

# Impact of the 2004 Sumatran tsunami on the diversity of intertidal brachyuran assemblages of Maavah, Laamu Atoll, Maldives

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**Abstract** A 2-year spatio-temporal survey of intertidal brachyuran crabs involving five sites was conducted in the Maavah reef system, Laamu Atoll, Maldives, from April 2001 to March 2003. In December 2004, the sites were hit by the catastrophic Sumatran tsunami. An 8-month-long study was carried in the same five sites after the tsunami, and the data obtained were compared with the pre-impact baseline data. A sand dune formed at the north-eastern side of the island as a result of the tsunami was also included in the post-tsunami study (site 6). Nine brachyuran crab species not recorded during pre-tsunami sampling in the five study sites were collected after the event. Of these, six species were recorded in site 6 during January 2005, and they started to appear in the other sites in the following months. Nine species of crabs collected during the pre-tsunami periods from four sites were not represented in the post-tsunami collections. Abundance, evenness and diversity of the post-tsunami brachyuran communities of sites 1 and 2 exhibited downward trends, and the evenness and diversity of the post-tsunami communities of site 4 exhibited upward trends when compared with pre-tsunami patterns. Multivariate analyses revealed that the tsunami had changed the post-tsunami brachyuran communities of sites 1–4. However, tests revealed that in site 4, the pre-tsunami brachyuran assemblage 1 (2001–2002) differed from pre-tsunami assemblage 2 (2002–2003) and post-tsunami assemblages. The roles of tsunami-transported species and site-specific dominant species in contributing to faunal dissimilarities between the pre- and post-tsunami brachyuran assemblages were found to be patchy. Further studies would reveal whether the population of any newly added species increases or decreases in the long term.

**Keywords** Brachyuran diversity · Tsunami · Evenness · Maavah · Laamu Atoll · Maldives

## 1 Introduction

The Sumatran tsunami was generated by an earthquake of 9.3 Mw magnitude (Stein and Okal 2005) at 3.3°N, near the northern end of Sumatra on 26 January 2004, and the energy

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released by the earthquake was equivalent to the combined energy released by all earthquakes between 1976 and 1990 (Park et al. 2005). The first wave arrived at Malé, the capital of Maldives 3.17 h after the onset of the earthquake (Merrifield et al. 2005), and most of the atolls were subjected to rapid surges unlike the big waves that affected Thailand and Sumatra (Spencer 2007). The reefs of Rasdhoo and Ari (Alifu) Atolls were covered by sediment immediately after the tsunami, and within 2 days, the reefs became sediment-free (Gischler and Kikinger 2007).

On a per-unit-area basis, the Central Indo-Pacific and the Caribbean coral reefs hold the greatest diversity of marine life including one-third of world's marine fish species (Paulay 1997). Coral formations act as buffers during storm surges and tidal waves (Ramachandran et al. 2005). Therefore, the impact of tsunami on a reef ecosystem is a matter of concern. Post-Sumatran tsunami surveys revealed that the coral reefs of Pulau Park of Malaysia, Andaman Sea, North Aceh region of Indonesia, Mu Ko Surin National Park of Thailand, Seychelles, Myanmar, Sri Lanka and the Maldives were scarcely damaged (Affendi et al. 2005; Brown 2005; Campbell et al. 2005; Comley et al. 2005; Obura and Abdulla 2005; Rajasuriya et al. 2006; Tun et al. 2006; Zahir et al. 2006), but those in the Gulf of Mannar as well as Andaman and Nicobar Islands were severely affected (Kumaraguru et al. 2005; Edward et al. 2006). Reefs affected by anthropogenic activities such as global warming and coral mining were more severely damaged by the tsunami (Baird et al. 2005; Foster et al. 2006). Studies on the impact of tsunamis on coral reef-associated fauna are very few. Cortes et al. (1993) studied the mass mortality among intertidal and reef-associated organisms caused by tsunami. A study of the post-tsunami changes in the benthic fauna at Marina beach, Chennai, India, was carried out by Altaff et al. (2005). Campbell et al. (2007) reported that reef fish diversity in Aceh, Northern Sumatra, was unaffected by the Sumatran tsunami.

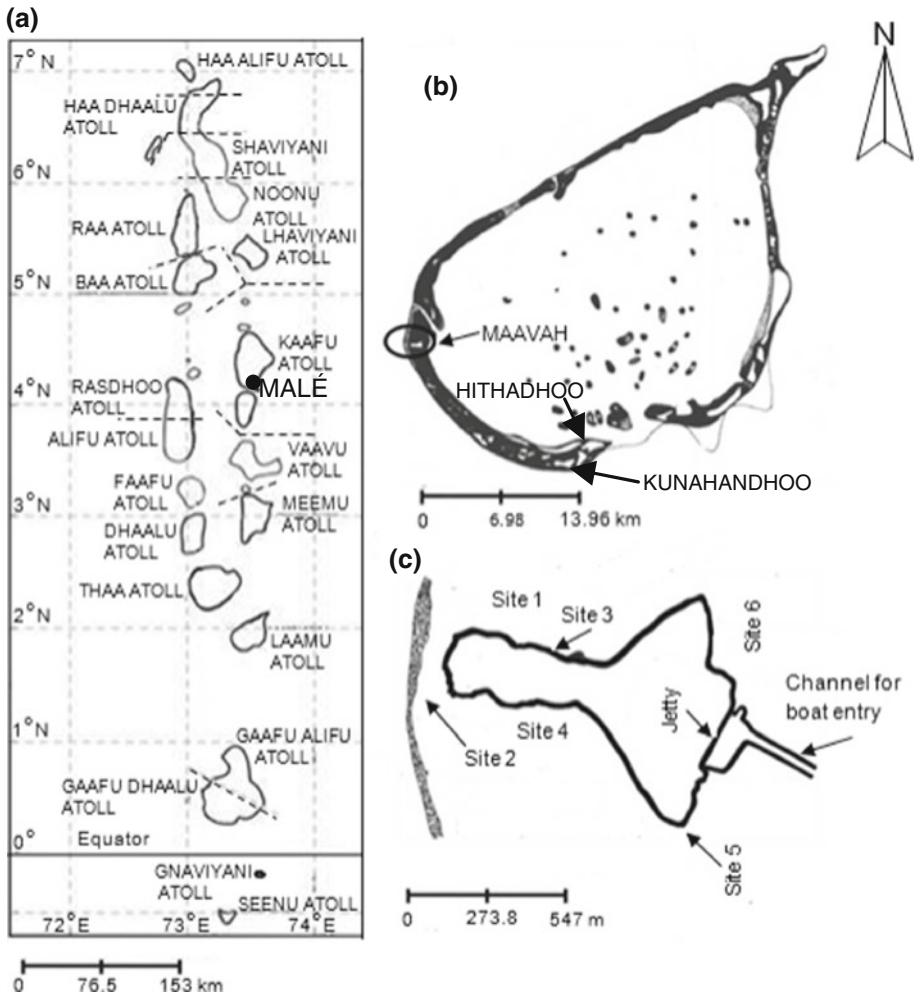
There is extensive literature on the impact of hurricanes on reef communities (Koehl et al. 1981; Woodley 1993; Bythell et al. 2000). Delicate coral forms like *Acropora* sp. were not seen in areas frequently exposed to typhoons (Randall 2003). However, the impact of tsunami on the ecology of reef systems has rarely been assessed (Bilham 2005; Hagan et al. 2007; Phongsuwan and Brown 2007). More accurate quantitative studies of damage caused by tsunamis are very rare (Tomascik et al. 1997). The initial reports on the impact of the Sumatran tsunami in Aceh, Northern Sumatra, were found to be exaggerated when the same area was quantitatively analysed later (Campbell et al. 2007). The lack of pre-tsunami baseline studies has hampered the accurate estimation of damage caused to coral reefs by the 2004 tsunami (Abdulla et al. 2006; Edward et al. 2006). Only a few studies have quantitatively estimated the damage incurred to coral reefs by the 2004 tsunami based on previous baseline works (Campbell et al. 2007; Phongsuwan and Brown 2007). At present, most of the tsunami-related published studies are based on either inaccurate rapid assessment methods (Hagan et al. 2007) or studies without pre-tsunami baseline data. This investigation steers clear of both these disadvantages as: (1) this is a long-term study and (2) a baseline pre-tsunami data set is available, which can be useful for comparing with post-tsunami data.

