, moving along the southeast-northwest axis dominated the sites during sampling (Appendix A). Current direction reflects slightly stronger ebbing (0.1-0.5 $ms^{-1}$) than flooding (0.1-0.3 $ms^{-1}$) tidal currents (Appendix A). Depths were similar between sampling times ($H$ = 6.08, $p > 0.10$), but onshore stations were shallower by 1-3 m compared to offshore stations with a mean depth of 8 m with shallowest mean depth of 3 m recorded in the Seagrass onshore site (Appendix B in the online supplemental information). Temperature varied little across depths justifying averaging (Appendix B), and average temperature varied significantly between sites ($H$ = 168.46, $p < 0.001$) and time ($H$ = 87.78, $p < 0.001$) but not between stations ($H$ = 0.36, $p > 0.55$). Temperature (29.8-31.2$^{o}$C) slightly elevated at the sandy site during daytime compared to the other sites. Salinity data were also vertically averaged as prompted by very low variation (Appendix B), and mean salinity values varied between sites ($H$ = 195.23, $p < 0.001$) but not between stations ($U$ = 3.39, $p > 0.34$) and time ($H$ = 5.54, $p > 0.13$). Highest salinity values (33.8-34.2) were obtained from the sand site. The vertically-averaged dissolved oxygen values varied significantly between sites ($H$ = 26.04, $p < 0.001$) and time ($H$ = 35.33, $p < 0.001$), but were similar between inshore and offshore stations ($U$ = 1.27, $p > 0.25$) (Appendix B). This was due to the widest range of dissolved oxygen values (5.32- 9.52 mg $L^{-1}$) at the Seagrass site. Ranging from 0.02-1.46 □g $L^{-1}$, chlorophyll *a* values were similar among site ($H$ = 3.39, $p > 0.18$), and between station ($U$ = 77, $p > 0.34$), and time ($U$ = 80, $p > 0.80$) (Appendix B).

Zooplankton abundance: spatial and temporal patterns

Overall, a total of 129 taxa were identified comprising 69 copepod species and 60 non-copepod taxa (Table 1; Appendices D and E in the online supplemental information). Copepod larvae (Nauplii and Copepodids I-V) dominated the small-fraction samples with appendicularians, *Oithona nana*, Molluscan veligers and *Parvocalanus elegans* as other most abundant (>7%) taxa (Table 1). Total density (individuals $m^{-3}$) of the small-fraction Zooplankton was four-fold higher than the large-fraction Zooplankton. Similarly, copepod copepodids, nauplii and adults (C6), and the harpacticoid *Metis* sp. outranked other dominant holoplankton (chaetognaths and appendicularians) and meroplankton (echinoderm, polychaete and cirripede larvae) in large-fraction samples (Table 1).

Due to the large variation, there was no distinct temporal trend of the total small and large fraction Zooplankton abundance at different sites and stations (Fig. 2). In contrast, the level of abundance differed significantly between sites ($H$ = 223.2, df = 2, $p < 0.001$), with smaller values in Seagrass than other sites ($U > 39516.0$, $p < 0.0001$ for all comparisons) for small fraction, and smaller values in Coral than other sites for larger fraction ($U > 118500.0$, $p < 0.0001$ for all comparisons) (Fig. 2). These indicate that large Zooplankton dominate in the Seagrass than in other sites. The dominance pattern in the smaller fractions differed markedly from those of the larger fractions, and showed a relative increase of copepodids, followed by nauplii, at the Coral and sandy sites, but much lower abundance of copepods at the Seagrass site ($H$ = 611.7, $p < 0.001$) (Fig. 3A). In contrast to the total Zooplankton, higher taxa of the larger fractions showed distinct temporal patterns in some sites (Fig. 3B). While copepods dominated at all sites, its dominance differed significantly between sites, with highest abundance in the Seagrass site. A swarm of the harpacticoid copepod *Metis* sp., was recorded in the sand and Coral sites at daytime in both onshore and offshore stations with marked decreases at particular times of the first night. In the Seagrass site, there was a marked increase of copepods at night and a pulse of echinoderm larvae (ophiuroid) both in the onshore and offshore stations (Fig. 3B). Dominant small fraction copepod species (*e.g. Oithona nana*, *Parvocalanus elegans*, *Oithona simplex*) and large fraction calanoid *Acrocalanus gibber* are abundant 24 hours and showed no clear diel patterns ($H$ = 0.10-0.23, df = 5, $p > 0.63$ for the four species). In contrast,

the calanoid copepod *Calanopia aurivilli* was essentially restricted in the Coral and sandy-bottom sites, with negligible occurrence in the Seagrass site, and showed high abundances at night.

Community structure of copepod species

Copepods were the most numerous component in both small (30-35%) and large (67-75%) fraction of bulk Zooplankton samples. A total of 69 copepod species were identified in combined small and large fraction samples. In total, 24 species belonged to the small fraction samples (Appendix D), and 21 of these were also found in the large that comprised 66 species (Appendix E). For small size fraction, the ranges of the number of species per sample were 6-13, 3-12, and 6-15 for the Coral, Seagrass and sand sites, respectively. *Oithona simplex*, *O. nana*, and *Parvocalanus elegans* numerically dominated in all sites, and these three species alone contributed 80% of the total abundance. In contrast, large size fraction samples had more species per sample, except for two samples from the Coral site and one sample from the Seagrass site. Three samples had exceptionally numerous species, specifically *Metis* sp. (2826 inds $m^{-3}$) for onshore day samples, *Calanopia aurivilli* (271 inds. $m^{-3}$) for night samples from the Coral site, and *Microsetella norvegica* (850 inds $m^{-3}$) from the onshore Seagrass samples collected at daytime. The Coral site had the widest range of species number per sample (7-29), followed by the sand site (9-25), and thirdly by the Seagrass site (7-23) Varied among sites and sampling time, the top three species (Coral site: *Acrocalanus gibber*, *Parvocalanus crassirostris*, *Calanopia aurivilli*; sand site: *P. aculeatus*, *Oncaea conifer*, *Calanopia aurivilli*; Seagrass site: *Microsetella norvegica*, *Oncaea conifer*, *Oithona simplex*) constituted 25-55% of the total assemblage.

