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Diel variation and trophic structure in coral-reef zooplankton of Peninsular Malaysia

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Abstract— Biomass in zooplankton (>100 μm) and particulate organic matter (POM) (0.7–100 μm) was investigated every 3 hours for two days at the fringing reef of Redang and Tioman Island, the east coast of Peninsular Malaysia. The zooplankton was size-fractionated into three fractions (100–200 μm, 200–335 μm, and >335 μm) and POM was divided into two size-fractions (0.7–35 and 35–100 μm). The POM (0.7–100 μm) accounted for more than 95% of the total biomass (POM+zooplankton) in the water column. The largest size fraction (>335 μm) was the most dominant in zooplankton biomass during the two days at both islands. Nocturnal vertical migration also occurred most strongly in the largest size fraction (>335 μm). The biomass of the largest fraction (>335 μm) may be supported by high growth rate in the smaller size zooplankton (100–200 and 200–335 μm) and the large amount of POM (0.7–100 μm). The contribution of phytoplankton biomass was approximately 10% of the POM (0.7–100 μm). The mean C/N ratio of the POM (0.7–100 μm) at Redang and Tioman Islands were 5.9 and 6.6, respectively. Most of the diet of particle-feeders in both study areas would mainly originate from mucus which was produced by corals.

Key words: zooplankton, particulate organic matter (POM), size-fraction, diel variation, trophic structure, coral-reef

Introduction

Coral reef zooplankton is an important trophic link between primary producers and higher trophic levels on reefs, including scleractinian corals and fish (Hobson and Chess 1978, Jacoby and Greenwood 1989, Heidelberg 2004). It has often been assumed that coral reef zooplankton largely came from surrounding oceanic water (Roman et al. 1990). However, coral reefs possess unique assemblages of zooplankton which live in association with the benthic substrate by day and migrate into the water column at night (Sale et al. 1976, Jacoby and Greenwood 1988, Heidelberg 2004). The behavior of the zooplankton dramatically changes total zooplankton densities in the water column between day and night (Roman 1990). This day/night difference makes it difficult to argue on the materials recycling in reef pelagic ecosystem. Densities of zooplankton can be seriously underestimated if based solely on day sampling. For example, in the Gulf of Siam, Thailand, demersal zooplankton density in the water column ranged from 90 inds. m^{-3} by day to 5676 inds. m^{-3} at night (Sorokin 1993). However, quantitative data on variations in the density of coral reef zooplankton with one to several hour intervals are scarce (Ohlhorst 1982, Goswami 1990, Roman et al. 1990, Madhupratap et al. 1991a, Harding 2001). The migration behavior of demersal zooplankton often produces density peaks at various times throughout the night (Ohlhorst 1982, Madhupratap et al. 1991b), sometimes near dusk and down. Thus, investigation with short time intervals allows unambiguous interpretation of variation patterns.

Size-fractioning the zooplankton communities have been widely used as an alternative to taxon-based investigation of abundance/biomass and it has an advantage to simplify a fairly complex community composition (Magnesen 1989). The use of size of zooplankton has been supported by the structure in pelagic communities (Sheldon et al. 1973) and by theoretical considerations (Kerr 1974). Also, ecophysiological rates such as respiration and excretion, and ecological measurements like feeding type and turnover rate are found to be strongly dependent on body size (Fenchel 1974, Banse and Mosher 1980).

The marine tropics can be readily divided into four major biogeographic regions: the Indo-West Pacific (IWP), eastern Pacific (EP), western Atlantic (WA), and eastern Atlantic (EA). Reefs dominate large areas of the IWP and WA, but are limited in their development and diversity in the EP and EA (Paulay 1997). Peninsular Malaysia is located in the IWP, the most diverse and extensive marine biogeographic region on the Earth (Veron 1995, Paulay 1997). For example, in the coral reefs of Malaysia there are more than 50 genera of about 700 species of corals as compared with the Caribbean Sea in the WA that has only 26 genera with less than 100 species. Most of reef zooplankton study has been conducted in the WA (at Caribbean Sea, e.g. Glynn 1973) and EP (for example at GBR, e.g. Alldredge and King 1977, and at French Polynesia, e.g. Charpy and Charpy-Roubaud 1990). Little is known, however, on the reef zooplankton in the IWP, especially in the coral reef of Peninsular Malaysia.