Studies on the impact of tsunamis on marine animals other than coral species are scarce. The 2-year spatio-temporal study carried out on the intertidal brachyuran assemblages of Maavah during the years 2001–2003 before the Sumatran tsunami in 2004 (Kumar and Wesley 2010) provided a rare opportunity to quantify the impact of the tsunami on the same animal fauna (Kumar 2008), and the results of the study are presented in this paper.

## 2 Materials and methods

### 2.1 Study site description

This study was conducted on the brachyuran assemblages of Maavah ( $1^{\circ}53'08.92''\text{N}$ ;  $73^{\circ}14'35.61''\text{E}$ ), in Laamu Atoll ( $2^{\circ}08'\text{N}$  and  $1^{\circ}47'\text{N}$ ), in the Maldives ( $7^{\circ}10'\text{N}$ – $0^{\circ}4'\text{S}$  and  $72^{\circ}30'$ – $73^{\circ}40'\text{E}$ ) (Fig. 1a–c) between 2001 and 2005. Pre- and post-tsunami studies were conducted on five sites of this island. Sites 1, 2 and 4 are between low water neap and low water spring tides, and these would be  $\sim 0.3\text{ m}$  to  $\sim 0.45\text{ m}$  above the chart datum. The sandy area of site 3 and the entire site 5 are between low water neap and high water neap tides ( $\sim 0.45$  to  $\sim 0.6\text{ m}$  above chart datum), and the coral shingle bed of site 3 is located in the splash zone, which is  $\sim 1.2\text{ m}$  above the chart datum. Site 1 is made of several



**Fig. 1** a The Maldives ( $7^{\circ}10'\text{N}$  and  $0^{\circ}4'\text{S}$  and  $72^{\circ}30'$  and  $73^{\circ}40'\text{E}$ ) showing Laamu Atoll; b Laamu Atoll ( $2^{\circ}08'\text{N}$  and  $1^{\circ}47'\text{N}$ ) showing Maavah (inside the circle); c Maavah ( $1^{\circ}53'08.92''\text{N}$  and  $73^{\circ}14'35.61''\text{E}$ ) showing the study sites

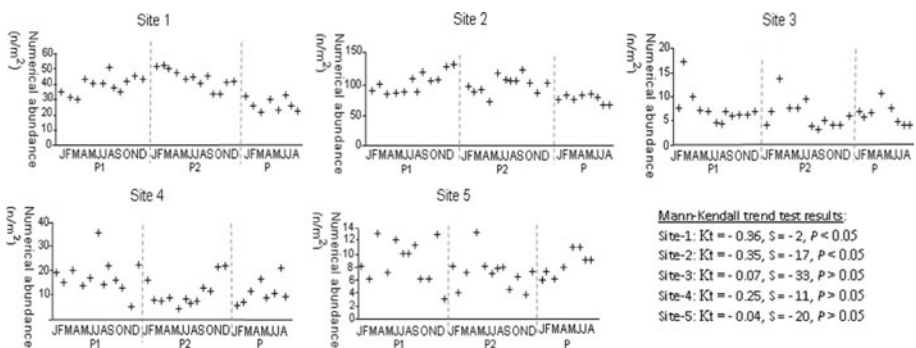
habitats such as sandy patches, seagrass bed, piles of coral clasts, boulder belts, muddy areas and *Porites* coral beds. Site 2 is homogeneous space-wise and made of myriads of different-sized coral boulders. Site 3 is made of sandy beach, conglomerate rocky beds, coral shingle beds, etc. Site 4 is made of seagrass bed, sandy patches and rolling boulders. Around one-fourth of site 5 is made of silty mud originating from domestic wastes, and the rest of the area is made of fine beach sand (Kumar and Wesley 2010). The tsunami had led to the formation of a new sand dune (site 6) in the eastern side of the jetty. This site was surveyed after the tsunami. This site is located between low water neap and low water spring tides, and these would be  $\sim 0.3$  to  $\sim 0.45$  m above the chart datum.

## 2.2 Sampling methodology

Pre- and post-tsunami survey samplings were done following the quadrat method along transects. Along a 200-m-long transect in each study site, a  $50 \times 50$  cm quadrat was used for sampling intervals of 5 m (40 samplings); the total survey area of each site was  $10 \text{ m}^2$ . Coral rocks of the sampling sites were carefully covered by gunny bags, taken to the beach and dismantled, and the crabs were collected. Pre-tsunami surveys were performed every month from April 2001 to March 2003. Post-tsunami surveys were conducted for 8 months (January 2005–August 2005); this period was sufficient to record the appearance of juvenile crabs from larval stages probably carried by the tsunami. Carapace length and breadth (in cm; carapace dimension) of the newly recorded species of crabs after the tsunami were also recorded.

## 2.3 Statistical analysis

The study period was divided into pre-tsunami period (PR) (April 2001–March 2003) and post-tsunami period (P) (January 2005–August 2005). For the purpose of statistical analysis, the pre-tsunami period was further divided into pre-tsunami period 1 (P1) (April 2001–March 2002) and pre-tsunami period 2 (P2) (April 2002–March 2003). The monthly abundance data of P1, P2 and P from the different sites shown in Fig. 2 were tested with nested analysis of variance (ANOVA) to determine the effect of year (nested with pre- and post-tsunami periods), month (nested with pre- and post-tsunami periods) and pre- and post-tsunami periods (Note: Years include pre- and post-tsunami years, and pre-tsunami