For small and large fraction copepod samples, Pielou's evenness index *J'* were similar among sites ($F$ = 1.18, $p > 0.05$), and between offshore and onshore stations ($F$ = 1.68, $p > 0.05$), and between sampling times ($F$ = 0.24, $p > 0.62$) (Appendix C). Mean values of *J'* range from 0.56 to 0.97. However, for small fraction samples, mean values of species richness ($S$) ($F$ = 77.79, $p < 0.001$) and Shannon diversity index, $H'$ ($F$ = 29.45, $p < 0.001$) were lower ($S$ = 5.0 to 11.0; $H'$ = 1 to 1.7) in the Seagrass site than those similar

values in Coral ($S$ = 8.7 to 12.2; $H'$ =1.5 to 1.8) and sand sites ($S$ = 9.7 to 12; $H'$ = 1.6 to 1.8). Offshore stations were more species rich (mean $S$ = 9.3 to 12) ($F$ = 14.03, $p < 0.001$) and diverse (mean $H'$ = 1.4 to 1.8) ($F$ = 23.47, $p < 0.001$) than those in onshore stations, but mean $S$ ($F$ = 3.08, $p > 0.05$) and $H'$ values did not differ significantly between day ($S$ = 1.0 to 1.8) and night ($H'$ = 1.4 to 1.7) samples ($F$ = 1.50, $p >$ 0.22). For large fraction copepods, mean values were higher in Coral ($S$ = 14.0 to 28.3; $H'$ = 1.8 to 2.8) and sand ($S$ =19 to 32; $H'$ =2.2 to 2.8) sites than in Seagrass ($S$ = 7 to 29; $H'$ = 1.5 to 2.5) sites for $S$ ($F$ = 4.31, $p < 0.05$) and the diversity index $H'$ ($F$ = 18.31, $p < 0.001$). Offshore stations showed higher mean values ($S$ = 14 to 30; $H'$ = 2.3 to 2.8) of $S$ ($F$ = 10.96, $p < 0.01$) and $H'$ ($F$ = 4.56, $p < 0.05$) than those in onshore stations ($S$ = 7 to 32; $H'$ = 1.5 to 2.6). Species richness ($F$ = 8.01, $p < 0.01$) and $H'$ diversity ($F$ = 7.85, $p < 0.01$) were lower at daytime ($S$ = 7 to 30; $H'$ = 1.5 to 2.7) than at nighttime ($S$ = 7 to 32; $H'$ = 2.2 to 2.8) samples.

Copepod indicator species and assemblage of species

Six groups, two in each site, were analyzed for the indicator species and assemblage of species for both small and large fraction samples (Table 2). Since small fraction copepod abundance was similar regardless of sampling time (day VS night), samples were grouped according to inshore (Group 1a) and offshore (Group 1b) stations for each site, but for large fraction samples, since abundances were similar regardless of the sampling station, the grouping for each site was based on day (Group1a) and night (Group 1b) sampling times. The groupings are based on the output groupings from CCA (Figs. 5A, B). For the small fraction samples, seven species topped by *Oncaea* spp. were indicators for Coral inshore sites and only *Parvocalanus crassirostris* for the Coral offshore site (Table 2). The only indicator species for the Seagrass inshore site was *Oithona decipiens*, but two species (*Kelleria* sp. and *Pseudocyclops* sp.) were indicators for the Seagrass offshore site. Seven species topped by *Parvocalanus elegans* were indicators for sand onshore site, and the top species *Paracalanus parvus* and nine other species for the offshore site. For the large fraction samples, *Oithona simplex* (with the highest indicator value of 84%)

and seven others were indicators for night samples at the Seagrass site (Table 2). Harpacticoid copepods *Microsetella norvegica* and *Macrosetella gracilis* were best indicators for the Seagrass day samples. *Metis* sp. and five others comprised the best indicators for day Coral samples, while for the Coral night samples *Calanopia aurivilli* was the top and only species. Nine for day samples and six for night characterized the sand site with *Paracalanus aculeatus* and *Microsetella rosea* topping the day and night sand samples, respectively.

Ordination of Zooplankton and environmental variables

The CCA triplot of taxa, samples and environmental variables for the small fraction Zooplankton is presented in Fig 4A. All four ordination axes had a low 0.084 total eigenvalue which suggests that the two statistically significant environmental variables (by Monte Carlo permutation test: dissolved oxygen [$F = 3.31$, $p < 0.01$] and depth [$F = 1.79$, $p < 0.01$]; correlation coefficients with the first ordination axis: dissolved oxygen [$r = -0.65$], depth [$r = -0.40$]) explained little variation of Zooplankton abundance. However, these CCA axes determined an abundance gradient of denser Zooplankton (e.g., *Oithona simplex*, *O. nana*, *Parvocalanus elegans*, Copepoda nauplii and copepodids) at inshore than offshore sampling depth where distinct Seagrass site samples were formed as against overlapping Coral and sand samples. Polychaete larvae were also characteristic in Seagrass samples while *Corycaeus* spp. and *Oncaea* spp. in sand and Coral samples. In contrast, all four CCA ordination axes (Fig 4 B) explained a high 34.3% of the variation of large fraction Zooplankton abundance, which had significant correspondence with dissolved oxygen ($F = 4.88$, $p < 0.01$), time ($F = 3.70$, $p < 0.01$), and salinity ($F = 3.49$, $p < 0.01$) by Monte Carlo permutation test. The first ordination axis had the highest correlation with dissolved oxygen ($r = -0.85$) while the second with time ($r = -0.68$) and salinity ($r = -0.58$). Distinct groupings of samples into sites were formed, but within a site, echinoderm larvae, *Metis* sp., and chaetognaths and appendicularians were most common in Seagrass, Coral, and sand samples, respectively, during day sampling (Fig 4 B).