The aims of this study are 1) to clarify characteristics of size-fractionated zooplankton community and 2) to reveal zooplankton contribution to the reef pelagic ecosystem. We also discuss the amount and quality of diet which support the biomass of the zooplankton community in the coral-reef.

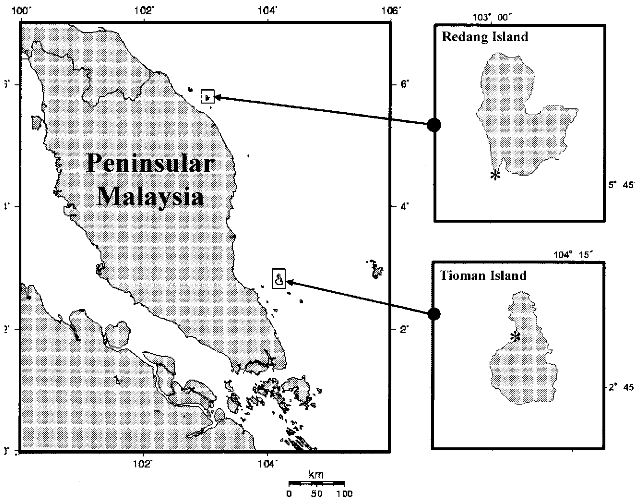

Fig. 1. Location of the sampling sites at Redang and Tioman Island off the east coast of Peninsular Malaysia.

Materials and Methods

Study sites and sampling periods

The two study sites are fringing reefs situated off the east-coast of Peninsular Malaysia: Redang Island (5°47′19″ N; 103°200′49″E) and Tioman Island (2°50′00″N; 104°10′ 00″E) (Fig. 1). The depth of the sampling site ranged between 2.8 to 3.9 m at Redang Island and 6.9 to 11.0 m at Tioman Island. The study periods were 5th to 7th August 2003 at Redang Island and 20th to 22nd October 2003 at Tioman Island. Sampling was conducted every 3 hours for 2 days at a jetty in the Marin Park of the respective islands.

The zooplankton (>100 μm)

Zooplankton was collected by five gentle vertical tows of a 100-μm plankton net (diameter: 30 cm; length: 100 cm) from 1 m above the bottom to the surface. In the present study, we assumed the filtration efficiency of the net to be 100% in all transects since the nets returned to the surface with no evidence of clogging. The filtration volume was calculated from the mouth area of the net and the distance towed. The samples collected were pooled and size-fractionated into three fractions (100–200, 200–335, and >335 μm) by mesh screens of 200 and 335 μm. Then the three fractions were divided into two aliquots with a Folsom plankton splitter. One aliquot was filtered onto a Whatman GF/A filter which was pre-combusted at 500°C for 4 h and pre-weighed for organic content analysis. Another aliquot was fixed with 5% formalin seawater for microscopic observation, and zooplankton was characterized into different groups and counted under a dissecting microscope.

Particulate organic matter (0.7–100 μm)

Water samples were obtained at 1-m depth and 1 m above the bottom each time from the water column with a 10-L Niskin bottle. Depth specific water temperature and salinity were measured. The seawater from the two depths were pre-filtered through a 100-μm mesh screen and later combined to form a 20-L sample for chlorophyll-*a* (Chl.-*a*) and particulate organic matter (POM) (mg C m^{-3}) analysis. 2 L of the seawater was filtered onto a Whatman GF/F filter for Chl.-*a* measurement. The remaining 18 L of seawater was size-fractionated into two fractions (<35 μm and 35–100 μm) by a 35-μm mesh screen. To measure the organic contents of the two fractions, the 35–100 μm sample on the 35-μm mesh screen and 2 L of the <35-μm sample were filtered onto pre-combusted and pre-weighed Whatman GF/A and GF/F filters, respectively.

Chemical analysis

Chl.-*a* concentrations were fluorometrically determined (Suzuki and Ishimaru 1990). The filters for organic content analysis were dried at 60°C for 24 hours in an oven (EYELA NDO-600ND). Measurements of organic carbon and nitrogen were performed with the method described by Hirota and Szyper (1975) and Nagao et al. (2001) using a CHN analyzer (FISON model NA1500NCS), a balance (SARTORIUS MC5) for weighing of samples, and an oven (ISUZU STR-28K) for combustion. To examine the amount of diet for the zooplankton, average POM (0.7–100 μm) concentration during the study period was calculated.