**Fig. 2** Time plots showing the time trends of P1, P2 and P in sites 1–5. P1, pre-tsunami period 1; P2, pre-tsunami period 2; P, post-tsunami period.  $K_t$  = Kendall's tau;  $S$  = average Kendall's tau. X-axis: months of the year from January to December (J–D)

years include P1 and P2). Years and months were considered as fixed factors and pre- and post-tsunami periods as random factors. Prior to the test, the data were subjected to Cochran *C*-test to determine the homogeneity of variance, and  $\log x + 1$  transformation was done whenever necessary. Calculations were done with the aid of the STATISTICA software (STATISTICA, '99 Edition, StatSoft, Inc.). Univariate diversity indices, such as numerical abundance (*N*), Pielou's evenness (Pielou 1977) (*J'*) and the  $\log_e$  Shannon–Wiener species diversity index (*H'*) (Shannon and Weaver 1949), were calculated for each month (PRIMER-E software package, Plymouth Marine Laboratory, UK; Clarke and Warwick 2001-demo version). The resultant data sets were analysed by one-way ANOVA to check for any deviation between periods. Before the test, normality and homogeneity tests were performed following the steps given in Appendix fig N1 provided in *Guidance for Data Quality Assessment* (USEPA 2000). Transformations did not improve the normality and homogeneity of *H'* values of site 4, so nonparametric Kruskal–Wallis test was applied for the same data sets. When the mean values of the different periods were found to be heterogeneous by one-way ANOVA, Tukey's honestly significantly different test was carried out to compare the groups. To understand the period-wise abundance trends, time plots were drawn for the monthly data sets (USEPA 2000), and Mann–Kendall test was applied to verify the significance of the trend (XLSTAT 2010 Addinsoft) and this test was extended to verify the time period trend of *J'* and *H'*. Bray–Curtis similarity index (Bray and Curtis 1957) was used to verify the similarity in square root-transformed, non-normalized, pooled species abundance data sets per P1, P2 and P, and SIMPER analysis was performed to understand faunal dissimilarity (PRIMER-E software package). Non-metric multidimensional scaling (MDS) was conducted on the similarity matrix of square root-transformed, non-normalized, monthly species-based abundance data sets of P1, P2 and P to find out the relationship between pre- and post-tsunami periods, and one-way analysis of similarity (ANOSIM) was performed on the same similarity matrix to examine the statistical significance of differences between periods.

## 2.4 Specimen depositories

Vouchers of the species collected during the study were deposited in the Natural History Museum, London (voucher nos. NHM 2008.50 to NHM 2008.152), Zoological Reference Collection, Raffles Biodiversity Museum, Singapore (ZRC 2007.0704 to ZRC 2007.0759; ZRC 2008.0264 to ZRC 2008.0266), and Marine Research Station, Maldives (MRC-CR-0001-2007 to MRC-CR-0062-2007).

## 3 Results

### 3.1 Impact of the tsunami on species composition

Nine previously unrecorded species of crabs were collected from the Maavah reef system after the Sumatran tsunami (Tables 1 and 2): *Chlorodiella cytherea*, *Cyclodius* sp., *Etisus laevimanus*, *Pilumnus* sp., *Macrophthalmus verreauxi*, *Ptychognathus barbatus*, *Paramedaeus* sp., *Platypodia granulosa* and *Epixanthus frontalis*. Species overlaps of the tsunami-transported species were found in sites 1, 2, 4 and 6. Of the nine species, six were collected in site 6 (tsunami-formed sand dune) in January 2005 itself, and these species slowly started to appear in the other sites in the following months (Table 2). Interestingly, *Liomera rugata*, *Paractea* sp., *Lydia annulipes* and *Tylocarcinus styx* from site 1, *Kraussia*

**Table 1** Pre- and post-tsunami (spatio-temporal) distribution of the brachyuran crabs at the study sites

No.	Name	Spatio-temporal distribution	No.	Name	Spatio-temporal distribution
1	<i>Calappa lophos</i>	S1 (P1, P2, P), S4 (P1, P2, P)	31	<i>Paractea</i> sp.	S1 (P1, P2)
2	<i>Portunus longispinosus</i>	S1 (P1, P2 <sup>b</sup> , P), S4 (P1, P2, P)	32	<i>Lybia tesellata</i>	S1 (P1, P2), S2 (P1, P2, P)
3	<i>Portunus orbitosinus</i>	S1 (P1, P2, P), S4 (P1, P2, P)	33	<i>Kraussia rugulosa</i>	S1 (P1, P2, P), S2 (P1, P2)
4	<i>Thalamita danae</i>	S1 (P1, P2, P), S4 (P1 <sup>c</sup> , P2 <sup>b</sup> )	34	<i>Palapedia rastripes</i>	S1(P1, P2, P), S2 (P1 <sup>b</sup> , P2 <sup>c</sup> ), S4 (P1, P2, P)
5	<i>Thalamita picta</i>	S2 (P1, P)	35	<i>Actumnus</i> sp.	S1 (P1, P2, P)
6	<i>Thalamita admete</i>	S1 (P1 <sup>d</sup> , P2 <sup>d</sup> , P <sup>d</sup> ), S4 (P1 <sup>d</sup> , P2 <sup>c</sup> , P <sup>c</sup> )	36	<i>Pilumnus</i> sp. <sup>a</sup>	S1 (P), S4 (P)
7	<i>Thalamita chaptalii</i>	S1 (P1 <sup>c</sup> , P2 <sup>c</sup> , P <sup>c</sup> ), S4 (P1 <sup>d</sup> , P2 <sup>b</sup> , P <sup>b</sup> )	37	<i>Eriphia scabricula</i>	S1 (P1 <sup>b</sup> , P2 <sup>b</sup> , P), S4 (P1 <sup>b</sup> , P2 <sup>b</sup> , P)
8	<i>Carpilius convexus</i>	S1 (P1, P2, P)	38	<i>Eriphia sebana</i>	S1 (P1, P), S2 (P1, P2, P), S3 (P1, P2, P)
9	<i>Leptodius</i> sp.	S1 (P1, P2, P), S2 (P1, P2, P)	39	<i>Epixanthus frontalis</i> <sup>a</sup>	S3 (P)
10	<i>Leptodius nudipes</i>	S2 (P1 <sup>f</sup> , P2 <sup>f</sup> , P <sup>f</sup> )	40	<i>Lydia annulipes</i>	S3 (P1, P2, P)
11	<i>Leptodius sanguineus</i>	S1 (P1, P2, P), S3 (P1, P2, P)	41	<i>Tylocarcinus styx</i>	S1 (P1, P2), S2 (P1, P2), S4 (P1, P2)
12	<i>Leptodius exaratus</i>	S1 (P1, P2, P), S2 (P1, P2, P), S3 (P1 <sup>c</sup> , P2 <sup>b</sup> , P), S4 (P1, P2, P)	42	<i>Camposcia retusa</i>	S1 (P1)
13	<i>Xanthias lamarckii</i>	S1 (P1 <sup>b</sup> , P2 <sup>b</sup> , P), S2 (P1, P2, P)	43	<i>Neopalicus contractus</i>	S1 (P1, P2), S4 (P1, P2, P)
14	<i>Liomera rugata</i>	S1 (P1, P2), S2 (P1 <sup>b</sup> , P2, P)	44	<i>Pseudozius caystrus</i>	S2 (P1, P2, P)
15	<i>Liomera</i> sp. 1	S1 (P1, P2, P), S2 (P1, P2, P)	45	<i>Eucrate</i> sp.	S1 (P), S2 (P1, P2, P)
16	<i>Liomera</i> sp. 2	S1 (P1, P2, P), S2 (P1, P2, P)	46	<i>Ocypode ceratophthalmus</i>	S3 (P1 <sup>b</sup> , P2, P <sup>b</sup> ), S5 (P1, P2, P)
17	<i>Euxanthus</i> sp.	S1 (P), S2 (P1 <sup>b</sup> , P2, P)	47	<i>Uca tetragonon</i>	S3 (P1, P2, P), S4 (P1, P2, P)
18	<i>Paramedaeus</i> sp. <sup>a</sup>	S2 (P), S4 (P)	48	<i>Macrophthalmus verreauxi</i> <sup>a</sup>	S1 (P)
19	<i>Platypodia granulosa</i> <sup>a</sup>	S4 (P)	49	<i>Macrophthalmus boscii</i>	S1 (P1, P), S3 (P)
20	<i>Etisus laevimanus</i> <sup>a</sup>	S1 (P), S4 (P)	50	<i>Grapsus albolineatus</i>	S1 (P1, P2, P), S3 (P1, P2, P)
21	<i>Etisus frontalis</i>	S1 (P1, P2, P), S4 (P1, P2, P)	51	<i>Grapsus longitarsis</i>	S3 (P2, P)
22	<i>Pilodius areolatus</i>	S1 (P1 <sup>c</sup> , P2 <sup>b</sup> , P), S2 (P1, P2, P)	52	<i>Pachygrapsus minutus</i>	S1 (P1 <sup>d</sup> , P2 <sup>d</sup> , P <sup>d</sup> ), S2 (P1 <sup>f</sup> , P2 <sup>f</sup> , P <sup>f</sup> ), S3 (P1, P2, P), S4 (P1, P2, P)