## Discussion

### Spatial and temporal patterns in Zooplankton community structure

Multivariate CCA aided this study in the identification of distinct communities of Seagrass, sand and Coral Zooplankton for small and large size fractions of samples over diel periods. The diel patterns reported in this study might be different in other seasons, but we do not expect great changes either, since seasonal changes are relatively minimal in the tropics compared to those in the temperate areas (Heidelberg et al., 2004; McKinnon et al., 2013). The present results inevitably involve uncertainties, due to the limitations of horizontal and longer term (e.g., seasonal) coverage. However, we believe that our study provides the first comprehensive dataset on the community structure of Zooplankton in different tropical habitats within a relatively short sampling period.

Although variability was low, the overall abundance of small Zooplankton was higher in onshore than offshore stations, and this is supported by the combined statistically significant correlation with depth and dissolved oxygen (DO) and the abundance of small Zooplankton. However, the short-term low values of DO in the Seagrass site at Tinggi Island may not be an important Zooplankton structuring force as these values are within normal limits that can go down up to 2 mg $L^{-1}$ in tropical Seagrass beds (Yarbro and Carlson, 2008). Copepod predation at the Seagrass site may be relevant in explaining the low abundance (Horinouchi et al., 2012), but we lack direct evidence on the impact of predation on small fraction copepods.

We found that small copepods were an order of magnitude higher in abundance than large copepods. This is in agreement with findings in other similar studies in the tropics (Hopcroft et al., 1998; Hopcroft et al., 2001; McKinnon et al., 2003; Heidelberg et al., 2004; Turner, 2004; Nakajima et al., 2008; Chew and Chong, 2011). However, this study differs from the previous ones because we report here two egg-carrying copepod species *Oithona simplex*, *O. nana* and a free-spawner *Parvocalanus elegans* that

dominated small fraction samples, and presumably the dominant copepod nauplii and copepodites were of these species. Amongst the possible biological explanations for the much higher density of small copepods are their long spawning period of the adults and heavy predation on the adult stages (Kiorboe and Sabatini, 1994), higher rates of reproduction of tropical small body size as against large body size copepod species (Hopcroft et al., 2001), and a high efficiency at converting primary production and protoZooplankton into biomass of small-sized copepod species (McKinnon et al., 2013).

Differences in Zooplankton abundance among sites were discerned among large fraction samples. Overall, total abundance in the Seagrass habitats was highest, intermediate in the sand site, and lowest in the Coral site. However, abundance was comparable in onshore and offshore stations in all three sites. The CCA identified a combination of sampling time, salinity and DO as the major environmental parameters explaining the observed patterns of Zooplankton distribution. We invoke the same reasoning used to explain the statistically significant correlation of DO with the abundance of small fraction Zooplankton. Also the slightly higher salinity values in the sandy bottom site may not be a dominant structuring force in Zooplankton. Sampling time, however, is widely reported to influence Zooplankton community structure. For instance, except for the daytime increase of Molluscan larvae in small and large fraction samples and of echinoderm larvae and the harpacticoid Copepod *Metis* sp., the rest of the small fraction taxa (mainly copepods) did not show marked diel change in abundance, suggesting that the Zooplankton assemblages in these sites are mixtures of species with diversely different temporal trends. However, the large fraction Zooplankton did show a relative nighttime increase in abundance in the major groups, which could be attributed to the effect of DVM that seems to vary among sites. For example, *Calanopia aurivilli* seems to emerge at night earliest in the sand site and much later in the Coral site. This is consistent with those reported by Nakajima et al. (2008, 2009) on diel patterns of Zooplankton in fringing reefs close to our study sites. Nighttime abundance peaks of large fraction Zooplankton may be due mainly to behaviourally driven emergence (Blackmon and Valentine, 2013) or may not be purely due to local DVM but by horizontal advection from offshore pelagic sites (Nakajima et al., 2009).

We assume that distance would not be a serious source of bias in the present analysis because the present three habitats are in very close proximity (less than 10 km apart) and within an area of similar oceanographic/climatic condition, as shown in the results on environmental parameters, particularly currents that would have enhanced dispersal and mixture of plankton communities among different sites. In fact, the close proximity and similar prevailing hydrodynamics of the Coral and sand sites explain the similar richness and Shannon diversity of both small and large Zooplankton samples. Similar observations have been reported in other tropical studies (e.g., Atayde and Bozelli, 1998; Carlton et al., 2001). This contrasts with the large spatial scale sampling in the Straits of Malacca where the diversity index differed between locations (Rezai et al., 2005). Overall mean diversity in the Seagrass site was lower, but at offshore Seagrass sites we obtained high values comparable to those in Coral and sand sites. However, maximum species richness of large fraction copepod assemblages is obtained if samples are taken at night from Coral substrates both at onshore and offshore stations. In all three sites, all offshore stations yielded more diverse Zooplankton communities. Higher diversity parameters for both large and small fractions at offshore stations could be explained by ecotonal effect of the mixing of offshore and reef plankton or oceanic-neritic affinity which is related to local hydrodynamics, narrowness of the shelf, and wind patterns (Hamner and Hauri, 1981; Alvarez-Cadena et al., 1998; Carlton et al., 2001; Nakajima et al., 2008). The importance of biological interactions in explaining the high Zooplankton diversity at offshore sites is worth investigating. The large fraction Zooplankton data showed the high taxonomic diversity-low abundance relationship found in other studies (e.g., Rezai et al., 2004, 2005). But it is surprising that despite the fewer number of species and significantly higher abundances, the Shannon diversity values in small fraction samples were as high as those in large fraction samples (Clarke and Warwick, 2001). This is explained partly by the higher evenness values (see Appendix C) and partly by higher turnover rates of the small sized species supported by high primary production in coastal waters. This finding implies that size fractionation of samples is very important particularly in the analysis of tropical Zooplankton community structure.

