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Diel variation in abundance, biomass and size composition of zooplankton community over a coral-reef in Redang Island, Malaysia

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Abstract: To understand coral-reef zooplankton ecology on a diel basis, zooplankton abundance, biomass and size composition from a fringing coral-reef of Redang Island, Malaysia, were investigated at three-hour intervals for a 48 hour period. Zooplankton was collected vertically and size-fractionated into three size-classes; 100–200 μm, 200–335 μm, and >335 μm. Diel variation of the zooplankton showed that the catches at night were always higher than those in the daytime and the nocturnal increase occurred most strongly in the large fraction (>335 μm). Zooplankton abundance steeply increased just after sunset, showed an abrupt increase 1.5 hour later and declined sharply thereafter. Observation of diel variation in coral-reef zooplankton from three-hour intervals revealed that the temporal variation was large in this study.

Key words: coral-reef, day and night, Malaysia, size-fraction, zooplankton

Introduction

It is well known that zooplankton biomass and abundance in the water column increases at night over coral-reefs (e.g. Glynn 1973, Ohlhorst 1982, Goswami & Goswami 1990, Sorokin 1993, Yahel et al. 2005a, b). For example, in the Gulf of Thailand, zooplankton density in the water column ranged from 90 indiv. m^{-3} by day to 5,676 indiv. m^{-3} at night (Sorokin 1993). The behavior of the zooplankton dramatically changes total zooplankton densities in the water column between day and night. This increase is caused by onshore advection of pelagic zooplankton which have diel migration offshore and/or migration of demersal zooplankton which stay during daytime in or on the substratum or near the bottom, and migrate into the water column at night (Alldredge & King 1977).

Zooplankton is an ecological community that has an important role in reef ecosystems as an energy source to benthic planktivores such as corals (Glynn 1973, Sebens et al. 1996, Coma et al. 1999). Corals feed on zooplankton to satisfy their requirements for inorganic nutrients and vitamins that cannot be supplied from photosynthesis by the coral's symbiotic algae (Sebens et al. 1987). Coral feeding preference on zooplankton depends on both zooplankton size and composition (Sebens et al. 1996, Palardy et al. 2006), and corals use tentacles to capture prey primarily during the night (Sebens et al. 1998). Since coral-reef zooplankton are known to show their peak in abundance at various times throughout the night, e.g. soon after sunset or before sunrise (Sorokin 1993), investigation on the size composition of zooplankton over short time intervals will provide fundamental information on potential prey to corals. Although diel variation in the density and biomass of coral-reef zooplankton with one to several hour intervals has been examined in several studies, relatively little is known about the size composition of zooplankton over coral-reefs (Table 1). Size-fractioning of zooplankton communities has been widely used in temperate waters as an alternative to investigation to the species level, and it has the advantage of simplifying complex community composition (Magnesen 1989). Size-fractioning the zooplankton community on a diel basis will also provide information on what size classes chiefly contribute to the diel variation.

In this study, we collected zooplankton at three-hour intervals for a 48 hour period and fractionated them into various size classes over a coral-reef at Redang Island, Peninsu-

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Table 1. Summary of coral-reef zooplankton studies with short time interval sampling, size-fractionatin or both. GBR: Great Barrier Reef. NA: not applicable

Study site	Sampling method	Mesh size (μm)	Short time interval sampling: Interval (hour)	Consectutive sampling period (day)	Replicate number of samplings	Size-fraction (μm)	Source
Laurel Cay, Puerto Rico	Net-tow	158	2	1	4	NA	Glynn 1973
Davies Reef, GBR	Net-tow	235	2	1	1	NA	Hamner & Carleton 1979
Discovery Bay, Jamaica	Trap	polyvinyl	day and 1, 2, 3–6, 7–15 after sunset	1	5	NA	Ohlhorst 1982
Laccadive, India	Net-tow	335	3	1	2	NA	Goswami & Goswami 1990
Davies Reef, GBR	Net-tow	200	3	3	1	NA	Roman et al. 1990
Laccadive, India	Net-tow	200	dawn, noon, dusk, midnight	1	1	NA	Madhupratap et al. 1991a
Laccadive, India	Core	NA	0.5 to 3	1	1	NA	Madhupratap et al. 1991b
Virgin Island, US	Net-tow	?	0.3 to 0.5	1	4	NA	McFarland et al. 1999
Helix Reef, GBR	Trap	1,000	2100–2200, 2400–0100, 0300–0400	3 nights	1	NA	Carleton et al. 2001
Tikehau atoll, Polynesia	Net-tow	35,200	NA	NA	NA	35–100, 100–200, 200–2000	Blanchot et al. 1989
Uvea atoll, New Caledonia	Net-tow	35,200	NA	NA	NA	35–200, 200–2000	Le Borgne et al. 1997
Padre Burgos, Philippine	Trap	80	1800–2400, 2400–0600, 0600–1800	1	1	80–202, 202–500, >500	Walter et al. 1981
Gulf of Aqaba, Red Sea	Pump	100	4	1	31	100–200, 200–500, 500–1350	Yahel et al. 2005a
Gulf of Aqaba, Red Sea	Pump	100	day, dusk, evening	17	1	500–710, 710–1000, >1000	Yahle et al. 2005b
Redang Island, Malaysia	Net-tow	100	3	2	1	100–200, 200–335, >335	This study

lar Malaysia. Although some research has been conducted at Redang Island on corals and other benthos (e.g. Rezai et al. 1999, Harborne et al. 2000), zooplankton studies are completely lacking. This paper presents results for the diel variation of zooplankton abundance, biomass and size composition to examine diel zooplankton behavior over the coral-reef.