**Table 1** continued

No.	Name	Spatio-temporal distribution	No.	Name	Spatio-temporal distribution
23	<i>Pilodius nigrocrinitus?</i>	S1 (P1, P2 <sup>b</sup> , P), S2 (P1, P2, P)	53	<i>Pachygrapsus plicatus</i>	S1 (P1 <sup>b</sup> , P2, P <sup>b</sup> ), S2 (P1 <sup>b</sup> , P2, P)
24	<i>Pilodius pugil</i>	S1 (P1, P2, P)	54	<i>Pachygrapsus</i> sp.	S1 (P1 <sup>c</sup> , P2 <sup>b</sup> , P), S2 (P1 <sup>c</sup> , P2 <sup>c</sup> , P <sup>d</sup> ), S3 (P1), S4 (P1, P2, P)
25	<i>Cyclodius scabriculus</i>	S1 (P1 <sup>b</sup> , P2 <sup>b</sup> , P <sup>b</sup> ), S2 (P1 <sup>b</sup> , P2 <sup>b</sup> , P)	55	<i>Parasesarma</i> sp.	S3 (P1, P2, P)
26	<i>Cyclodius granulatus</i>	S1(P1 <sup>b</sup> , P2 <sup>b</sup> , P), S2 (P1, P2, P)	56	<i>Metasesarma obseum</i>	S3 (P2, P)
27	<i>Cyclodius areolatus</i> <sup>a</sup>	S1 (P), S4 (P <sup>b</sup> )	57	<i>Ptychognathus barbatus</i> <sup>a</sup>	S3 (P)
28	<i>Chlorodiella nigra</i>	S1 (P1 <sup>b</sup> , P2 <sup>b</sup> , P), S2 (P1 <sup>b</sup> , P2 <sup>b</sup> , P)	58	<i>Acmæopleura</i> sp.	S3 (P1 <sup>b</sup> , P2, P)
29	<i>Chlorodiella cytherea</i> <sup>a</sup>	S1(P), S4 (P)	59	<i>Percnon planissimum</i>	S1 (P1, P2, P), S2 (P1, P2, P)
30	<i>Actaeodes tomentosus</i>	S1 (P1 <sup>c</sup> , P2 <sup>c</sup> , P), S2 (P1, P2 <sup>b</sup> , P)			

Average abundance (no./m<sup>2</sup>) for each time period (P1, P2, P) is mentioned; species with average abundance lesser than 1(no./m<sup>2</sup>) is not indicated

S1 site 1, S2 site 2, S3 site 3, S4 site 4, S5 site 5, P1 pre-tsunami period 1, P2 pre-tsunami period 2, P post-tsunami period

<sup>a</sup> Tsunami-brought species

<sup>b</sup> abundance in between 1 & 2

<sup>c</sup> abundance in between 2 & 5

<sup>d</sup> abundance in between 5 & 10

<sup>e</sup> abundance in between 10 & 20

<sup>f</sup> abundance above 20

*rugulosa*, *Tylocarcinus styx* and *Camp oscia retusa* from site 2, *Pachygrapsus* sp. from site 3 and *Thalamita danae* from site 4 were found during the pre-tsunami period but not during the post-tsunami period (Table 1).

### 3.2 Impact of the tsunami on brachyuran abundance and diversity

Time plots of sites 1 and 2 showed that there is fall in abundance of the post-tsunami brachyuran community when compared with the pre-tsunami community, and the Mann–Kendall trend analysis confirmed that these time trends are negative and statistically significant (Fig. 2); the nested ANOVA performed for the same data sets of time plots has also confirmed that the pre- and post-tsunami periods have statistically significant variations (Table 3). In site 4, the time plot revealed that P2 and P were similar abundance-wise, although this trend was not statistically significant as per the Mann–Kendall trend analysis (Fig. 2). However, these variations between periods were detected by the nested ANOVA (Table 3), and this is presumably because the nested ANOVA may be more sensitive in detecting changes between abundances of periods than the Mann–Kendall trend analysis.

**Table 2** Numerical abundance and size range of the brachyuran species recorded after the tsunami, 2004, from the study sites