Data analysis

To determine the difference between day and night biomass and density for each fraction, a Mann-Whitney *U*-test was used (Fowler et al. 1998). Cluster analysis was performed on zooplankton abundance in the three size-fractions at both islands. Data were $\log_{10}(X+1)$ transformed prior to analysis, and the results are summarized by dendrograms. Calculations were performed using the SPSS® software.

Results

Environmental conditions

The water temperature was 29.4±0.3°C at Redang Island and 27.3±0.4°C at Tioman Island. The salinity was 32.7±0.8 PSU and 33.9±0.6 PSU at Redang Island and Tioman Island, respectively. Chl.-*a* was 0.62±0.27 mg m^{-3} at Redang Island and 0.36±0.21 mg m^{-3} at Tioman Island.

Mean biomass of size-fractionated zooplankton and POM

Total biomass (POM+zooplankton) in the entire water column was 300.8±45.1 mg C m^{-3} and 234.1±77.4 mg C m^{-3}, at Redang and Tioman Islands, respectively (Table 1). The contribution of each size fraction (0.7–35, 35–100, 100–200, 200–335, and >335 μm) to the total biomass was 74.1, 21.9, 0.9, 1.1 and 2.1% at Redang Island, and 77.5, 19.8, 0.5, 0.6 and 1.5% at Tioman Islands. The biomass of the water column at Redang and Tioman Islands was mainly occupied by the <100 μm fraction at 96.0% and 97.3% of total biomass, respectively. The mean C/N ratio of the POM (0.7–100 μm) was 5.9±2.4 at Redang Island and 6.6±0.8 at Tioman Island during the study periods.

Day/night change in zooplankton biomass

The total biomass (mg C m^{-3}) of zooplankton (>100 μm) in the water column over the coral reef was significantly higher during the night at Redang Island ($p<0.05$), but not at Tioman Island (Fig. 2). At Redang Island, the biomass at night (18.50±9.70 mg C m^{-3}) was on average 3.2 times higher than that during the day (5.75±2.64 mg C m^{-3}).

At Redang Island, the largest fraction (>335 μm) was the most dominant size fraction in the total zooplankton biomass during both day and night, contributing 38±12% and 55±4% to the total zooplankton biomass (>100 μm), respectively (Fig. 3). At Tioman Island, the largest fraction (>335 μm) was also the most dominant size fraction in the total zooplankton biomass during both day and night, contributing 51±10% and 68±7% to the total zooplankton biomass, respectively (Fig. 3).

At Redang Island, the three size fractions increased at night with a 2.4-fold increase in the smallest size fraction (100–200 μm), a 3.0-fold increase in the middle size fraction (200–335 μm), and a 4.1-fold increase in the largest size fraction (>335 μm) ($p<0.01$, $p<0.05$ and $p<0.01$, respectively) (Fig. 2). At Tioman Island, the diel variation appeared most evident in the largest size fraction (>335 μm) where the day/night increase was significant ($p<0.01$) but was less evident in the smaller size fractions (100–200 and 200–335 μm) where the day/night increase was not significant ($p>0.05$) (Fig. 2). During the night, the biomass of the largest fraction (>335 μm) was 1.9-fold of day time biomass.

Table 1. Mean organic carbon contents in different size-fractions of particulate organic matter (POM). Values are in mg C m^{-3}, with percentage of the total in parentheses.

Size-fraction (μm)	Redang Island		Tioman Island	
0.7–35	222.9±31.9	(74.1)	181.5±54.8	(77.5)
35–100	65.7±29.9	(21.9)	46.4±19.9	(19.8)
100–200	2.6±0.9	(0.9)	1.2±0.6	(0.5)
200–335	3.4±1.1	(1.1)	1.4±0.6	(0.6)
>335	6.2±2.1	(2.1)	3.5±1.6	(1.5)
Total	300.8±45.1		234.1±77.4	

Zooplankton abundance and composition

At Redang Island, the diel variation in total zooplankton abundance over the reef was a 3.1-fold increase of zooplankton density at night compared to day (9126±4319 and 2960±1781 inds. m^{-3}, respectively). At Tioman Island, there was no clear difference between day and night and it was a 1.4-fold increase at night in comparison to day (5678±1572, and 4015±1530 inds. m^{-3}, respectively) (Fig. 2). In Redang Island, the maximum day/night differences in abundance in the three fractions (100–200, 200–335, and >335 μm) were remarkable, showing a 7-fold, 96-fold and 81-fold, respectively. In Tioman Island, it was 6.8-fold, 4.3-fold and 9-fold increase, respectively.