Indicator copepod species and assemblage of species

The identification of indicator species or assemblage of species is important in the ecology, conservation, monitoring and management of biological resources (Dufrene and Legendre, 1997). However, studies using indicator Zooplankton species and assemblages in Coral reefs are rare. In this study, all sites had different top indicator species for the small fraction samples. The indicator assemblage of species had similar composition but the top indicator species varied from one group to another. The top two species for the Coral, Seagrass, and sand sites were *Oncaea* sp. and *Parvocalanus crassirostris*, *Oithona decipiens* and *Kelleria* sp., and *Parvocalanus elegans* and *Paracalanus parvus*, respectively. These may be regarded as site-specific indicator species and assemblage of species. Using the same indicator value index, Tseng et al. (2008) declared *E. acutifrons* and *O. nana* as indicator species in the shelf region of the subtropical East China Sea. McKinnon et al. (2003) noted that *O. attenuata* and *O. nana* are typical species of shallow coastal waters. To our knowledge, this study is one of the first efforts in examining indicator species on a small-scale comparison among Coral, Seagrass and sand substrates. Interestingly, apart from an indicator of the Coral site, *Oncaea* sp. seems to conform to the high abundance of appendicularians at the same site. Oncaeids are reported to feed on phytoplankton and microbes attached on appendicularian houses (McKinnon et al., 2013).

Respective daytime and nighttime indicator species were identified for the large fraction samples, namely, *Metis* sp. and *Calanopia aurivilli* at the Coral site, *Microsetella norvegica* and *Oithona simplex* at the Seagrass site, and *Paracalanus aculeatus* and *Microsetella rosea* at the sand site. *Metis* sp. is a harpacticoid copepod species known to form swarming densities in Coral habitats, and is also known to have close association with benthic invertebrates, such as holothurians (Gilby et al., 2012). Pontellid *Calanopia* species are known nocturnal species that inhabit very close to the bottom in the daytime (e.g. Mulyadi and Ueda, 1996; Cohen and Forward, 2005) and *C. aurivilli* is our identified nocturnal species at the Coral site. *Oithona simplex* were found dominant in Seagrass beds in the Great Barrier Reef (Robertson et al., 1988), but the Seagrass daytime indicator species *Microsetella norvegica* is a

cosmopolitan species which may have been advected to our Seagrass site (Razouls et al., 2013). The largest indicator assemblage of species was recorded in the two-dimensional sand site, but its composition suggests a mix of neritic species, e.g. *Temora turbinata* and *Farranula gibbula* are considered offshore pelagic species (Alvarez-Cadena et al., 1998). Similarly, *Acrocalanus gibber*, *Canthocalanus pauper*, *Cosmocalanus darwini*, *Centropages furcatus*, and *Temora discaudata* are also considered neritic (Hwang et al., 2007).

**Conclusion**

This study underscores the importance of size-fractionation in the analysis of nearshore tropical copepod communities because different size fractions generally differ in community structural properties. Univariate and multivariate approaches are useful in demonstrating that the different microhabitats sampled differed in copepod community structure as shown in large fraction samples. Although both small fraction and large fraction copepod communities appeared to be correlated with DO, depth, time and salinity, other resource dimensions including food, predators, competitors, microscale island and large scale basin-wide hydrodynamics, and most importantly microscale structural complexity may also be relevant. This short term study strengthens the fact that Zooplankton assemblages can differ among tropical nearshore habitats, but highest Zooplankton diversity at population and community levels is found in the most structurally complex Coral substrates. The use of copepod communities in tropical environmental biomonitoring would need accurate copepod taxonomy, nighttime and daytime and onshore and offshore sampling, and univariate and multivariate analytical strategies as outlined in this study.

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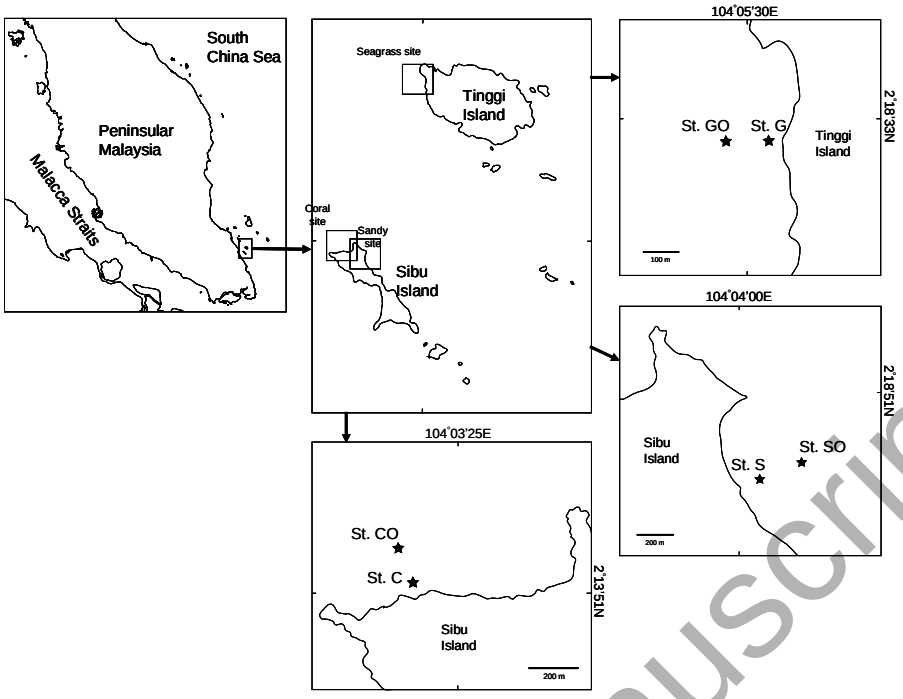



Fig. 1. Location of sampling site and stations in Tinggi Island for the Seagrass substrate, and in Sibu Island for the sand and Coral substrates. St. CO = offshore Coral station, St. C = onshore Coral station; St. SO = offshore sand station, St. S = onshore sand station; St. GO = offshore Seagrass station, St. G = onshore Seagrass station.