Site	No.	Name of the crabs recorded after the tsunami	Number of crabs in different months (n/m <sup>2</sup> )												Size range in cm	
			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Breadth	Length				
1	1	<i>Chlorodiella cytherea</i>	0	0	0	0.05	0.15	0	0	0	0	0	0	0.8–1.2	0.5–0.8	
	2	<i>Cyclodius areolatus</i>	0	0	0.05	0.1	0.15	0	0.05	0.15	0	0.05	0.15	0.6–1.9	0.4–1.5	
	3	<i>Etisus laevimanus</i>	0	0	0	0.15	0.15	0.2	0	0.1	0.2	0	0.1	1.9–3.4	1.5–3.0	
	4	<i>Pilumnus</i> sp.	0	0	0	0.05	0	0.05	0	0	0.05	0	0	0.6–0.7	0.6–0.7	
	5	<i>Macrophthalmus verreauxi</i>	0	0	0	0.05	0.05	0	0	0	0	0	0	1.7	1.2	
2	1	<i>Paramedaeus</i> sp.	0.2	0.05	0	0	0	0	0	0	0	0	0	0.5–0.9	0.3–0.6	
3	1	<i>Pychognathus barbatus</i>	0.25	0.5	0.1	2.25	0	0.75	0.3	0.05	0.05	0.05	0.05	0.5–1.0	0.5–1.1	
	2	<i>Epixanthus frontalis</i>	0	0	0	0	0.1	0	0	0.05	0	0	0.05	2–3.6	1.7–2.8	
4	1	<i>Chlorodiella cytherea</i>	0	0	0.1	0.75	0.35	0	0.2	0.1	0.2	0.1	0.1	0.6–1.1	0.4–0.8	
	2	<i>Cyclodius</i> sp.	0	0	1.9	0.75	0.95	0.35	0.85	0.3	0.85	0.3	0.3	0.7–1.9	0.5–1.5	
	3	<i>Etisus laevimanus</i>	0	0	0	0.35	0.55	0.4	0.15	0.25	0.15	0.25	0.25	1.2–2.7	0.8–2.2	
	4	<i>Pilumnus</i> sp.	0	0	0	0	0	0.1	0.05	0	0.05	0	0	0.6–0.8	0.6–0.8	
	5	<i>Paramedaeus</i> sp.	0	0	0	0.05	0	0	0	0	0.2	0.3	0.3	0.7–1.0	0.5–0.7	
	6	<i>Platypodia granulosa</i>	0	0	0	0.05	0	0	0	0	0	0	0	2	1.7	
6	1	<i>Chlorodiella cytherea</i>	0.45	0.3	0.9	0.7	1.05	0.3	0.6	0.4	0.6	0.4	0.4	0.7–1.2	0.5–0.8	
	2	<i>Cyclodius</i> sp.	0.7	0.35	1.6	1.2	0.85	0.4	1.55	0.8	1.55	0.8	0.8	0.6–1.9	0.4–1.5	
	3	<i>Etisus laevimanus</i>	0.5	0.35	0.45	0.6	0.15	0.3	0.35	0.2	0.35	0.2	0.2	1.0–2.7	0.7–2.2	
	4	<i>Pilumnus</i> sp.	0.6	0.7	0.3	0.9	20	1.15	0.45	0.35	0.45	0.35	0.35	0.6–1.1	0.6–1.0	
	5	<i>Paramedaeus</i> sp.	0.85	0.95	0.95	1.2	1.5	0.25	0.6	0.95	0.6	0.95	0.95	0.5–1.4	0.3–1.1	
	6	<i>Platypodia granulosa</i>	1.1	0.6	0.4	0.55	0.3	0.35	0.45	0.15	0.45	0.15	0.15	1.1–2.5	0.8–1.9	

In site 5, no new species were recorded after the tsunami

Site 1 North Lagoon, Site 2 Reef Front, Site 3 North Beach, Site 4 South Lagoon, Site 6 Eastern Side of Jetty



**Table 3** Results of the nested ANOVA obtained for the pre- and post-tsunami period’s abundance data sets at the study sites

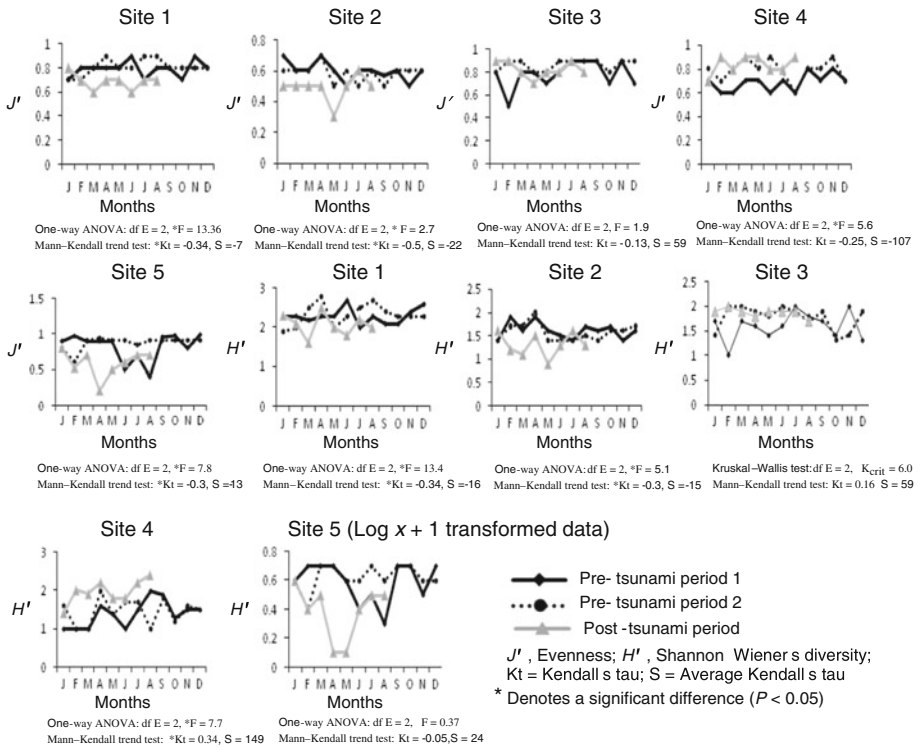
Sites	1–5	1		2		3		4 <sup>a</sup>		5	
Effects	Df	SS	F	SS	F	SS	F	SS	F	SS	F
Year (PR-P)	1	44.61	0.63	265.2	1.2	8.64	0.65	0.4004	9.10*	9.83	1.2
Months (PR-P)	18	974.19	0.77	2487.0	0.62	268.01	1.12	1.0578	1.34	132.25	1.0
PR-P	1	1253.10	17.8*	4458.4	20.1*	0.0	0.00001	0.595	1.34	3.5	0.43
Error	11	775.2		2435.7		146.14		0.4819		89.95	
Total	31	3047.13		9646.2		422.79		1.9996		235.64	
Cochran C results		C = 0.55, P > 0.05		C = 0.57, P > 0.05		C = 0.462, P > 0.05		C = 0.494, P > 0.05		C = 0.47, P > 0.05	

PR pre-tsunami period, P post-tsunami period

\* Denotes a significant difference (P < 0.05)