The most significant diel change was found for the largest fraction (>335 μm) at both islands. Zooplankton in the largest fraction was of low abundance from the water column during the day (255±232 inds. m^{-3} at Redang Island, and 699±638 inds. m^{-3} at Tioman Island), while at night its density increased by an order of magnitude (1732±963 inds. m^{-3} at Redang Island, and 1361±803 inds. m^{-3} at Tioman Island). All zooplankton fractions at Redang Island increased at night with peak abundances at 21:00 h on both days. However, at Tioman Island the peak abundance occurred at 3:00 h in only the largest fraction (>335 μm) during the study period (Fig. 2).

At both islands, zooplankton community consisted mostly of holoplanktonic taxa (copepods including copepodites, naupliar copepods, ostracods, amphipods, siphonophores, chaetognaths, and appendicularians) and a few meroplanktonic groups (e.g. echinoderm larvae, polychaetes) (Fig. 4). The smallest fraction (100–200 μm) mainly consisted of naupliar copepods and copepods at both islands which occupied about 99% of the total number. In the middle fraction (200–335 μm), copepods were the most abundant organisms (72%) at Redang Island. Naupliar copepods accounted for 17% of the total number, 5% and 4% being appendicularians and chaetognaths, respectively. At Tioman Island, copepods were the dominant taxon, constituting 51% of the 200–300 μm fraction followed by naupliar copepods (41%). Ap-

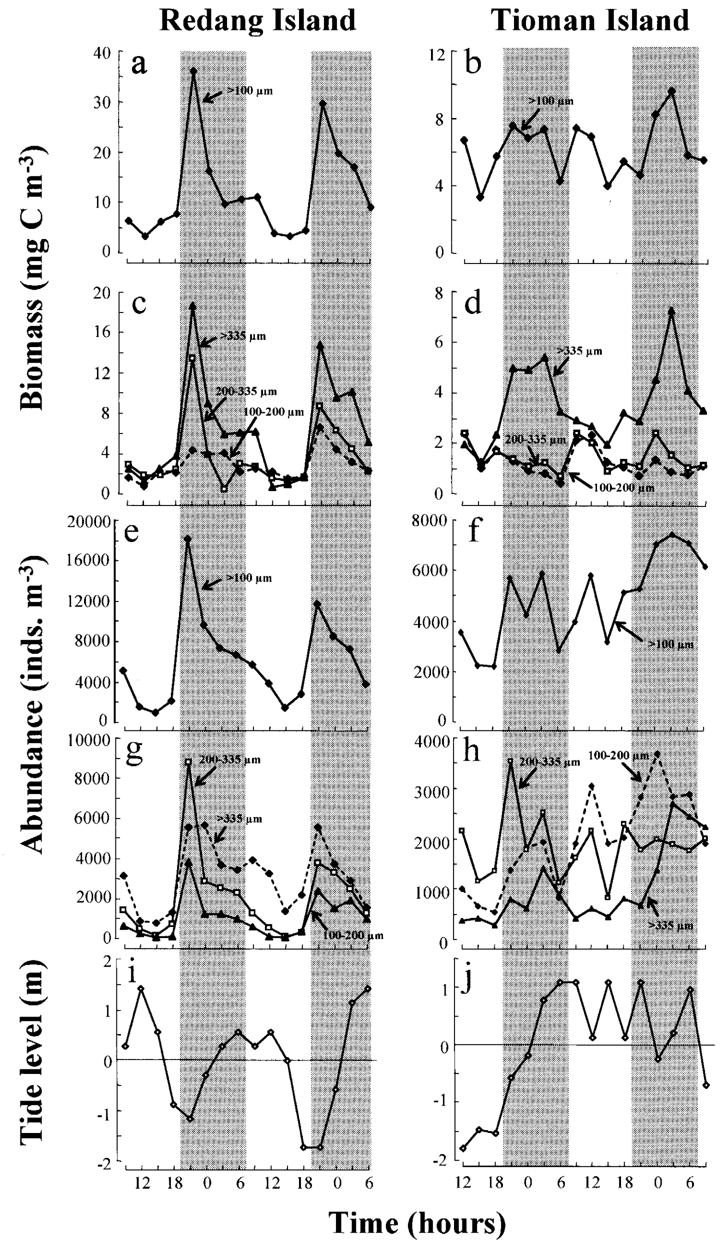

Fig. 2. Diel variation of biomass and abundance in total zooplankton (a, b, e, f) and size-fractionated zooplankton (c, d, g, h) during the two days at Redang and Tioman Islands. Black bars indicate hours of night.