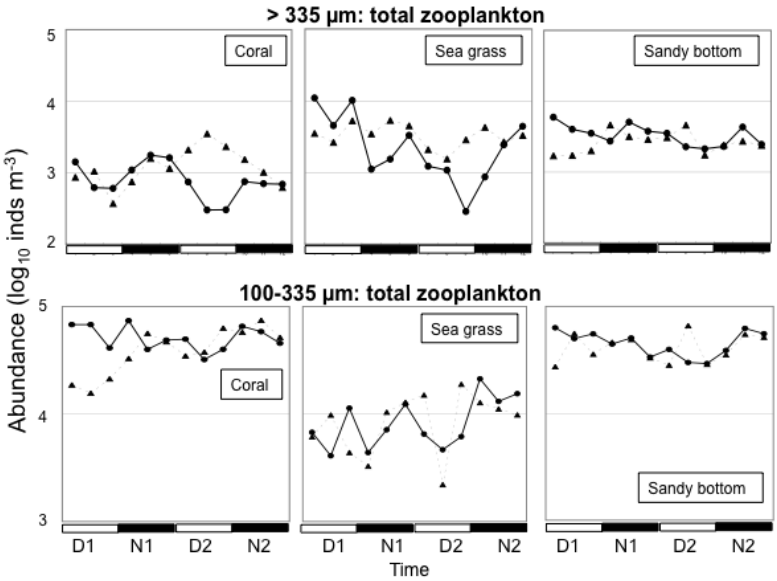
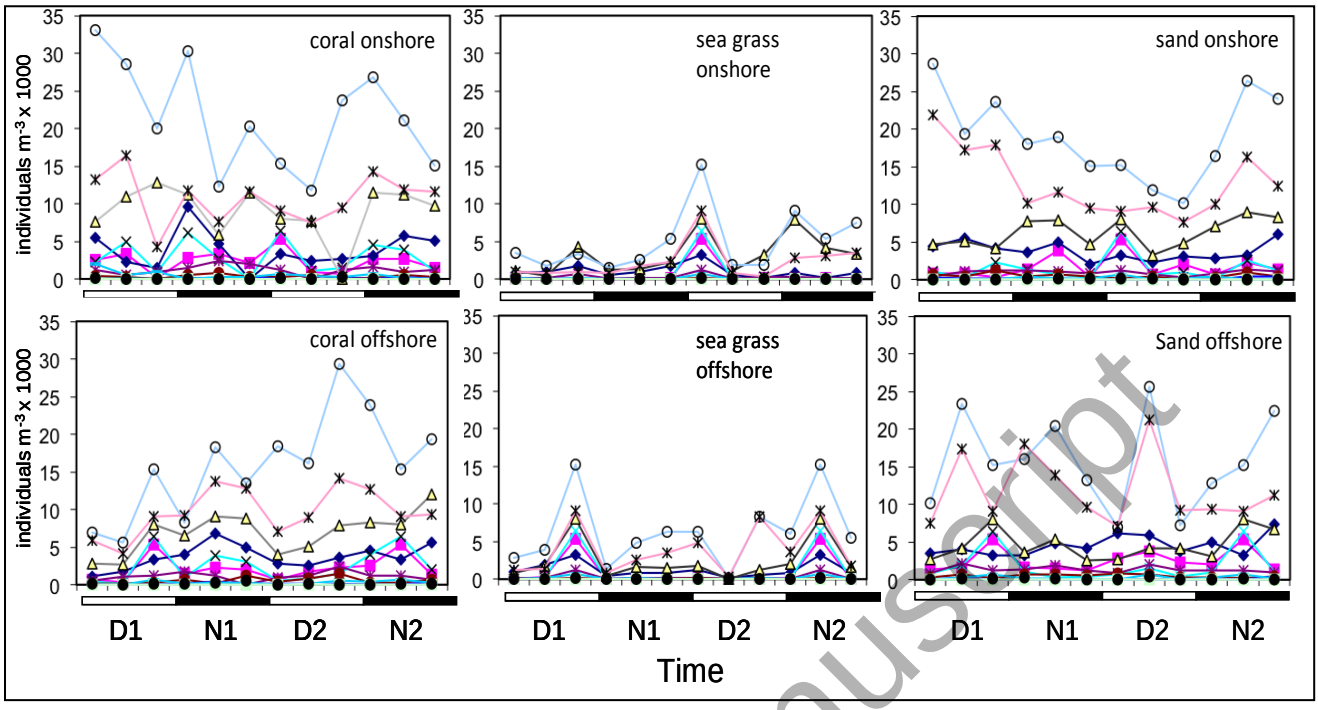



Fig. 2. Temporal (48 hours) patterns of total abundance ($log_{10}$) of small and large fraction Zooplankton taxa from onshore (solid circles) and offshore (solid triangles) stations in Coral, Seagrass, and sandy bottom sites in Tinggi and Sibu Islands, Malaysia. White and black horizontal bars represent daytime (D) and nighttime (N) sampling, respectively.

