Teoh *et al. Zoological Studies* 2014, **53**:67
http://www.zoologicalstudies.com/content/53/1/67

Zoological Studies
a SpringerOpen Journal

RESEARCH **Open Access**

Influence of habitat heterogeneity on the assemblages and shell use of hermit crabs (Anomura: Diogenidae)

Hong Wooi Teoh[1,2*], Muhammad Ali Syed Hussein[1] and Ving Ching Chong[2,3]

Abstract

Background: Two contrasting intertidal habitats on the western Sabah coast (Malaysia), one is a rocky-sandy-mud flat at Sepangar (N6°02′18.57″; E116°06′40.07″) and the other is a mangrove foreshore at Sulaman (N6°15′33.00″; E116°18′49.80″), are characterized by substrate zonation and homogeneous substrate (mud), respectively. Hermit crabs are one of the most conspicuous benthic macrofauna at both sites. The study examined the influence of habitat heterogeneity on the assemblages and shell use pattern of hermit crabs.

Results: The heterogeneous intertidal flat at Sepangar (five species) supported a higher diversity and abundance of hermit crabs compared to Sulaman mangrove foreshore (two species). Hermit crabs at Sepangar used a greater variety of shells (30 species) compared to those at Sulaman (two species). Zonation of hermit crab species occurred at Sepangar where *Diogenes klaasi* dominated at the high-tide mark and two *Clibanarius* species (*C. striolatus* and *C. merguiensis*) dominated at the low-tide mark. Considerable overlap in habitat use (mid- and lower shore) occurred between *D. tumidus* and the two *Clibanarius* species which appeared to influence shell use pattern.

Conclusions: This study supports the work of others showing that structurally complex habitats will allow habitat partition among species thus explaining the greater diversity and abundance of hermit crabs. Such a heterogeneous habitat provides a wider choice of shells for the hermit crabs, minimizing interspecific competition for the available shell resources.

Keywords: Hermit crabs; Diversity; Habitat heterogeneity; Tropical intertidal

Background

Hermit crabs are one of the most conspicuous and ecologically important groups of animals inhabiting intertidal and subtidal habitats (Schembri 1982). These animals are unique for their dependency on gastropod shells as a 'mobile home' to protect them from predators (Elwood et al. 1995) and reduce the risk of desiccation during emersion at low tide (Bertness and Cunnigham 1981). Despite the many world-wide studies on hermit crabs, those pertaining to hermit crab-shell interactions are more common than studies investigating habitat partitioning which are scarce especially in the Indo-Pacific region. The available literature on both macro- and micro-habitat preferences of hermit crabs including shell use pattern may indicate adaptations to reduce interspecific competition (Leite et al. 1998). Habitat partitioning has been demonstrated since closely related species show variable use of gastropod shells depending on the shell size, shape and availability (Teoh and Chong 2014), while a more heterogenous habitat provides more niches and ways to exploit the available resources (Bazzaz 1975).

At the intertidal zone, landmark studies on biological zonation are well established (Knox 2001; Harley 2003; Veloso et al. 2003; Rodil et al. 2006; Sacrosati and Heaven 2007), attributable to the accessibility of sites and the diversity of species of sessile and slow-moving animals that are readily enumerated (e.g. Connell 1972). There are several important factors influencing intertidal biological zonation which include wave exposure (Stephenson 1961; Knox 2001; Harley 2003), temperature (Wethey 1983), salinity (Druehl 1967) and substrate composition (Rai-mondi

---

* Correspondence: teohhongwooi@gmail.com
[1]Borneo Marine Research Institute, Universiti Malaysia Sabah, Sabah, Malaysia
[2]Present address: Institute of Biological Sciences, Faculty of Science, University of Malaya, Kuala Lumpur, Malaysia
Full list of author information is available at the end of the article

1988). Among these factors, sediment texture may invoke a relatively greater influence on distribution and maintenance of anomuran populations (Fransozo et al. 2008) as sediment is utilized by these animals as shelter and food source (Abele 1974). The adaptation of intertidal animals towards different environmental settings resulted in the formation of distinct ecological niches along the intertidal zone. This is exemplified by the unique features of rocky shores that exhibit prominent horizontal bands formed by different types of animals and plants (Nybakken 1982).