Materials and Methods

Study site

This study was carried out on 5th to 7th August 2003 at the fringing coral-reef of Redang Island (5°44′49″N, 102°59′60″E) situated off the east-coast of Peninsular Malaysia (Fig. 1). Zooplankton sampling was conducted at a jetty in the marine park at a satellite island of Redang Island (Fig. 1). The maximum depth of the sampling site was 3.9 m during high tide. The live coral coverage of the sampling site was 49% with 8% of dead corals and 43% of other bottom substrata (e.g. sand and rock). The dominant coral at the sampling site was *Acropora formosa* (Dana) which accounted for 54% of live corals (Kok 2003). The sea condition at the sampling site was calm with no strong wind or rainfall during the study period.

Sampling and analysis

We collected zooplankton every three-hours: starting at 0900 h on 5th and with last sampling at 0600 h on 7th August. The number of sampling times (n) was 16 since we collected samples every three-hours for 48 hours. Of the 16 sampling times, 8 represented samples taken during the day (0900, 1200, 1500, and 1800 h for two daytime periods) and the other 8 represented night samples (2100, 0000, 0300, and 0600 h for two nighttime periods). The timing of sunrise and sunset was 0703 h and 1925 h, respectively. Additionally, we took samples only once just after sunset (1930 h) on 6th August.

At each sampling time, zooplankton were collected by five gentle vertical tows of a plankton net (mesh size, 100 μm; diameter, 30 cm; length, 100 cm) with a flowmeter from 1 m above the sea bottom to the surface. The filtration volume was calculated from the mouth area of the net, the value of the flowmeter and the distance towed. The samples collected were pooled and immediately brought back to the laboratory of the marine park within 5 min. Prior to the zooplankton collection, depth was measured to determine the tide levels and water was sampled with a 10 L Niskin bottle from the surface and 1 m above the bottom for water temperature and salinity measurements. Temperature was measured with a mercury thermometer and salinity was determined with a light-refraction salinometer (Shibuya S-10). The Spearman rank correlation was calculated to assess the correlation between the tide level and temperature or salinity.

The net-collected samples (>100 μm) were size-fraction-

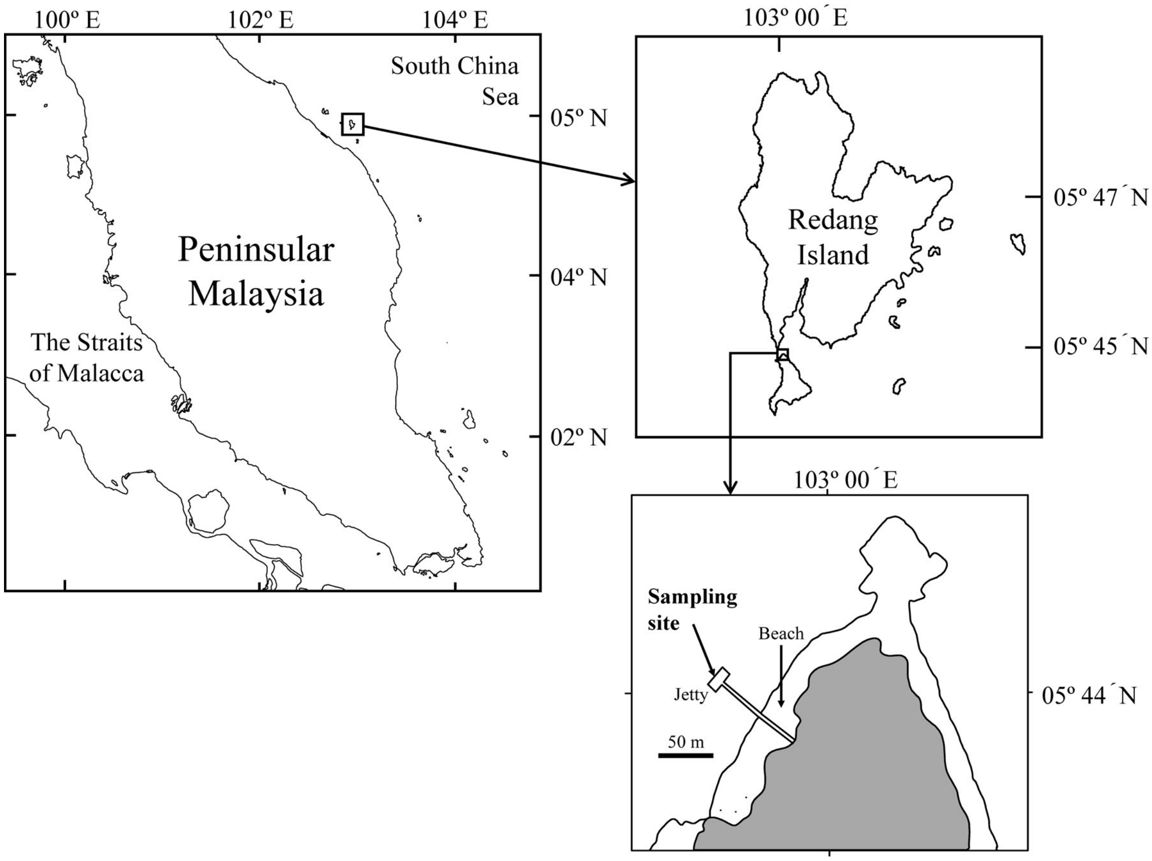

Fig. 1. Map of the sampling site at Redang Island off the east-coast of Peninsular Malaysia (5°44′49″N, 102°59′60″E).