**(A)**




(B)

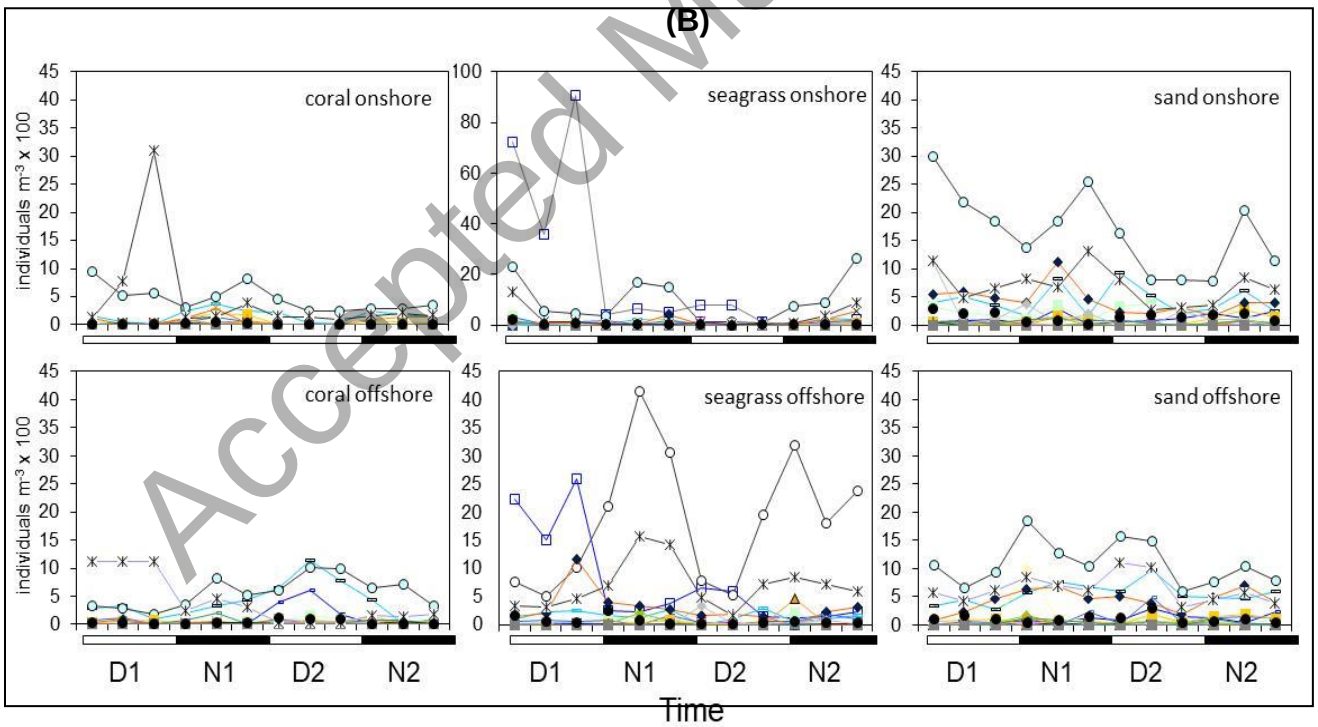
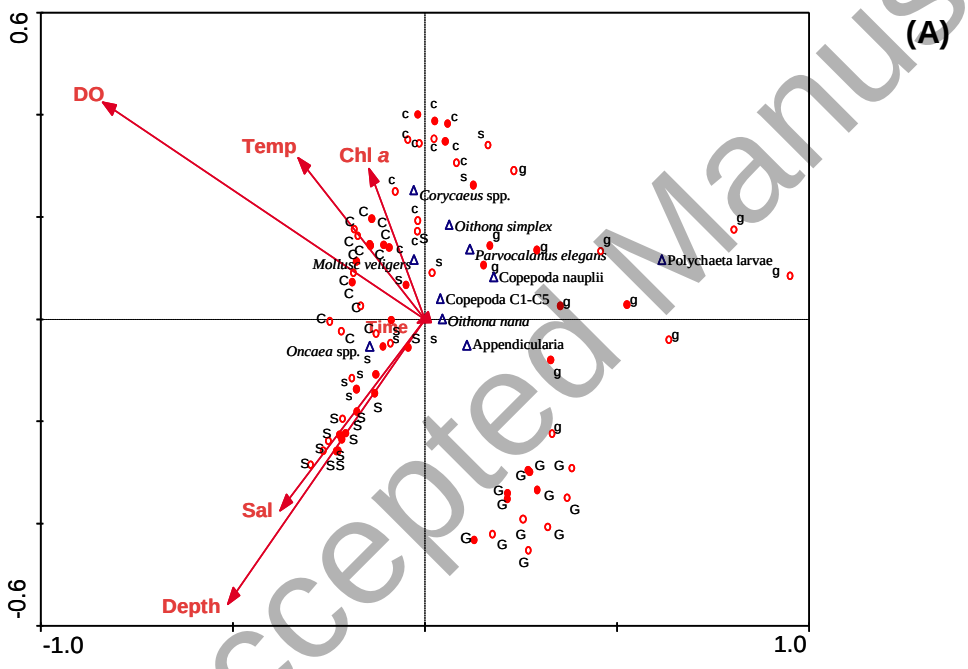


Fig. 3. Temporal (48 hours) patterns of abundance of small (A) and large (B) fractions Zooplankton taxa from onshore and offshore stations in Coral, Seagrass, and sandy bottom sites in Tinggi and Sibu Islands, Malaysia. White and black horizontal bars represent daytime and nighttime sampling, respectively. Small fraction Zooplankton individuals x 1000. Large fraction Zooplankton individuals x 100. Symbols for dominant taxa: – Copepod C1-C5, – adult Copepods, – Copepod nauplii, – appendicularians, – Molluscan veligers, – echinoderm larvae, – Chaetognaths.