Shells influence the growth and reproduction of hermit crabs (Fotheringham 1976; Bertness 1981a; Elwood et al. 1995), and thus, the selection of a shell of optimum size and shape is essential for their survival. Hermit crab populations are limited by the availability, size and quality of their shells (Vance 1972). Since they rely on empty shells and rarely predate on gastropods or remove the flesh from dead gastropods, hermit crabs compete intra- or interspecifically for the shell resource (Bach et al. 1976). Although the availability of empty shells may be subjected to advective forces such as tides and waves as well as the hermit crabs themselves, the co-occurring assemblage of living gastropods typically reflects the availability of shells in intertidal mud habitats (Teoh and Chong 2014).

In the western coast of Sabah, Malaysia, the heterogeneous environment of Sepangar intertidal flat (Figure 1) is characterized by distinct substrate zonation ranging from a mixture of sand-mud, gravels, rocks, coral rubbles to large rocky boulders. On the other hand, Sulaman mangrove fringe, which is located about 30 km northeast from Sepangar, is characterized by homogenous environment dominated by sand-mud substrate. Hermit crabs are one of the most conspicuous benthic macrofauna at both sites. However, the contrasting habitat settings appear to evoke different adaptations among the hermit crab species, possibly influencing their diversity, abundance and shell use pattern. In this study, spatial distribution and shell use of the hermit crab community in Sepangar and Sulaman shores were quantified to answer the following research questions: 1) Does a structurally heterogeneous habitat host greater diversity and abundance of hermit crabs than homogeneous habitat? 2) Are shells used by hermit crabs more diverse in a heterogenous habitat than homogeneous habitat? 3) How are hermit crab species ecologically partitioned (distribution and shell use pattern) in relation to substrate zonation in the heterogenous habitat?

Methods

Field work

Field samplings were carried out in an intertidal rocky flat (N6°02′18.57″; E116°06′40.07″) at Sepangar Bay and fringing mangrove forest (N6°15′33.00″; E116°18′ 49.80″) at Sulaman, both sites located in the State of Sabah, Malaysia. A vast part of the intertidal rocky shore at Sepangar is uncovered during spring low tide to approximately 200 m from the highest tide mark. The Sulaman's mangrove area however has a lower, bare and muddy zone of about 50 m from the mangrove fringe to the sea which is completely exposed during spring low tide. Samplings were performed at both sites, each on three separate occasions in December 2007 and January 2008 during spring low tide.

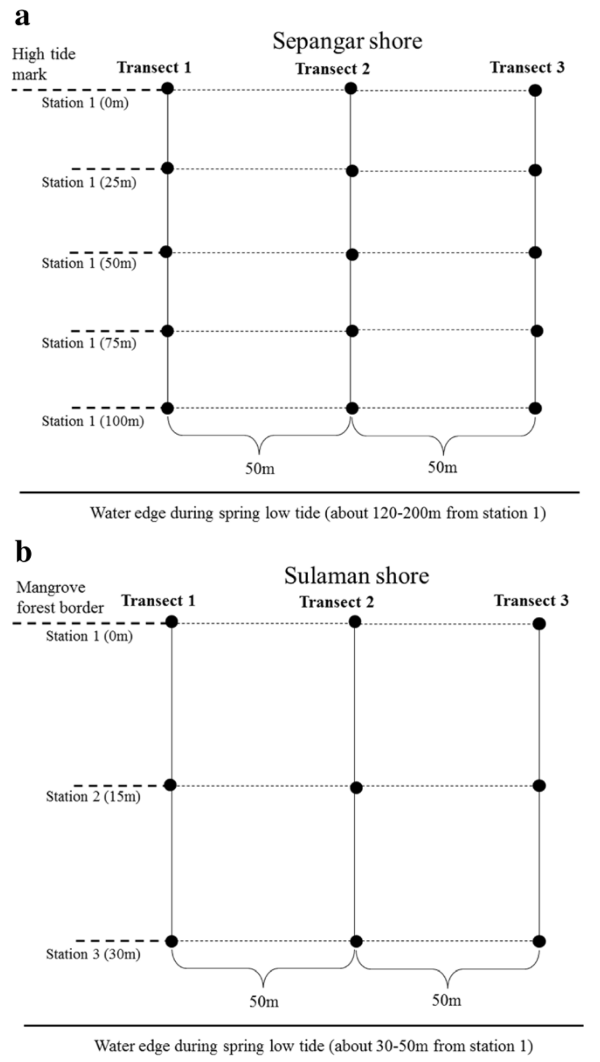

Figure 1 Schematic diagrams of sampling design at (a) Sepangar and (b) Sulaman shores.