ated into three size-classes (100–200 μm, 200–335 μm and >335 μm) by mesh screens of 200 μm and 335 μm. The three fractions were each divided into two aliquots with a Folsom plankton splitter (Omori & Ikeda 1984). One aliquot was used to determine organic carbon weight and the other for abundance and taxonomic analysis. The aliquot for weight determination was immediately filtered onto a GF/A filter (Whatman) which was pre-combusted at 500°C for 4 h and pre-weighed. The filters were subsequently dried and then organic carbon weight was measured following Nagao et al. (2001) using a CN analyzer (Fisons EA 1108 CHNS/O). The aliquot for abundance and taxonomic analysis was fixed with 5% formalin seawater and zooplankton was characterized into different groups and counted under a dissecting microscope. Copepod adults were identified to genus level whenever possible. The sample collected at 1930 h on 6th August was used only for abundance estimation.

The statistical difference in the density and biomass of zooplankton for each size-fraction between Day 1 (0900 h on 5th to 0600 h on 6th) and Day 2 (0900 h on 6th to 0600 h on 7th) and day (0900 to 1800 h) and night (2100 to 1600 h) were determined by Mann-Whitney's *U* test. The statistical difference in the density and biomass of zooplankton at four tidal levels (low tide, low to high tide, high tide, and high to low tide) were examined with the Kruskal–Wallis test.

Results

Environmental factors

Minimum tidal height was observed at 2100 h during the study period (Fig. 2). There was no difference in temperature and salinity between the surface and 1 m above the bottom and thus the water column was quite homogeneous throughout the study period. Mean temperature at the two depths ranged from 29.0°C at 0000 and 0900 h on 6th August and at 0000, 0300 and 0600 h on the 7th to 29.9°C at 1500 h on the 6th (overall average=29.4±0.3°C), while mean salinity was 31.0 psu at 0900 h on the 6th to 34.0 psu at 0000 h on the 7th (overall average=32.7±0.7 psu) (Fig. 2). Temperature and salinity were not correlated to the tidal level (temperature, $r=-0.001$, $p=0.998$; salinity, $r=-0.286$, $p=0.283$). Also, there were no significant differences in temperature or salinity between day and night (temperature, $p=0.328$; salinity, $p=0.442$).

Day/night change in zooplankton abundance and biomass

There were no significant differences in abundance and/or biomass of total zooplankton (>100 μm) between

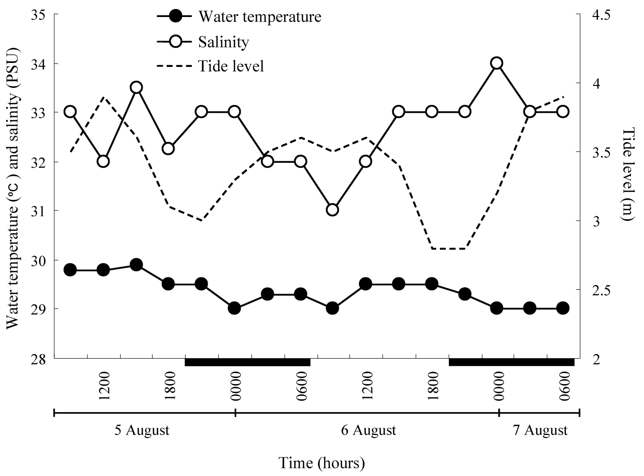

Fig. 2. Diel variation in mean water temperature and salinity in the water column and tidal level at Redang Island. Black bars indicate hours of nighttime.

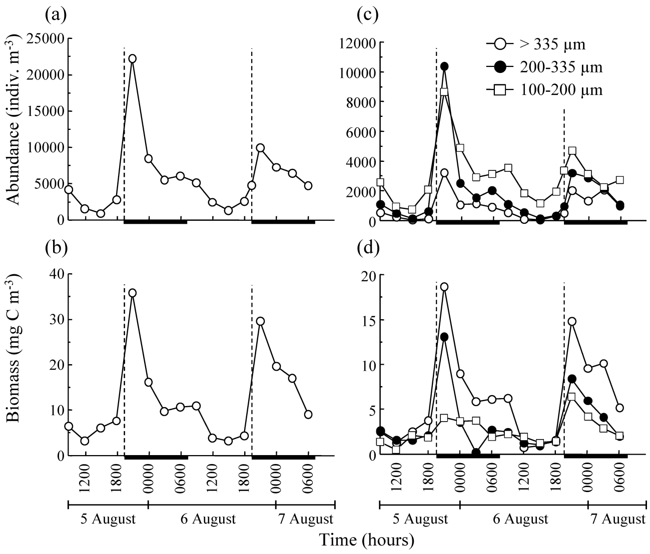

Fig. 3. Diel variation in abundance and biomass of total zooplankton (a, b) and size-fractionated zooplankton (b, d) at Redang Island. Black bars indicate hours of nighttime. Dotted vertical lines indicate the time of sunset.