<sup>a</sup> Log x + 1-transformed data set

Wherever variations in  $J'$  and  $H'$  values were witnessed (Fig. 3) between pre- and post-tsunami periods, there one-way ANOVA and Mann–Kendall trend tests showed statistically significant changes in temporal trends in sites 1–5, and there is one exception to this generalization,  $J'$  of site 4 (Fig. 3), in which Mann–Kendall trend analysis could not detect statistically significant trend changes. Tukey’s test revealed that mean values of pre- and post-tsunami groups (P1 and P; P2 and P) of  $J'$  and  $H'$  varied unlike the mean values of two pre-tsunami groups (P1 and P2) in sites 1, 2, 4 and 5 (Table 4). This suggests that there are changes in terms of evenness and diversity between pre- and post-tsunami brachyuran communities of sites 1, 2 and 4. Bray–Curtis analysis showed in sites 1–4 that pre-tsunami (P1 and P2) and post-tsunami periods (P) formed separate clusters (Fig. 4). The similarity level in these sites varied between ~62 % (site 4) and ~83 % (site 2). In site 5, P1 and P clustered together leaving P2 as an out-group (Fig. 4). SIMPER analysis revealed that in sites 1–4 dissimilarities between pre- and post-tsunami periods were considerably higher than those between either pre-tsunami periods (P1 and P2) (Table 5). In site 5 also a similar trend was seen, although the trend was not as prominent as in the other sites (Table 5). The first few species that contributed to 50 % dissimilarity within and between pre- and post-tsunami are shown in Table 6. This analysis revealed that the contribution of species recorded after tsunami and site-specific dominant species to dissimilarity within and between pre- and post-tsunami periods was patchy. Tsunami-transported species were never found to be among the species that contributed to 50 % dissimilarity in sites 1 and 2; in site 3 *Ptychognathus barbatus* was the lone species that contributed satisfactorily (18 %) to faunal dissimilarity between P2 and P and between P1 and P. Only in site 4 was the contribution of tsunami-transported species to dissimilarity prominent; this may be due to: (a) *Cyclodius areolatus*, a tsunami-transported species contributed to 9 % dissimilarity between P1 and P time periods, (b) about 31 % dissimilarity between P2 and P was accounted for three tsunami-transported species (Table 6). *Cyclodius areolatus*, *Paramedaeus* sp., *Etisus laevimanus*, *Pachygrapsus minutus*, *Thalamita admete* and *Thalamita chaptalii* were the dominant species in site 1 (Table 1). However, their contribution to dissimilarity was less than that of the less abundant species. In site 2, *Leptodius nudipes*,



**Fig. 3** Evenness ( $J'$ ) and Shannon–Wiener's diversity ( $H'$ ) of the brachyuran crabs during the pre- and post-tsunami periods of the study sites

*Pachygrapsus minutus* and *Pachygrapsus* sp. were the dominant species (Table 1). Between P1 and P2, *Leptodius nudipes* contributed to 14 % dissimilarity and the contribution of the other two species was meagre. The contribution of these three species to dissimilarity between P1 and P was higher (36 %). Between the time periods P2 and P, *Pachygrapsus minutus* and *Pachygrapsus* sp. contributed to 29 % dissimilarity and the contribution of *Leptodius nudipes* to dissimilarity was inconspicuous (Table 6). Although some species were dominant in terms of abundance in sites 3–5, their magnitude of dominance was not as strong as the species dominance of sites 1 and 2.

Stress values of MDS plot (Fig. 5) ranged between 0.2 (site 3) and 0.05 (site 5). In sites 1 and 2, post-tsunami months were grouped together well vertically, and in sites 3 and 4, pre- and post-tsunami months were well separated although some pre- and post-tsunami months were found to be overlapped; in site 5, post- and pre-tsunami months were separated horizontally. One-way ANOSIM revealed that P1 and P2 were similar in all the sites and that P1 and P and P2 and P were dissimilar in all the sites, implying that pre- and post-tsunami brachyuran faunal characteristics have changed (Table 7).

#### 4 Discussion

Post-tsunami brachyuran assemblages were dissimilar in terms of abundance, evenness and diversity in general when compared with pre-tsunami brachyuran assemblages. Species

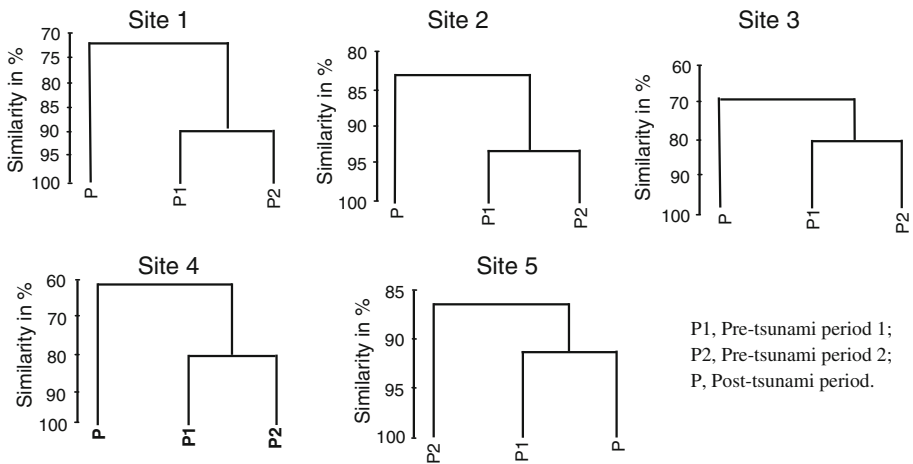
**Table 4** Results of the Tukey’s test, comparing the mean values of P1 and P2, P1 and P and P2 and P relative to  $J'$  and  $H'$

SI	Results of $J'$				Results of $H'$			
	Contrast	Diff.	Std. diff	Crit Val	Contrast	Diff.	Std. diff	Crit val
1	P1 versus P2	0.01	0.25	2.05	P1 versus P2	0.04	0.38	2.47
	P1 versus P*	0.12	4.5	2.05	P1 versus P	0.25	2.17	2.47
	P2 versus P*	0.12	4.73	2.05	P2 versus P*	0.28	2.5	2.47
2	P1 versus P2	0.02	0.7	2.47	P1 versus P2	0.02	0.26	2.47
	P1 versus P*	0.12	4.8	2.47	P1 versus P*	0.27	2.95	2.47
	P2 versus P*	0.1	4.1	2.47	P2 versus P*	0.25	2.72	2.47
4	P1 versus P2	0.07	2.29	2.47	P1 versus P2	0.04	0.33	2.47
	P1 versus P*	0.12	3.22	2.47	P1 versus P*	0.53	3.65	2.47
	P2 versus P	0.04	1.17	2.47	P2 versus P*	0.49	3.36	2.47
5	P1 versus P2	0.06	0.86	2.47				
	P1 versus P*	0.24	3.06	2.47				
	P2 versus P*	0.30	3.83	2.47				

Post hoc tests not conducted for the  $J'$  and  $H'$  values of site 3 and the  $H'$  values of site 5 as one-way ANOVA or Kruskal–Wallis tests could not detect any changes between periods

SI sites, P1 pre-tsunami period 1, P2 pre-tsunami period 2, P post-tsunami period,  $J'$  evenness,  $H'$  Shannon–Wiener’s diversity

\* Significant at 0.05 level



**Fig. 4** Bray–Curtis cluster analysis showing the similarities between pre- and post-tsunami periods in the study sites

compositions of the sites were altered by the entry of nine previously unrecorded species of crabs and the loss of nine species from the habitats. Abundance, evenness and diversity of post-tsunami brachyuran communities of sites 1 and 2 declined, whereas evenness and diversity of post-tsunami brachyuran assemblages of site 4 increased. The role of dominant species and newly recorded species after the tsunami in contributing to faunal

**Table 5** SIMPER results showing dissimilarity within pre-tsunami and between pre- and post-tsunami periods

Periods	Dissimilarity in %		
	P1 versus P2	P1 versus P	P versus P2
Site 1	7.5	34	35
Site 2	8	27	27
Site 3	22	43	34
Site 4	18	49	40
Site 5	12	14	18