At Sepangar shore, three 100-m transect lines were laid perpendicular to the shoreline 50 m apart between transects. Along each transect line, five stations were designated at intervals of 25 m. These stations were marked as 0, 25, 50, 75 and 100 m from the high-tide mark (Figure 1a). The 0 m marked the highest tide mark. At each station, 1 × 1 m quadrate sampling in triplicates were performed within a 5-m radius from each station point, taking care that unsampled quadrates were not disturbed while sampling. All hermit crabs that were found within each quadrate were collected starting from the sides of the quadrate to minimize escapement of hermit crabs. A similar sampling method was employed for Sulaman's bare mangrove zone, but given its narrow shore width (maximum 50 m), 30-m transect lines were laid with three designated stations set 15 m apart (Figure 1b). The 0-m mark however marked the lowest fringe of the mangrove forest. Substrates at the intertidal flat at Sepangar Bay were visually characterized based on the distinctive mixture of substrates present (Table 1) whereas the sediment at Sulaman's bare mangrove zone was characterized as homogenously dominated by sand-mud.

Laboratory procedures and data analyses

Hermit crabs were removed from their shell by gently pulling and twisting the crab against the direction of shell spiral. In the event when crabs were unable to be retrieved from their shell, a light hammer was used to gently crack the shell before pulling out the crab. Both hermit crabs and their shells were identified to the lowest taxa. The cephalothoracic length (SL) of each hermit crab, measured from the rotral tip to the posterior margin of the hardened portion of the carapace by using a pair of Vernier calipers (accuracy to 0.05 mm), was recorded. Sex of hermit crabs was determined based on position of gonopores; males have gonopores on the coxae of the fifth pereopods while females have gonopores on the coxae of the third pereopods. Density of hermit crabs was estimated as follows:

$$\text{Density}\ \left(\text{ind/m}^2\right) = \frac{\text{Number of individuals for species in a quadrate}}{\text{Area of each quadrate}\ \left(1\text{m}^2\right)}$$

Diversity and species richness of hermit crabs and their shells were quantified using Shannon-Wiener diversity index and Pielou's index of evenness expressed as follows:

- Shannon-Wiener index, $H' = -\Sigma(p_i \ln p_i)$,
  where p_i is the number of individuals for species i/ total number of individuals
- Pielou's index, $J' = H'/\ln s$
  where s is the total number of species

One-way analysis of variance (ANOVA) at 5% significance level was performed to determine the significant difference in density among sampling stations for each hermit crab species. All data were log transformed [log (x + 1)] if requirements for normality and homogeneity in variance as checked by Kolmogorov-Smirnov's and Levene's tests, respectively, were not fulfilled (Zar 2010). This analysis was performed using SPSS software version 12.0. Chi-square test at 5% significance level was performed to determine whether the distribution of the various hermit crab species is associated/dependent on sampling stations at both Sepangar and Sulaman shores.

Canonical correspondence analysis (CCA) was used to analyse and visualize the relationships between species of hermit crabs and their shells according to stations (Ter Braak 1986) at Sepangar rocky shore but not at Sulaman mangrove because of the low number of hermit crabs and shell species. The species data set comprised of hermit crab species with sex. The site or sample of data set comprised of sampling stations along the transect lines. The proportion of shell species used by hermit crabs were treated as environmental variables (co-variables) which comprised of the five most common shell types used by hermit crabs (*Clypeomorus batillariaeformis*, *Clypeomorus bifasciata*, *Cerithium zonatum*, *Rhinoclavis sinensis* and *Tenguella musiva*). The CCA was performed using CANOCO 4.5 software (Ter Braak and Smilauer 2002).