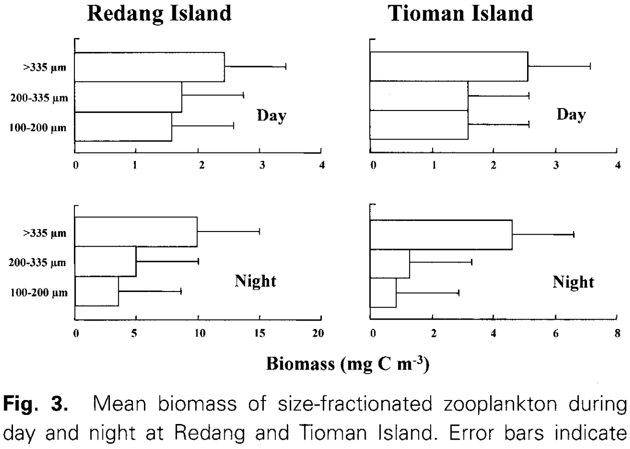

Fig. 3. Mean biomass of size-fractionated zooplankton during day and night at Redang and Tioman Island. Error bars indicate the standard deviation.

pendicularians and chaetognaths accounted for 3% and 1%, respectively. In the largest fraction (>335 μm), copepods were the dominant taxon at Redang Island, constituting 55% of the total number. Chaetognaths and appendicularians were secondly abundant (18 and 10%). Siphonophores and echinoderm larvae accounted for 7 and 5%, respectively. At Tioman Island, copepods were also markedly dominant in the >335 μm fraction, accounting for 54% of the total number. Echinoderm larvae, chaetognaths and appendicularians were secondly abundant (9.4, 9 and 10%). Ostracods and siphonophores accounted for 0.7 and 0.3% of the total, respectively.

Total percentage of primarily particle feeders in the three fractions considered by general feeding preference of each taxa was estimated at 98% in the 100–200 μm, 71% in

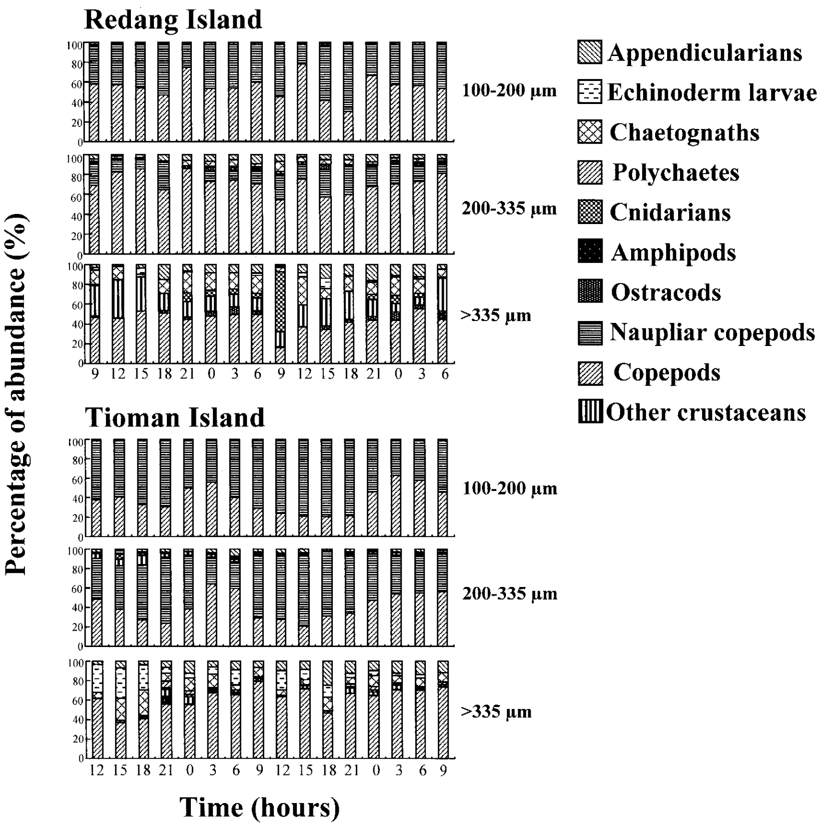

Fig. 4. Relative abundance of zooplankton taxa in three size-fractions during the two days at Redang and Tioman Islands.

the 200–335 μm, and 62% in the >335 μm fraction at Redang Island while it was 99% in the 100–200 μm, 95% in the 200–335 μm and 70% in the >335 μm fraction at Tioman Island. They included calanoid, harpacticoid and cyclopod copepods, appendicularians and echinoderm larvae. The ratio of particle feeders decreased with increasing size fraction. The largest fraction (>335 μm) comprised mainly of large-sized carnivorous taxa (e.g. chaetognaths and siphonophores; 38% at Redang Island and 30% at Tioman Island).