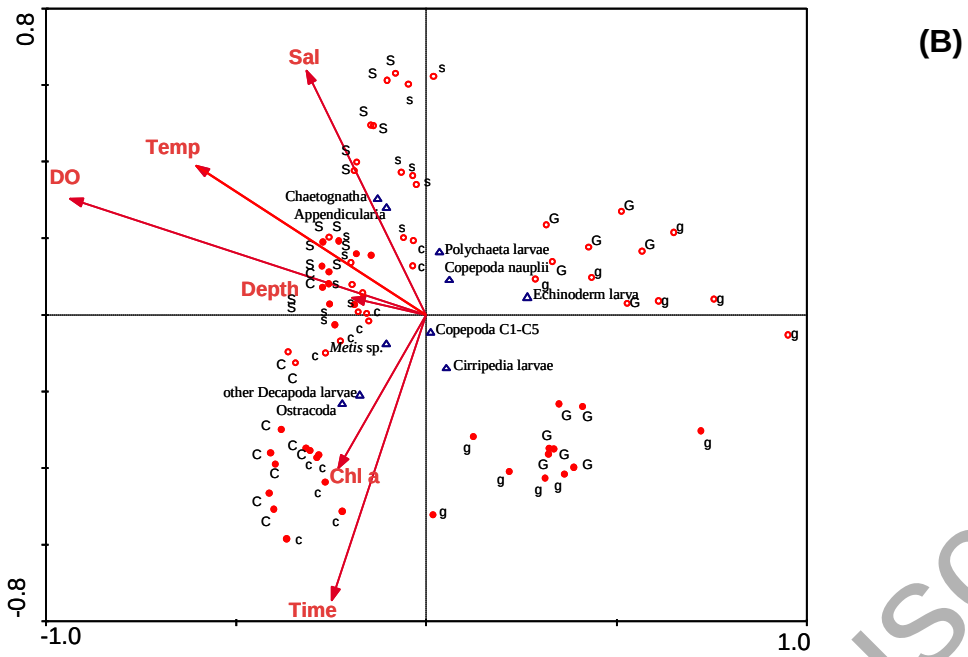



Fig 4. Canonical correspondence analysis triplot of environmental parameters (DO - dissolved oxygen, Depth, Chl a - chlorophyll *a*, Temp - temperature, Time - sampling time, and Sal - salinity), small (A) and large (B) fraction Zooplankton samples from Coral onshore (C) and offshore (c) stations, sand offshore (S) and sand onshore (s) stations and sea grass offshore (G) and onshore (g,) stations collected at daytime (open circles) and nighttime (solid circles). Triangles represent top 10 most abundant taxa.

Table 1. Abundance (individuals $m^{-3}$) and percentage frequency of occurrence of small and large Zooplankton taxa that contributed >2% of overall total abundance.

| **Small Size Fraction (100-335 □m)** | | | **Large Size Fraction (>335 □m)** | | |
|---|---|---|---|---|---|
| Taxon | Abundance | % | Taxon | Abundance | % |
| Copepodites I-V stages | 872511 | 36 | Copepodites I-V stages | 79021 | 33 |
| Copepoda nauplii | 357099 | 15 | Echinoderm larva | 36528 | 15 |
| Appendicularia | 216719 | 9 | Copepoda adults (CVI) | 20031 | 9 |
| *Oithona nana* | 183435 | 8 | Chaetognatha | 21620 | 8 |
| Mollusc veligers | 175967 | 7 | Appendicularia | 16509 | 7 |
| *Parvocalanus elegans* | 174254 | 7 | Copepoda nauplii | 5362 | 2 |
| *Oithona simplex* | 126209 | 5 | Polychaeta larvae | 4919 | 2 |
| Copepoda adults (CVI) | 120368 | 5 | *Metis* sp. | 4263 | 2 |
| Polychaete larvae | 60295 | 2 | Cirriped larvae | 3918 | 2 |

(Other small fraction taxa: harpacticoid copepodids, *Corycaeus* sp., *Microsetella norvegica*, Chaetognatha, *Euterpina acutifrons*, barnacle nauplii/cypris, *Oithona attenuata*, decapod larvae, Ostracoda, *Oithona rigida*, *Metis* sp., Isopoda, *Paracalanus parvus*, *Parvocalanus crassirostris*, *Macrosetella gracilis*, *Acrocalanus gibber*, Harpacticoida spp., *Clytemenestra scutellata*, *Oithona plumifera*, *Kelleria* sp., *Paracalanus aculeatus*, Calanoida spp., Amphipoda, Cladocera, *Oithona decipiens*, *Pseudocyclops* sp., *Sapphirella*-type copepod, *Metacalanus* sp., *Bestiolina similis*. Relative abundance of each taxon is shown in Appendix A)

(Other large fraction taxa: Mollusca veligers, *Microsetella norvegica*, *Oncaea conifera*, *Acrocalanus gibber*, Mysida, *Acartia pacifica*, *Calanopia aurivilli*, *Corycaeus asiaticus*, *Oithona rigida*, *Parvocalanus crassisrostris*, Luciferidae, brachyuran larvae, *Paracalanus aculeatus*, *Oithona simplex*, *Euterpina acutifrons*, *Oithona nana*, Cnidaria, *Oithona plumifera*, *Subeucalanus subcrassus*, *Microsetella rosea*, *Corycaeus crassiusculus*, *Corycaeus erythraeus*, *Centropages furcatus*, Cladocera, *Temora turbinata*, *Macrosetella gracilis*, *Farranula gibbula*, *Canthocalanus pauper*, *Parvocalanus elegans*, Pteropoda, *Metacalanus aurivilli*, other harpacticoid spp., *Temora discaudata*, *Kerellia* spp., *Calanopia elliptica*, *Oithona attenuata*, Amphipoda, *Corycaeus andrewsi*, Cumacea, *Corycaeus* spp., Caridean, fish egg, fish larva, *Farranula concinna*, Isopoda, *Oncaea* spp., cyphonaute larva, *Acartia erythraea*, *Labidocera minuta*. Relative abundance of each taxon is shown in Appendix B)