Table 1 Substrate characteristics of each station along a transect line at Sepangar shore

Station (m)	Substrate characteristics
0	Narrow sandy strip bordered by sand-mud with sparse gravels, rocks and coral rubbles
25	Sand-mud with sparse gravels, rocks and coral rubbles
50	Sand-mud overlain by dense gravels, rocks and coral rubbles
75	Gravels, rocks and coral rubbles
100	Large boulders and coral rubbles

Results

Diversity and abundance of the hermit crab community

Sepangar shore

A total of 850 specimens were collected comprising of five species belonging to two genera from the family Diogenidae: *Clibanarius merguiensis*, *C. striolatus*, *Diogenes klaasi*, *D. pallescens* and *D. tumidus*. The largest species was *C. striolatus* (SL 5.64 ± 2.55 mm), followed by *C. merguiensis* (5.45 ± 2.48 mm), *D. pallescens* (4.37 ± 2.39 mm), *D. klaasi* (4.28 ± 2.37 mm) and *D. tumidus* (4.14 ± 1.86 mm). The greatest diversity was recorded at 100 m ($H' = 1.09$) while the lowest at 0 m ($H' = 0.00$) where only one species (*D. klaasi*) was present. Hermit crab species at 100 m were the most evenly distributed ($J' = 0.79$) while they were the least evenly distributed at 0 m ($J' = 0.00$) (Table 2).

The overall highest density was reported for *D. tumidus* (8.98 ± 6.52 ind/m^2) which peaked at 50 m (16.95 ± 12.35 ind/m^2) but absent at 0 m (Figure 2a). This species was dominant at both 50 and 75 m stations (Figure 3a).

Table 2 Number of species, H′ and J′ values of hermit crabs at Sepangar shore

Station (m)	Number of species (*s*)	Shannon-Wiener (H′)	Pielou (J′)
0	1	0.00	0.00
25	4	0.91	0.65
50	5	1.04	0.64
75	3	0.71	0.65
100	4	1.09	0.79

Density of *D. tumidus* decreased gradually towards 100 m. On the other hand, *D. klaasi* was present in the first three stations (0, 25 and 50 m) and absent at 75 and 100 m. It was the sole species at 0 m with density of 6.25 ± 7.39 ind/m^2. Peak density of this species was observed at 25 m (10.64 ± 15.44 ind/m^2) (Figure 2b). Densities of both *Clibanarius* species generally increased towards the sea. At the highest station (0 m), *C. striolatus* was absent but gradually increased in density from 25 m (0.22 ± 0.54 ind/m^2) to 100 m (5.33 ± 8.92 ind/m^2) (Figure 2c). Similarly, *C. merguiensis* was absent at 0 m but had density peak at 100 m (6.11 ± 7.20 ind/m^2). Lowest density of this species was recorded at 75 m (1.17 ± 2.07 ind/m^2) (Figure 2d). The results from ANOVA showed no significant difference ($p > 0.05$) in density among stations for all species. The least abundant species in the study was *D. pallescens* which was present at 50 m (0.11 ± 0.17 ind/m^2) and 100 m (0.11 ± 0.27 ind/m^2). Chi-square test revealed strong dependency/association ($\chi^2 = 57.18$, df = 16, $p < 0.0001$) of hermit crab species on stations/zones in Sepangar shore.

Sulaman shore

There were only two species at Sulaman shore; the dominant *D. foresti* (SL 2.83 ± 1.03 mm) and another *Diogenes* sp. (Figure 3b) which was too small (SL 1.53 ± 0.42 mm) to be fully identified. Diversity and evenness indices were not computed for hermit crabs in Sulaman due to a low number of species. Density of *D. foresti* generally decreased from 3.33 ± 2.65 ind/m^2 at 0 m to 0.16 ± 0.28 ind/m^2 at 30 m (Figure 2e). *Diogenes* sp. was absent at 30 m and occurred in small number with an overall mean density of 0.21 ± 0.32 ind/m^2. Chi-square test revealed no association ($\chi^2 = 0.15$, df = 2, $p > 0.05$) between hermit crab species and station in Sulaman shore.