Day 1 and Day 2 (abundance, $p=1.000$; biomass, $p=0.916$). The abundance and biomass of total zooplankton in the water column was significantly higher during the night ($p<0.01$) (Fig. 3a, b). The nocturnal abundance (8,846±5,658 indiv. m^{-3}) was 3.4 times higher in comparison to that during the day (2,619±1,454 indiv. m^{-3}). The total biomass at night (18.50±9.70 mg C m^{-3}) was also 3.2 times higher than that during the day (5.75±2.64 mg C m^{-3}). Both the abundance and biomass of total zooplankton attained peaks at 2100 h, declined sharply at 0000 h and kept declining at a slower pace thereafter. The minimum abundances were recorded at 1500 h (Fig. 3a).

In terms of size-fractions, the most significant diel change in abundance and biomass was found for the large fraction (>335 μm) (Fig. 3c, d). The day/night differences in abundances in the three size-fractions were remarkable, showing a 2.2-fold difference ($p<0.01$) in the 100–200 μm, 5.9-fold difference ($p<0.01$) in the 200–335 μm and 6.8-fold difference ($p<0.01$) in the >335 μm fractions (Fig. 3c). The biomass of the three size-fractions also significantly increased at night with a 2.1-fold ($p<0.01$), a 2.7-fold ($p<0.05$), and a 3.8-fold increase ($p<0.01$), respectively (Fig. 3d). All three size-fractions showed peaks in abundance at 2100 h (Fig. 3c). There were no significant differences in either abundance or biomass in any of the size-fractions at the four tidal levels ($p>0.05$).

Total zooplankton abundance before sunset (1800 h on 6th August; 2,566 indiv. m^{-3}) increased 1.9-fold just after sunset (1930 h; 4,777 indiv. m^{-3}) and further increased 2.1-fold in the next 1.5-h (2100 h; 9,950 indiv. m^{-3}) (Fig. 3a). In all three size-fractions abundances increased just after sunset with a 1.7-fold increase in the 100–200 μm, a 3.0-fold increase in the 200–335 μm, and a 1.6-fold increase in the >335 μm size-fractions (Fig. 3c). Abundances in all three size-fractions further increased over the next 1.5-h with a 1.4-fold increase in the 100–200 μm, 3.3-fold increase in the 200–335 μm, and 4.2-fold increase in the >335 μm fractions.

Zooplankton taxa in each size-fraction

The dominant organisms found in the small fraction (100–200 μm) were copepods (adult+copepodites) and copepod nauplii (Table 2). On average, copepods comprised 51.3% of the total number of organisms, the remainder being copepod nauplii (47.1%), and they were responsible for the diel pattern observed for this fraction (Fig. 4a). Copepods and copepod nauplii increased in number significantly at night and their peaks in abundance were at 2100 h. *Paracalanus*, *Oithona*, *Oncaea* and their copepodites were dominant among the copepod community (Table 3), and these taxa significantly contributed to the nocturnal increase in copepods (Fig. 5a, b, d). The day and night difference in *Microsetella* (adult+copepodites) in the small fraction was statistically not significant (Table 3), but a sharp nocturnal increase was observed at 2100 h on the first night (Fig. 5c).

In the mid fraction (200–335 μm), copepods (adult+copepodites) were the most abundant organisms throughout the study period and comprised 74.3% of the total abundance, determining the diel variation observed for this fraction (Table 2, Fig. 4b). Copepod nauplii accounted for 13.0% of the total number of zooplankters, with 5.3% and 4.0% being larvaceans and chaetognaths, respectively. Copepods (adult+copepodites), copepod nauplii, ostracods (myodocopids), other crustaceans, chaetognaths and larvaceans were responsible for the abrupt increase at 2100 h (Fig. 4b, c). The dominant copepod taxa in this fraction included *Paracalanus*, *Oithona*, *Microsetella* and *Oncaea*

Table 2. Abundance and percent composition (%) of common zooplankton taxa in different size-fractions at Redang Island. p values pertain to the abundance differences between day and night (**: $p<0.01$; *: $p<0.05$; ns: not significant).

Size-class (μm)	Zooplankton taxa	Abundance (indiv. m^{-3})									
		Day	n	%	Night	n	%	p	Total	n	%
100–200											
	Ostracods (Myodocopids)	9±8	8	0.5	13±19	8	0.3	ns	11±14	16	0.4
	Copepods (adult+copepodites)	896±438	8	48.7	2125±1126	8	52.5	**	1510±1041	16	51.3
	Copepod nauplii	904±614	8	49.1	1868±1038	8	46.1	*	1386±963	16	47.1
	Chaetognaths	6±5	8	0.3	6±4	8	0.1	ns	6±4	16	0.2
	Larvaceans	18±18	8	1.0	32±20	8	0.8	ns	25±20	16	0.8
200–335											
	Ostracods (Myodocopids)	9±6	8	1.6	68±54	8	2.1	**	38±48	16	2.0
	Copepods (adult+copepodites)	354±207	8	64.5	2443±2560	8	75.9	**	1398±2059	16	74.3
	Copepod nauplii	122±109	8	22.2	369±198	8	11.5	**	246±201	16	13.0
	Other crustaceans	1±1	8	0.1	8±5	8	0.3	**	4±6	16	0.2
	Chaetognaths	27±37	8	4.9	123±126	8	3.8	**	75±103	16	4.0
	Larvaceans	27±30	8	5.0	174±126	8	5.4	**	101±117	16	5.3
>335											
	Hydrozoans	44±120	8	19.0	113±83	8	7.2	**	79±106	16	8.7
	Polychaetes	1±2	8	0.3	7±7	8	0.4	*	4±6	16	0.4
	Ostracods (Myodocopids)	2±3	8	1.1	63±32	8	4.0	**	33±38	16	3.6
	Copepods (adult+copepodites)	103±107	8	44.9	731±351	8	46.3	**	417±409	16	46.1
	Amphipods	1±2	8	0.5	11±24	8	0.7	*	6±17	16	0.7
	Other crustaceans	2±3	8	0.9	58±53	8	3.7	**	30±47	16	3.3
	Chaetognaths	36±38	8	15.6	263±190	8	16.7	**	149±177	16	16.5
	Echinoderm larvae	7±7	8	3.0	24±22	8	1.5	ns	15±18	16	1.7
	Larvaceans	13±11	8	5.5	150±102	8	9.5	**	81±99	16	9.0

n, number of samples.