Cluster analysis of zooplankton community structure showed different groups in the three fractions at both islands (Fig. 5). Zooplankton community in the largest fraction for the two days was largely divided into two groups, which coincided on the basis of sampling time of day and night (percentage dissimilarity: ca 10% at Redang Island and ca 17% at Tioman Island). In the middle fraction (200–335 μm) at Redang Island, zooplankton community was also largely divided into day and night sampling time (percentage dissimilarity: ca 7%) though at Tioman Island the clusters were not clear. In the smallest fraction (100–200 μm) at both islands the clusters were not clear.

Discussion

Zooplankton abundance may be higher at high tides if shelf waters are the main source of reef zooplankton (Roman et al. 1990). It is easy to separate tidal effect from day/night differences in our zooplankton data because all night samples were coincidently taken at low tides at both islands (Fig. 2). Indeed, most of the taxonomic groups in samples collected during the night such as amphipods, calanoid, cyclopoid, and harpacticoid copepods, ostracods, chaetognaths, and polychaetes, have been described as demersal (e.g. Alldredge and King 1977, Jacoby and Greenwood 1988, Roman et al. 1990). The higher abundance in zooplankton at night compared to the day on these Malaysian reefs is likely a reflection of the nocturnal migration of demersal zooplankton.

Examination of the diel variation in the biomass of different size-fractions revealed that nocturnal vertical migration occurred most strongly in the largest fraction (>335 μm) at both islands. The largest fraction mostly contributed to the diel dynamics in the zooplankton community structure in this study area. Ohlhorst (1982) measured body size of zooplankton which were collected every an hour from dusk throughout the night in Discovery Bay, Jamaica, and reported that larger sized zooplankton predominantly showed nocturnal