Table 2. Top ten small and large fraction copepod species ranked using the indicator value (in parentheses) or % $IndVal_{ij}$ index of Dufrene and Legendre (1997). Grouping is defined by CCA as illustrated in Figure 5. Species in bold letters had indicator values ≥ the threshold value of 25%. Abbreviations: *Par*. = *Parvocalanus*; *Mic*. = *Microsetella*; *Mac*. = *Macrosetella*; *Cor*. = *Corycaeus*; *Cly*. = *Clytemenestra*; *Eut*. = *Euterpina*; *Para*. = *Paracalanus*; *Can*. = *Canthocalanus*; **Sapphirella*-type copepod.

| *Small Fraction (Day and Night Time)* | | | | | |
|---|---|---|---|---|---|
| CORAL | | SEAGRASS | | SAND | |
| Group1a | Group1b | Group2a | Group2b | Group3a | Group3b |
| Inshore | Offshore | Inshore | Offshore | Inshore | Offshore |
| Species | Species | Species | Species | Species | Species |
| ***Oncaea* spp. (37)** | ***Par. crassirostris* (25)** | ***Oithona decipiens* (25)** | ***Kelleria* sp. (25)** | ***Par. elegans* (41)** | ***Para. parvus* (52)** |
| ***Corycaeus* spp. (35)** | *Mic. norvegica* | *Oithona* | ***Pseudocyclops*** | ***Oithona simplex*** | ***Mic. norvegica*** |

| | | | | | |
|---|---|---|---|---|---|
| | (20) | *plumifera* (12) | **sp. (25)** | **(35)** | **(42)** |
| ***Mic. norvegica* (33)** | *Corycaeus* spp. *(15)* | *Oithona simplex* (8) | *Oithona plumifera* (15) | ***Oithona nana* (34)** | ***Corycaeus* spp. (41)** |
| ***Oithona attenuata* (30)** | *Oithona nana* (14) | *Oithona nana* (5) | *Acartia pacifica* (13) | ***Eut. acutifrons* (32)** | ***Cly. scuttelata* (35)** |
| ***Oithona nana* (28)** | *Par. elegans* (13) | *Par. elegans* (4) | *Oithona simplex* (11) | ***Oncaea* spp. (26)** | ***Oncaea* spp. (35)** |
| ***Oithona simplex* (27)** | *Oithona simplex* (12) | *Mic. norvegica* (4) | *Mic. norvegica* (10) | ***Corycaeus* spp. (25)** | ***Eut. acutifrons* (32)** |
| ***Par. elegans* (27)** | *Oithona rigida* (12) | *Oncaea* spp. (1) | *Par. elegans* (9) | ***Oithona attenuata* (25)** | ***Oithona nana* (31)** |
| *Oithona rigida* (22) | *Oncaea* spp. (12) | *Sapphirella** (1) | *Mac. gracilis* (9) | *Sapphirella** (22) | ***Oithona rigida* (30)** |
| *Eut. acutifrons* (21) | *Oithona attenuata* (10) | *Corycaeus* spp. (1) | *Oithona nana* (8) | *Metacalanus* sp. (13) | ***Oithona simplex* (26)** |
| *Acrocalanus gibber* (13) | *Eut. acutifrons* (9) | *Oithona attenuata* (1) | *Oncaea* spp. (6) | *Mic. norvegica* (10) | ***Metacalanus* sp. (25)** |

*Large Fraction (Inshore and Offshore Stations)*

| CORAL | | SEAGRASS | | SAND | |
|---|---|---|---|---|---|
| Group1a | Group1b | Group2a | Group2b | Group3a | Group3b |
| Day | Night | Day | Night | Day | Night |
| Species | Species | Species | Species | Species | Species |
| ***Metis* sp. (66)** | ***Calanopia aurivillli* (27)** | ***Mic. norvegica* (49)** | ***Oithona simplex* (84)** | ***Para. aculeatus* (52)** | ***Mic. Rosea* (66)** |
| ***Oncaea* spp. (43)** | *Oithona setigera* (14) | ***Mac. gracilis* (39)** | ***Eut. acutifrons* (53)** | ***Acrocalanus gibber* (45)** | ***Calanopia aurivillli* (48)** |
| ***Cor. lubbocki* (39)** | *Acartia pacfica* (11) | *Oithona plumifera* (22) | ***Kerellia* spp. (49)** | ***Centropages furcatus* (39)** | ***Oithona rigida* (41)** |
| ***Copilia* sp. (25)** | *Calanopia elliptica* (10) | *Acartia pacfica* (18) | ***Oncaea conifera* (36)** | ***Farranula gibbula* (37)** | ***Metacalanus aurivilli* (28)** |
| ***Delius* sp. (25)** | *Anawekia* sp. (7) | *Cor. asiaticus* (14) | ***Mic. norvegica* (33)** | ***Can. pauper* (37)** | ***Acrocalanus gibber* (27)** |

| | | | | | |
|---|---|---|---|---|---|
| ***Tortanus forcipatus* (25)** | *Bestiolina cf. similis* (7) | *Oncaea* spp. (14) | ***Oithona attenuata* (27)** | ***Temora discaudata* (34)** | ***Temora turbinata* (27)** |
| *Cor. andrewsi* (25) | *Calanopia australica* (7) | *Par. crassirostris* (13) | ***Par. crassirostris* (25)** | ***Cor. asiaticus* (33)** | *Calanopia elliptica* (23) |
| *Par. elegans* (18) | *Cor. latus* (7) | *Oithona oculata* (13) | ***Oithona plumifera* (25)** | ***Cor. crassiusculus* (31)** | *Para. aculeatus* (21) |
| *Pseudocyclops* sp. (14) | *Cor. speciosus* (7) | *Eudactylops latipes* (13) | *Oithona nana* (23) | ***Labidocera minuta* (26)** | *Centropages furcatus* (19) |
| *Par, crassirostris* (13) | *Oncaea mediterranea* (7) | *Tortanus barbatus* (13) | *Corycaeus* spp. (20) | *Cor. erythraeus* (24) | *Cor. erythraeus* (19) |