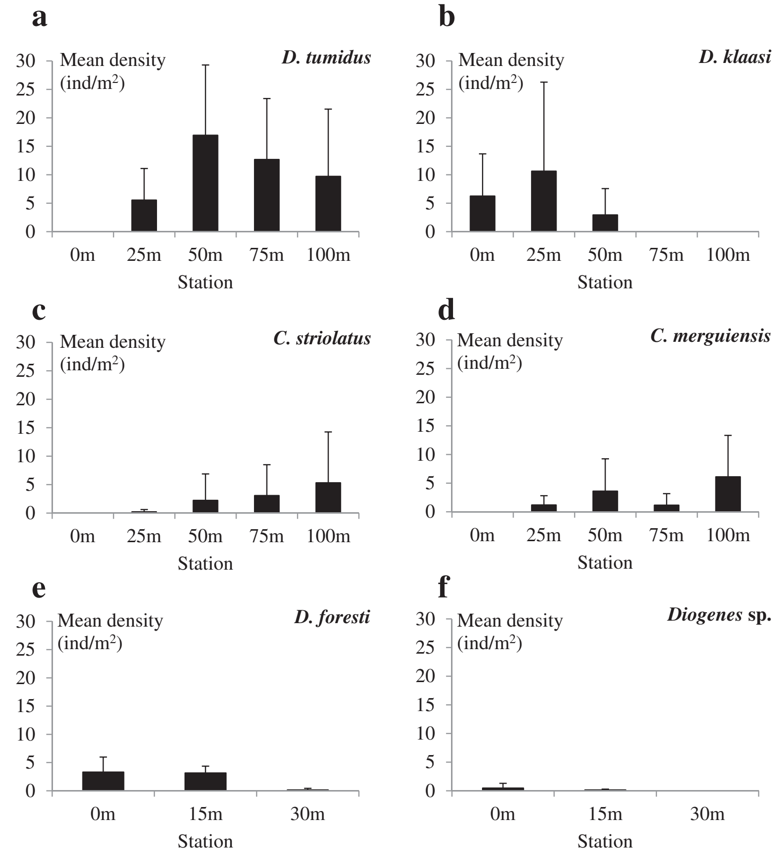

Figure 2 Mean density (+SD) of hermit crabs by species at Sepangar (a-d) and Sulaman (e-f) shores. *D. pallescens* from Sepangar was not included due to very low density and was absent in most stations.

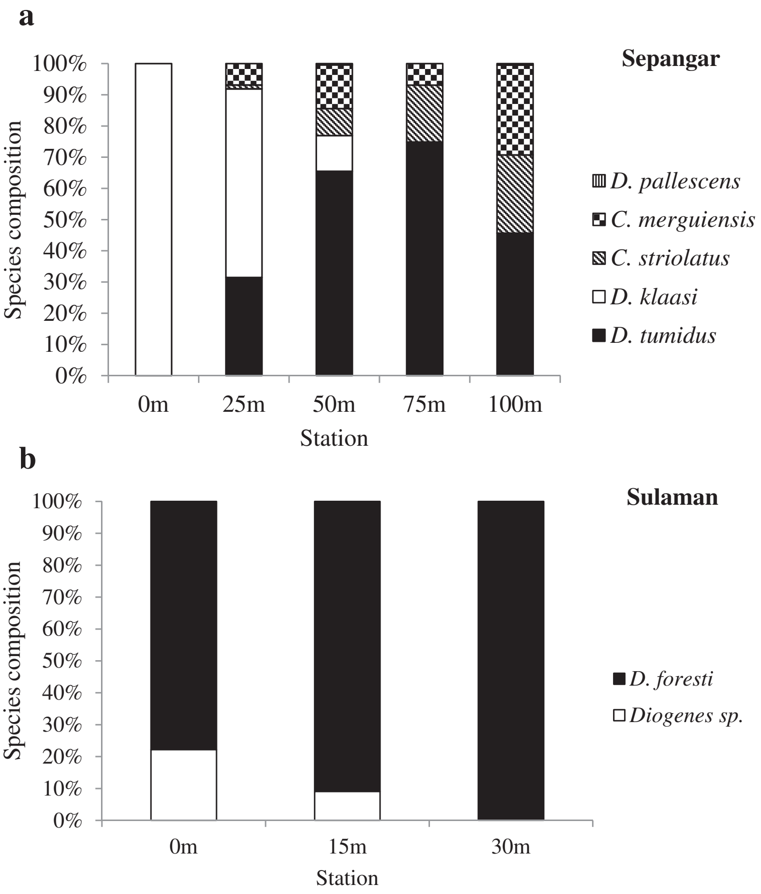

Figure 3 Species compositions of hermit crabs at (a) Sepangar and (b) Sulaman intertidal shores.