P1 pre-tsunami period 1, P2 pre-tsunami period 2, P post-tsunami period

dissimilarities between pre- and post-tsunami periods was sometimes not obvious. There is a tendency to believe that the changes that have been noted in the post-tsunami brachyuran assemblages when compared with the pre-tsunami assemblages reported in this study might have occurred during the 21-month gap between the pre- and post-tsunami surveys. This possibility cannot be ruled out; however, during these intervening 21 months, no major events such as cyclones or typhoons or swells were reported in the study region. Moreover, during the 48-month pre-tsunami study, no changes in species composition were found, implying that the study sites are rather stable in terms of species richness. The nine species of crabs recorded after the tsunami were not collected even once during the pre-tsunami period in 24 samplings made in a 240-m<sup>2</sup> area in toto (10 m<sup>2</sup> per 1 month sampling). Six species recorded after the tsunami were collected in site 6 in January 2005, and they slowly started to appear in the other sites, revealing that these species were probably transported to site 6 initially by the tsunami and then spread to other sites. Had these six species already existed in the vicinity of the future site 6 before the tsunami, it is likely that they would also have been collected from the other pre-tsunami sites, which were similar in habitat. Some islands like Kunahandhoo and Hithadhoo are very close to Maavah and are separated from each other by very shallow lagoons; pre-tsunami collections from these islands included *Ptychognathus barbatus* and *Macrophthalmus verreauxi* (Kumar 2008). Kunahandhoo and Hitadhoo are located to the east of Maavah, and it is probable that the tsunami waves might have travelled from east to west as the tsunami waves originated in the east (Sumatra). Considering all these facts and based on the results of this study, it may be concluded that the tsunami has brought changes in the brachyuran assemblages of the study sites.

The nine species of crabs recorded after the tsunami in the Maavah reef system are common to Indo-Pacific ocean regions (Sakai 1976). *Chlorodiella cytherea*, *Platypodia granulosa*, *Macrophthalmus verreauxi* and *Ptychognathus barbatus* had already been reported in the Maldives (Borradaile 1902; Rathbun 1902; Garth 1974).

*Tylocarcinus styx* (from North Lagoon, Reef Front and South Lagoon), *Liomera rugata*, *Neopalicus contractus*, *Paractea* sp., *Lybia tessellata* (from North Lagoon), *Kraussia rugulosa*, *Camposcia retusa* (from Reef Front), *Pachygrapsus* sp. (from South-east Beach) and *Thalamita danae* (from South Lagoon) were probably dislodged by the tsunami waves or lost from the system under changed physico-chemical conditions. Certainly, a long-term study is required to confirm this speculation. Populations small in size will be difficult to sample accurately (Mantelatto et al. 2004). In the present sites too, such a phenomenon should be considered, for most of these species are less abundant. The decrease in the

**Table 6** The species contributing to 50 % dissimilarity within pre-tsunami and between pre- and post-tsunami periods in sites 1–5

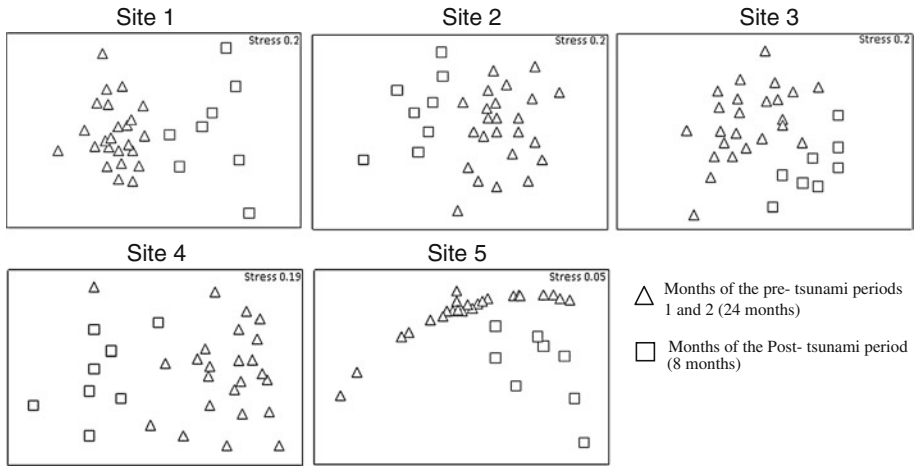
Sites	Species P1 versus P2	CSD%	Species P1 versus P	CSD%	Species P2 versus P	CSD%
1	<i>Portunus longispinosus</i>	11	<i>Pachygrapsus</i> sp.	6	<i>Portunus longispinosus</i>	6
	<i>Kraussia rugulosa</i>	10	<i>Chlorodiella nigra</i>	6	<i>Thalamita chaptalii</i>	6
	<i>Liomera rugata</i>	8	<i>Pilodius areolatus</i>	6	<i>Chlorodiella nigra</i>	5
	<i>Pachygrapsus plicatus</i>	7	<i>Thalamita chaptalii</i>	6	<i>Pachygrapsus</i> sp.	5
	<i>Eriphia sebana</i>	6	<i>Thalamita admete</i>	6	<i>Xanthias lamarckii</i>	5
	<i>Pachygrapsus minutus</i>	5	<i>Actaeodes tomentosus</i>	5	<i>Pachygrapsus minutus</i>	5
	<i>Carpilius convexus</i>	4	<i>Xanthias lamarckii</i>	5	<i>Actaeodes tomentosus</i>	5
			<i>Liomera rugata</i>	4	<i>Pilodius areolatus</i>	5
			<i>Pachygrapsus plicatus</i>	4	<i>Thalamita admete</i>	5
			<i>Pachygrapsus minutus</i>	4	<i>Liomera rugata</i>	4
2	<i>Leptodius nudipes</i>	14	<i>Pachygrapsus minutus</i>	16	<i>Pachygrapsus minutus</i>	17
	<i>Pachygrapsus plicatus</i>	14	<i>Pachygrapsus</i> sp.	11	<i>Pachygrapsus</i> sp.	12
	<i>Thalamita picta</i>	8	<i>Leptodius nudipes</i>	9	<i>Cyclodius scabriculus</i>	8
	<i>Kraussia rugulosa</i>	6	<i>Cyclodius scabriculus</i>	8	<i>Palapedia rastripes</i>	7
	<i>Leptodius</i> sp.	6	<i>Pachygrapsus plicatus</i>	7	<i>Eucrate</i> sp.	6
	<i>Liomera rugata</i>	5	<i>Palapedia rastripes</i>	6	<i>Eriphia scabricula</i>	5
3	<i>Metasesarma obseum</i>	15	<i>Leptodius exaratus</i>	18	<i>Leptodius exaratus</i>	18
	<i>Ocypode ceratophthalmus</i>	12	<i>Grapsus longitarsis</i>	15	<i>Ptychognathus barbatus</i> <sup>a</sup>	18
	<i>Grapsus longitarsis</i>	12	<i>Ptychognathus barbatus</i>	14	<i>Eriphia sebana</i>	12
	<i>Eriphia sebana</i>	10	<i>Lydia annulipes</i>	8	<i>Grapsus longitarsis</i>	12
	<i>Pachygrapsus minutus</i>	10				
4	<i>Thalamita chaptalii</i>	33	<i>Thalamita danae</i>	18	<i>Thalamita danae</i>	19
	<i>Thalamita admete</i>	21	<i>Thalamita chaptalii</i>	14	<i>Cyclodius areolatus</i> <sup>a</sup>	13
			<i>Thalamita admete</i>	13	<i>Paramedaeus</i> sp. <sup>a</sup>	9
			<i>Cyclodius areolatus</i> <sup>a</sup>	9	<i>Thalamita admete</i>	9
				<i>Etisus laevimanus</i> <sup>a</sup>	8	