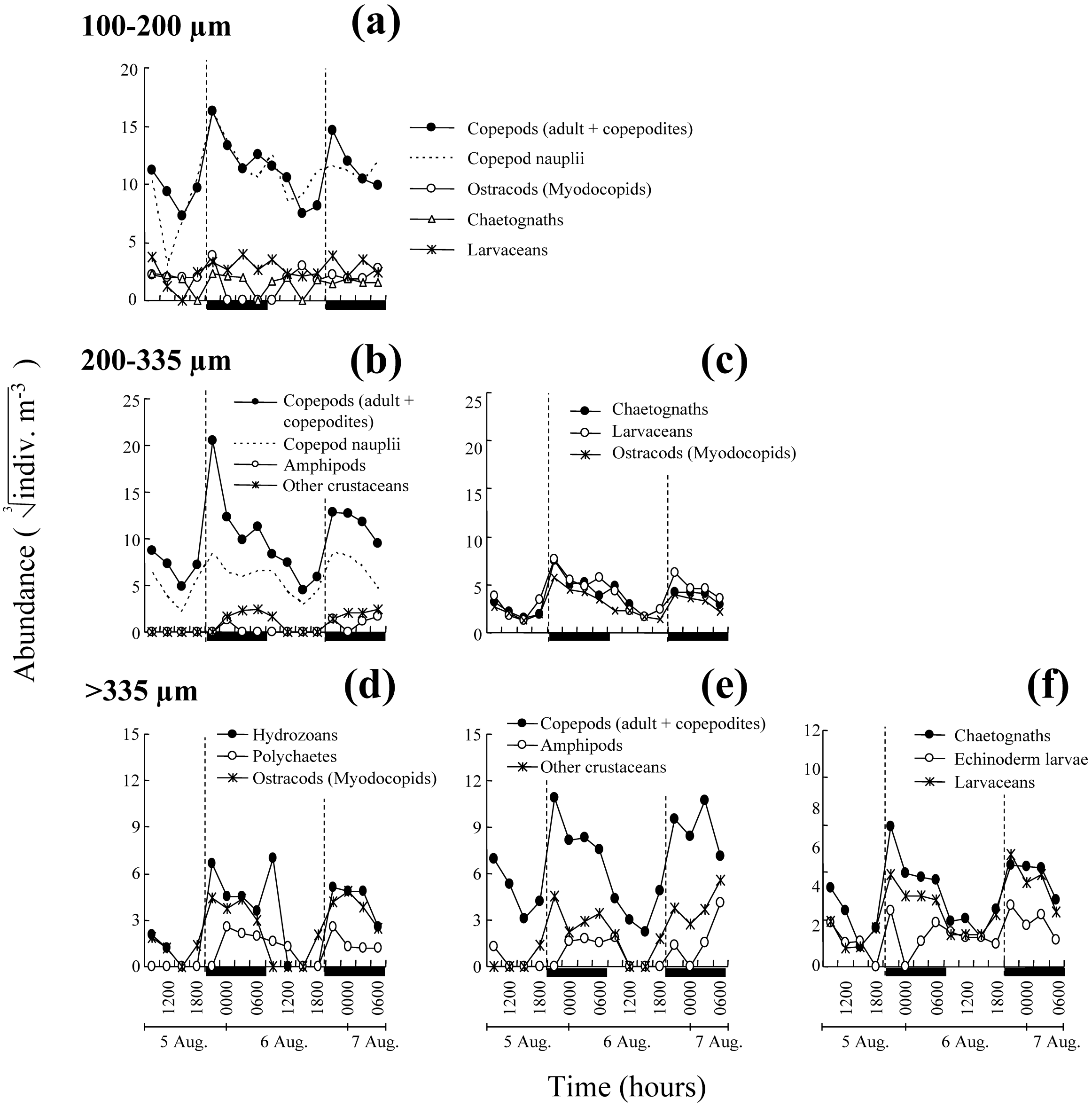

Fig. 4. Diel variation in abundance of common zooplankton taxa in the three size-fractions (a, 100–200 μm; b, c, 200–335 μm; d, e, f, >335 μm) at Redang Island. Black bars indicate hours of nighttime. Dotted vertical lines indicate the time of sunset.

(Table 3). These copepods and their copepodites increased significantly in number at night, peaking at 2100 h (Fig. 5e–i).

The common zooplankton taxa identified in the large fraction (>335 μm) throughout the study period were copepods (adult+copepodites) (46.1%), followed by chaetognaths (16.5%), larvaceans (9.0%), hydrozoans (8.7%), ostracods (myodocopids) (3.6%) and other crustaceans (3.3%) including cumaceans, crab zoea and mysids (Table 2). Hydrozoans were dominant at 0900 h on 6th August, coinciding with the minimum salinity value, due to the occurrence of large numbers of siphonophores, comprising 65.3% of the total zooplankton abundance (Fig. 4d). Hydrozoans, ostracods (myodocopids), copepods, other crustaceans, chaetognaths and larvaceans significantly increased at night, peaking at 2100 h (Fig. 4d, e, f). The dominant copepod taxa included *Acartia*, *Canthocalanus*, *Paracalanus*, *Acrocalanus*, *Oithona*, *Microsetella*, *Corycaeus* and *Oncaea* (Table 3). The abundance of many copepod taxa increased sharply at 2100 h (Fig. 5j–q).