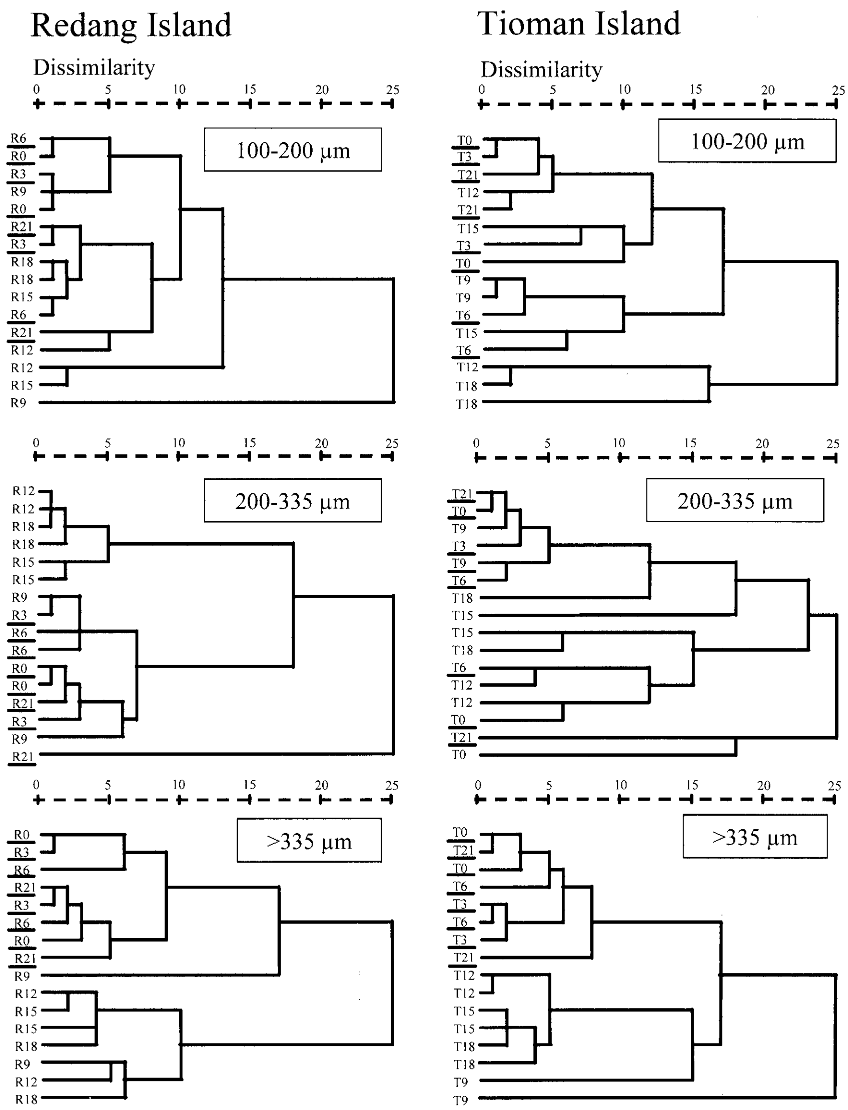

Fig. 5. Dendrogram resulting from classification analysis of zooplankton samples during the two days. Numbers on the left of the dendrogram refer to sampling times (hour). Underlines indicate hours of night.

vertical migration. Intense daytime zooplanktivory by fish may be the major factor determining diel variation in the large sized zooplankton in coral reef (Muscatien and Porter 1977). Larger zooplankton experience a greater susceptibility to visual predators (Hays et al. 2001) and hence their increased need to descend and spend the daytime on, or within substrata (e.g. Alldredge and King 1977). This behavior in the largest size-fraction may cause strong day/night difference in the community structure in this study area.

The largest size-fraction (>335 μm) was most dominant among three size-fractions during the two days, and mean size-fractionated zooplankton biomass at both day and night showed a reverse pyramidal structure at both islands (Fig. 3). What supports the largest fraction (>335 μm) which comprised about 35% of carnivorous zooplankton such as chaetognaths? There are two possibilities. One is the fast turn over rates in smaller sized zooplankton (100–200 and 200–335 μm). Hopcroft et al. (1998) revealed that small sized zooplankton such as naupliar copepods and small copepods have high growth rates in tropical waters. Another possibility is the large amount of POM (0.7–100 μm) concentration. The largest fraction (>335 μm) comprised about 65% of particle feeders. They may readily capture the 35–100 μm fraction as food source (Sheldon et al. 1977). Indeed, the concentration of the 35–100 μm fraction was more than 10-fold the largest size-fraction. Simultaneously, the 0.7–35 μm fraction is also potentially fed on by smaller sized zooplankton (100–200 and 200–335 μm), which mainly comprised of particle-feeders (about 90%). The concentration of the 0.7–35 μm fraction was approximately 60-fold of the smaller zooplankton fraction (100–200 and 200–335 μm). This large amount of POM is considered to support the high growth rates in small zooplankton in tropical waters.

We can roughly estimate the composition of POM (0.7–100 μm) by their Chl.-*a* concentrations and C/N ratio (Hata et al. 2002). The concentrations of Chl.-*a* in the POM at both islands was $0.62 \pm 0.27\,\mathrm{mg\,m^{-3}}$ at Redang Island and $0.36 \pm 0.21\,\mathrm{mg\,m^{-3}}$ at Tioman Island. Assuming that the C/Chl.-*a* ratio=50 (Blanchot et al. 1989), the contribution of phytoplankton biomass to POM was estimated to be 10.8% for Redang Island and 7.9% for Tioman Island. So this size-fraction would mainly consist of detritus or non-autotrophic organisms. The C/N ratios of some potential sources of POM have been reported: 6 to 8 for phytoplankton (Parsons et al. 1961), 20 for benthic marine plants (Atkinson and Smith 1967), 6.9 to 13.7 for fluid coral mucus (Johannes 1967), 4.8 to 5.9 for mucous sheet of coral (Coffroth 1990) and more than 30 for terrestrial vascular plants (Alexander 1977). The C/N ratio of the POM obtained in this study was 5.9 at Redang Island and 6.6 at Tioman Island. We suppose that the POM at Redang Island mainly originates from mucous sheet of coral. At Tioman Island, the POM may be derived from phytoplankton and coral mucus. However, phytoplankton contribution was quite low there. Therefore, most of the diet of particle-feeders in both study areas would mainly originate from mucus produced by corals.

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