Site 5 is not included as no new species were recorded there after the tsunami

P1 pre-tsunami period 1, P2 pre-tsunami period 2, P post-tsunami period, CSD% contribution of species to dissimilarity in %

<sup>a</sup> Tsunami-transported species

abundance of the brachyuran crabs in sites 1 and 2 during post-tsunami (Fig. 2) would otherwise be difficult to explain since abiotic and biotic changes caused by the tsunami are unknown. Sedimentation of coral colonies was reported by Zahir et al. (2006) and Gischler



**Fig. 5** Multidimensional scaling plots of the Bray–Curtis faunal similarity obtained for the square root-transformed abundance data obtained during the pre- and post-tsunami periods on a monthly basis from the five study sites. The faunal similarity between periods is shown by the relative distance

**Table 7** One-way ANOSIM results testing differences in brachyuran structure between pre- and post-tsunami periods

Global ANOSIM and pairwise comparison	Site 1		Site 2		Site 3		Site 4		Site 5	
	R	SL	R	SL	R	SL	R	SL	R	SL
Global ANOSIM	0.6	0.1	0.4	0.1	0.4	0.1	0.5	0.1	0.21	0.4
P1 versus P2	0.4	82.8	0.01	38.5	0.1	3.9	0.15	1.1	−0.02	59.2
P1 versus P	0.7	<b>0.1</b>	0.6	<b>0.1</b>	0.8	<b>0.1</b>	0.8	<b>0.1</b>	0.3	<b>0.3</b>
P2 versus P	0.7	<b>0.1</b>	0.68	<b>0.1</b>	0.5	<b>0.1</b>	0.62	<b>0.1</b>	0.48	<b>0.1</b>

Significant values are shown in bold (at 5 % level)

P1 pre-tsunami period 1, P2 pre-tsunami period 2, P post-tsunami period

and Kikinger (2007) in the Maldives reef systems as a consequence of tsunami, 2004, and Foster et al. (2006) showed that sedimentation has long-term effects on reefs.

Evenness and diversity of all sites were affected by the tsunami (Fig. 3), and these two components were stable in relative to temporal changes (Kumar and Wesley 2010). Figure 3 shows that  $J'$  and  $H'$  values of sites 1, 2 and 4 have changed in the post-tsunami period. From this figure, a trend is clear—an increase or decrease in  $J'$  value is concomitant with that of the  $H'$  value: (a)  $J'$  and  $H'$  values of sites 1 and 2 were found to have decreased in the post-tsunami period; (b) in site 4, both  $J'$  and  $H'$  values were increased during the post-tsunami period. Proportional diversity ( $H'$ ) is sensitive to both species richness and evenness (Pielou 1966). Excepting site 5, in all the other sites species richness changed in the post-tsunami brachyuran communities because of the addition of previously unrecorded species and the loss of species already present in sites.

In sites 1 and 2, pre- and post-tsunami brachyuran assembly changes were detected by Bray–Curtis analysis and nested ANOVA tests. Time plots and Mann–Kendall trend

analyses seemed to explain the reasons for these changes as they show a decrease in abundance during P (Fig. 2) in these sites. The addition of six species to the post-tsunami brachyuran community of site 1 might also have influenced the result. In site 3, a change in abundance was not apparent in the time plots and was not detected by the Mann–Kendall trend test. However, the results of the Bray–Curtis test distinguished pre- and post-tsunami brachyuran assemblages, and this is probably due to the shift in species composition of the post-tsunami brachyuran community.

The results for site 4 are ambiguous, and the Bray–Curtis analysis suggests that both the pre-tsunami brachyuran communities are more similar than the post-tsunami brachyuran community. Time period analysis revealed that the P2 and P brachyuran communities are more similar abundance-wise than P1. However, Mann–Kendall trend test showed that this trend is statistically insignificant. Nested ANOVA results also predicted within-year period changes. Table 1 shows that *Thalamita admete* and *Thalamita chaptalii* are the dominant species in this site and that their abundance is comparatively higher during P1, and this might have reflected in the time-series graph. Therefore, it appears that P1 and P brachyuran communities are more similar in abundance (result of time-series graph) and that the pre-tsunami brachyuran communities are more similar in species composition and abundance (Bray–Curtis analysis). It appears that the time plots show a decline within P2 at sites 1 and 2 and that continues into the post-tsunami period; Mann–Kendall trend analysis can detect changes in trends in general only and not trends between different periods. It must be noted that the nested ANOVA detected changes between pre- and post-tsunami periods in sites 1 and 2, and therefore, certainly there is a statistically significant abundance change between pre- and post-tsunami periods.

Tsunami-transported species and site-specific dominant species had no strong signatures in contributing to faunal dissimilarities between pre- and post-tsunami periods in sites 1 and 2; in sites 3 and 4, the contribution of tsunami-transported species to faunal dissimilarity is rather obvious. These two habitats are not species-rich like sites 1 and 2. It was observed that tsunami-transported species contributed to dissimilarity in small species-rich brachyuran communities.

Multivariate analyses compare two communities based on the number of common species they share at comparable level of abundance (Clarke and Warwick, 2001). Therefore, either alteration in species composition during the post-tsunami period in the study sites or changes in the brachyuran abundance during the post-tsunami period or the combined influence of these two factors on the brachyuran communities might have resulted in the spatial separation of pre- and post- brachyuran assemblages in MDS ordination and the detection of statistically significant differences between post- and pre-tsunami brachyuran communities by one-way ANOSIM in the study sites.

## 5 Conclusion

The December 2004 tsunami affected the species composition, abundance, evenness and diversity of the brachyuran assemblages of most of the sites. Species composition of the sites was altered by the appearance of nine previously unrecorded species of crabs and loss of nine species from the habitats after the tsunami. Abundance, evenness and diversity were found to be decreased because of the effect of the tsunami in many sites. Although faunal dissimilarities were conspicuous between pre- and post-tsunami periods, the roles of species recorded after the tsunami in contributing to these dissimilarities were prominent only in small species-rich sites (sites 3 and 4) and the role of dominant species in

contributing to faunal dissimilarities between pre- and post-brachyuran fauna is not prominent in general in all the study sites.

Several changes may be expected in the sites relative to changes in the population size of the newly recorded species or relative to their interaction with other indigenous species. In a sense, the population size of the immigrant species may increase or decrease or become obsolete because of the presence of favourable or unfavourable abiotic or biotic factors in their new environment, or the newly recorded species may out-compete the indigenous species, leading to the decline in their population. Therefore, it would be interesting to monitor the structural changes taking place in the brachyuran community in the study sites, influenced by the newly recorded species after the Sumatran tsunami.

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