Discussion

This study examined zooplankton community variation over a fringing reef in Malaysia to better understand the diel variations of coral-reef zooplankton communities. Although the sampling period included only two nights, zooplankton exhibited a substantial increase in abundance and biomass at night.

The examination of the diel variation of different size-

Table 3. Abundance and percent composition (%) of common copepod taxa in different size-fractions at Redang Island. *p* values pertain to the abundance differences between day and night (**: $p<0.01$; *: $p<0.05$; ns: not significant).

Size-class (μm)	Copepod taxa	Abundance (indiv. m^{-3})									
		Day	n	%	Night	n	%	*p*	Total	n	%
100–200											
	Calanoid										
	Paracalanus	42±32	8	4.7	162±124	8	7.8	**	102±108	16	6.8
	Copepodites	233±175	8	26.2	528±470	8	25.3	*	381±375	16	25.6
	Cyclopoid										
	Oithona	54±43	8	6.0	191±105	8	9.1	**	122±105	16	8.2
	Copepodites	226±164	8	25.3	559±260	8	26.8	*	392±271	16	26.3
	Harpacticoid										
	Microsetella (adult+copepodites)	30±17	8	3.4	88±126	8	4.2	ns	59±92	16	4.0
	Other copepodites	7±7	8	0.8	1±4	8	0.1	ns	4±6	16	0.3
	Poecilostomatoid										
	Oncaea	5±5	8	0.5	32±40	8	1.5	ns	19±31	16	1.2
	Copepodites	290±236	8	32.5	518±254	8	24.8	*	404±265	16	27.1
200–335											
	Calanoid										
	Paracalanus	57±56	8	17.9	442±665	8	18.2	**	249±498	16	18.2
	Copepodites	74±60	8	23.4	582±733	8	24.0	**	328±567	16	23.9
	Cyclopoid										
	Oithona	23±16	8	7.1	273±359	8	11.3	**	148±277	16	10.8
	Copepodites	19±15	8	6.0	182±189	8	7.5	**	101±154	16	7.3
	Harpacticoid										
	Microsetella (adult+copepodites)	88±67	8	27.7	253±228	8	10.4	**	170±183	16	12.4
	Other copepodites	0±0	8	0.0	2±6	8	0.1	ns	1±4	16	0.1
	Poecilostomatoid										
	Corycaeus	8±9	8	2.7	24±13	8	1.0	*	16±14	16	1.2
	Oncaea	19±19	8	6.0	467±256	8	19.2	**	243±290	16	17.7
	Farranula	2±2	8	0.5	6±4	8	0.3	ns	4±4	16	0.3
	Copepodites	21±17	8	6.6	178±252	8	7.4	**	100±191	16	7.3
>335											
	Calanoid										
	Acartia	2±3	8	1.7	40±32	8	5.6	**	21±30	16	5.1
	Canthocalanus	0±0	8	0.0	20±17	8	2.8	**	10±16	16	2.5
	Calocalanus	2±3	8	1.6	7±6	8	1.0	*	4±5	16	1.0
	Centropages	0±0	8	0.0	16±22	8	2.2	**	8±17	16	1.9
	Clausocalanus	0±0	8	0.0	2±2	8	0.3	*	1±2	16	0.2
	Candacia	0±0	8	0.0	2±2	8	0.3	*	1±2	16	0.2
	Eucalanus	0±0	8	0.0	5±2	8	0.7	**	2±3	16	0.6
	Paracalanus	5±6	8	5.4	103±52	8	14.3	**	54±62	16	13.3
	Acrocalanus	1±2	8	0.8	21±20	8	3.0	**	11±17	16	2.7
	Calanopia	0±0	8	0.0	3±4	8	0.5	*	2±3	16	0.4
	Copepodites	6±7	8	7.0	119±128	8	16.5	**	63±105	16	15.4
	Cyclopoid										
	Oithona	1±1	8	1.4	52±36	8	7.2	**	27±36	16	6.6
	Copepodites	4±5	8	4.1	11±7	8	1.5	*	7±7	16	1.8
	Harpacticoid										
	Microsetella (adult+copepodites)	68±60	8	74.1	206±160	8	28.6	**	137±137	16	33.8
	Poecilostomatoid										
	Corycaeus	0±1	8	0.2	24±27	8	3.3	**	12±22	16	3.0
	Oncaea	1±2	8	1.5	72±60	8	10.1	**	37±55	16	9.1
	Farranula	0±1	8	0.3	6±5	8	0.9	**	3±4	16	0.8
	Copepodites	1±2	8	0.9	2±3	8	0.3	ns	2±3	16	0.4

n, number of samples.

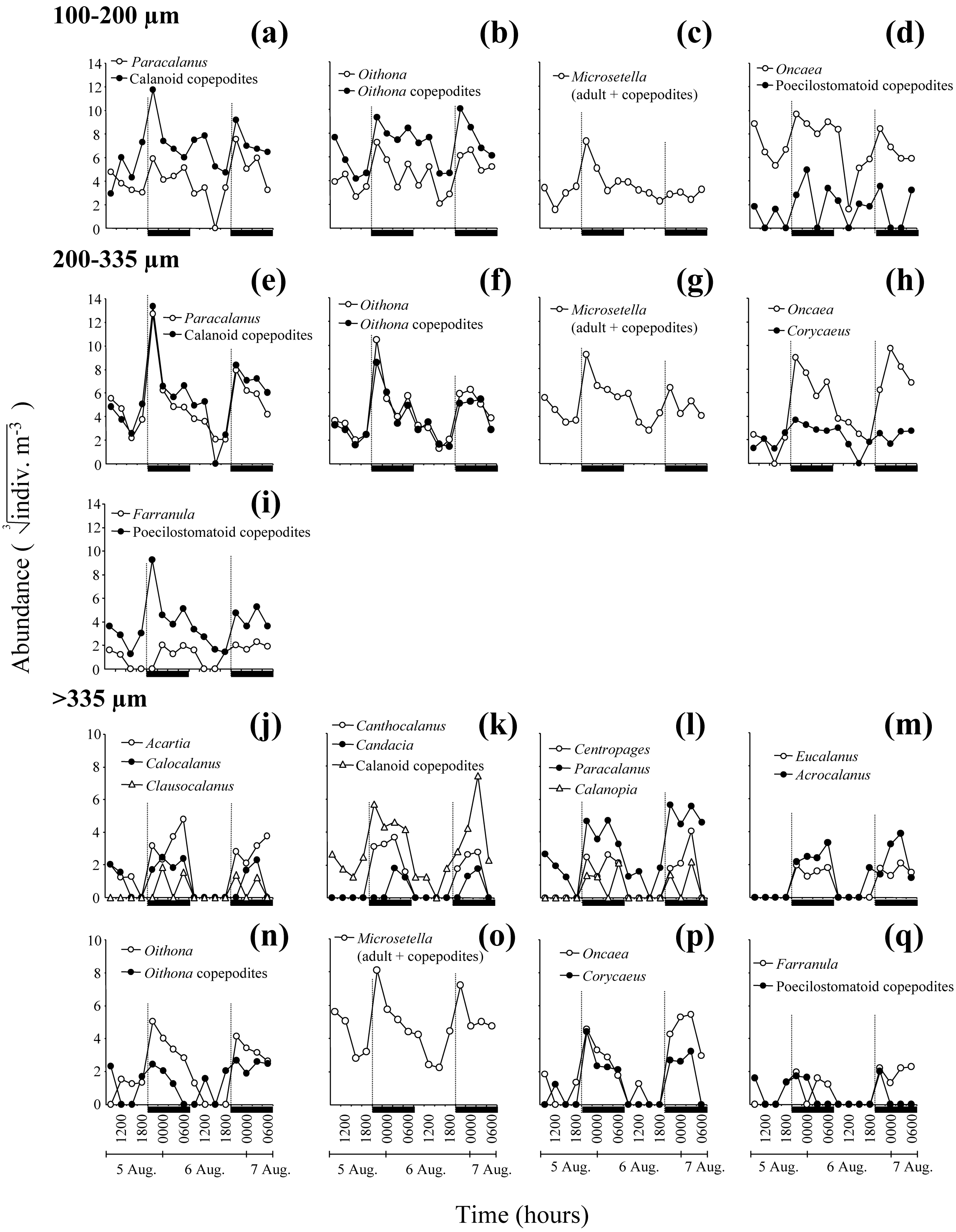

Fig. 5. Diel variation in abundance of common copepod taxa in the three size-fractions (a–d, 100–200 μm; e–i, 200–335 μm; j–q, >335 μm) at Redang Island. Black bars indicate hours of nighttime. Dotted vertical lines indicate the time of sunset.

fractions revealed that the nocturnal increase occurred most strongly in the large fraction (>335 μm). This result is similar to that in a report from the Gulf of Aqaba, Red Sea, that a nocturnal increase in zooplankton biomass was generally due to an increase in larger-sized zooplankton (>200 μm) (Yahel et al. 2005a). Intense daytime zooplanktivory by fish may be one of the major factors determining diel variation in coral-reef zooplankton (Muscatine & Porter 1977). Some larger individuals experience a greater susceptibility to visual predators (Hays et al. 2001) and hence they need to descend and spend the daytime near the bottom or in the crevices of the coral substratum. This behavior in the large sized zooplankton may have caused the strong day/night difference.

Temporal variations in zooplankton concentration in shallow water depend generally on two factors: (1) transport of pelagic species by horizontal currents and (2) vertical migrations of the organisms themselves (Morgado et al. 2003). During ebb tide, when the external influence is minimal, zooplankton samples collected over patch reefs and reef flats contain almost exclusively demersal zooplankton (Sorokin 1993). We found an abrupt increase in zooplankton abundance early in the night (2100 h) coinciding with the minimum tide level. Neither zooplankton abundance nor biomass exhibited a significant difference between tidal levels, and there was no vertical stratification in the water column or strong winds. Under these conditions the observed high zooplankton abundance at 2100 h was probably due more to diel vertical migration by demersal zooplankton than by horizontal advection. Demersal zooplankton on reefs is mainly comprised swarmers and epibenthic forms (Heidelberg et al. 2004). The swarmers, active aggregations of individuals, maintain position near the bottom or around coral formations without settling on the substratum during the day and disperse at night (Hamner & Carleton 1979), while the epibenthic species reside on and/or within the bottom substrate or coral formations during the day and some migrate into the water column at night (Mees & Jones 1997, Jacoby & Greenwood 1988). Among the zooplankton taxa that increased at 2100 h, cumaceans, ostracods (myodocopids), amphipods and polychaetes are categorized as epibenthic species (Jacoby & Greenwood 1988, Cahoon & Tronzo 1992), while mysids, *Acartia* and *Centropages* (mainly *Acartia erythraea* (Giesbrecht) and *Centropages orsinii* (Giesbrecht)) are categorized as swarmers (Hamner & Carleton 1979, Omori & Hamner 1982, Ueda et al. 1983). Some *Oithona* species are known to be swarmers at various coral-reefs (e.g. Heidelberg et al. 2004), but we do not know whether the *Oithona* in the present study are swarmers since we did not identify them to species level and thus pelagic species originating from offshore might be included. The pelagic zooplankton including chaetognaths, larvaceans, *Clausocalanus*, *Calocalanus*, *Paracalanus*, *Calanopia*, *Microsetella*, *Corycaeus* and *Oncaea* (Sale et al. 1976, Jacoby & Greenwood 1988, Webber & Roff 1995, Shimode & Shirayama 2004) also substantially increased at 2100 h. Heidelberg et al. (2004) reviewed data showing that some species traditionally characterized as pelagic forms behave like typical demersal zooplankton when they inhabit a coral-reef environment. For example, they may change behaviors when residing on reefs to prevent being swept off the reef by surface currents or to avoid heavy predation by abundant visual predators such as fish. It is also possible that pelagic species, which have a diel migration offshore, maintain vertical migration when advected into the reef but cannot reach their normal maximum depth (Heidelberg et al. 2004). Therefore, the abrupt nocturnal increase at 2100 h may be caused by both demersal zooplankton and the pelagic species that behave like demersal zooplankton when they inhabit coral-reef environments.

Zooplankton abundance in the present study increased steeply just after sunset (1930 h) and peaked 1.5 hour later (2100 h). The mid fraction (200–335 μm) increased just after sunset, while the large fraction (>335 μm) increased most substantially 1.5-h after sunset. In a similar observation, abrupt increase at sunset was attributed to an increase in smaller zooplankton, whereas larger zooplankton emerged one hour after sunset in the Gulf of Aqaba, Red Sea (Yahel et al. 2005b). High zooplankton abundance in the early hours of the night has been reported from various coral-reefs: e.g. the number of zooplankton rose steeply within 30 min after sunset, and peaked one or a few hours later in the U. S. Virgin Islands (McFarland et al. 1999), and in the Laurel Reef in Puerto Rico, zooplankton was most abundant from about 1800 to 2200 h (Glynn 1973). The numerical abundance of zooplankton increased between 2000 and 0200 h in Minocoy lagoon and Kavaratti atoll, India (Goswami & Goswami 1990), while at Helix Reef in Great Barrier Reef, the total catch was most abundant early in the night (2100 to 2200 h) (Carleton et al. 2001). A question arises as to why zooplankton show an abrupt nocturnal increase early in the night. Yahel et al. (2005b) showed using acoustic back-scattering that the abrupt emergence of reef zooplankton occurred soon after sunset when many diurnal planktivorous fish are still foraging but their prey-capture efficiency is greatly decreased and corals had not yet expanded their tentacles. Some zooplankton individuals which stay in, on or near corals may emerge soon after sunset before the corals fully expand their tentacles. This active bottom avoidance may partially contribute to the intense nocturnal emergence of coral-reef zooplankton early in the night (Yahel et al. 2005b). Interestingly, over a sandy bottom with only a few small patches of coral, a peak in zooplankton biomass occurred later at night, rather than at dusk at Tioman Island, Malaysia (Nakajima et al. in press). Similarly, in the Gulf of Aqaba, zooplankton showed a less pronounced diel pattern over a sandy seagrass meadow where the closest corals were found some 70 m away (Yahel et al. 2005a).

Coral feeding preference on zooplankton depends on both zooplankton size and composition (Sebens et al. 1996, Palardy et al. 2006). The dominant corals found in the study area were *Acropora formosa* (54% of live corals), *Pocillopora damicornis* (Linnaeus) (12%), *Acropora elseyi* (Brook) (11%) and *Acropora digitifera* (Dana) (9%) (Kok 2003). These corals have relatively small sized polyps and may feed on a similar size-range of prey. For example, *P. damicornis* has 1.0 mm diameter polyps, which preferentially feed on 200–400 μm sized zooplankton and rarely capture zooplankton smaller than 200 μm (Palardy et al. 2006). Thus, zooplankton in the mid fraction (200–335 μm) and a portion of the large fraction (>335 μm) may be mainly fed on by the corals in our study site. However, faster swimming taxa such as copepods may only be rarely captured (Sebens et al. 1996, Palardy et al. 2006). Sebens et al. (1996) found that scleractinian corals showed the lowest feeding rate on copepods (e.g. *Oithona* species) than on other prey zooplankton in Discovery Bay, Jamaica. According to this, poor swimming and relatively abundant taxa in the $>200\,\mu$m fraction in this study, such as chaetognaths, polychaetes, and larvaceans, may potentially be important prey for the corals.

This study provided data on changes in zooplankton communities over short time intervals above a Malaysian coral-reef. Observation of diel variation in zooplankton abundance and biomass at three-hour intervals revealed that the temporal variation was large in this study. Careful consideration of the temporal representativeness of coral-reef zooplankton samples should be made when designing sampling protocols.

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