Shell use

At Sepangar shore, a total of 30 shell species were used by hermit crabs with most occupied shells being *Clypeomorus batillariaeformis* (75.59%) followed by *C. bifasciata* (8.61%) and *Rhinoclavis sinensis* (4.13%) while utilization of other type of shells were markedly low (Table 3). Shells used by hermit crabs at station 5 appeared to be the most diverse (H′ = 1.31, J′ = 0.51) among all stations whereas station 2 was the least diverse (H′ = 0.66, J′ = 0.30) (Table 4). The composition of hermit crabs based on the four most occupied shells is shown in Figure 4. The shell category 'others' represents the collective proportion of hermit crabs by species that used the remaining 26 shell types. The empty shells of *C. batillariaeformis* comprised the majority of shells used by all hermit crab species whereas shells of *C. bifasciata* represented substantial proportion of shells used by *C. striolatus* (17%), *D. tumidus* (11%) and *D. klaasi* (6%) (Figure 4). At Sulaman shore, only two shells were used by hermit crabs: *Nassarius livescens* and *Cerithidea cingulata* with the latter occupied by 98% of the hermit crabs (Table 3).

Distribution and shell use of hermit crabs: influence of spatiality

The CCA triplots ordination is shown in Figure 5. The first two axes of the species-environment relation explained 95.5% of the variation. The dominance of *D. klaasi* at station 1 and station 2 resulted in the most apparent spatial separation of this species with other hermit crab species. Despite *C. batillariaeformis* being the most commonly used shells by all hermit crab species (Figure 4), *D. klaasi* appeared relatively more exclusive in the use of this shell. The proportional use of *C. bifasciata* shells by *D. tumidus* was higher at stations 3 and 4 where the hermit crab was most dominant. The species *D. tumidus* exhibited higher degree of habitat overlap with *Clibanarius* species than with *D. klaasi*. At station 5, *Clibanarius* species were dominant where the proportional use of *T. musiva*, *C. zonatum* and *R. sinensis* shells was the highest among all stations. Unlike the *Diogenes*, both *Clibanarius* species exhibited a higher degree of habitat overlap. There was no observable spatial separation between sexes for all hermit crab species.

Table 3 Overall compositions (%) of shell types used by hermit crabs at Sepangar and Sulaman shores

Shell type	Sepangar (%)	Sulaman (%)
Angaria delphinus	0.24	-
Angaria sp.	0.12	-
Canarium labiatum	0.12	-
Canarium urceus	0.24	-
Cerithidea cingulata	-	98.00
Cerithium zonatum	2.00	-
Clypeomorus batillariaeformis	75.59	-
Clypeomorus bifasciata	8.61	-
Clypeomourus pellucida	0.24	-
Cronia buccinea	0.35	-
Conomurex luhuanus	0.24	-
Drupella concatenata	0.24	-
Drupella cornus	0.12	-
Euchelus asper	0.24	-
Morula fiscella	0.24	-
Nassarius livescens	-	2.00
Nassarius olivaceus	0.12	-
Natica stellata	0.12	-
Neritopsis radula	0.12	-
Nodilittorina biangulata	0.12	-
Patelloida saccharina	0.24	-
Pictocolumbella ocellata	0.12	-
Pyrene sp.	0.24	-
Rhinoclavis sinensis	4.13	-
Rhinoclavis sp.	0.24	-
Tenguella musiva	2.95	
Terebralia palustris	0.12	-
Trochus maculatus	0.12	-
Turbo argyrostomus	0.47	-
Umbonium vestiarium	0.12	-
Unidentified A	1.53	-
Unidentified B	0.71	-

Table 4 Number of species and H′ and J′ values of occupied shells at Sepangar shore

Station (m)	Shannon-Wiener (H′)	Pielou (J′)	Number of species
0	1.17	0.53	9
25	0.66	0.30	9
50	0.99	0.35	17
75	1.08	0.43	12
100	1.31	0.51	13

Discussion

This study reveals the apparent influence of habitat heterogeneity towards the diversity and abundance of hermit crabs. The more complex intertidal shore with distinct substrate zonation at Sepangar hosts higher diversity and abundance of hermit crabs as compared to the homogeneous (sand-mud) mangrove shore at Sulaman. Such disparity in hermit crab assemblages between habitats has also been observed by De Grave and Barnes (2001) at the coastal shores of Mozambique islands where *Clibanarius virescens* dominated the small island shores that were less heterogeneous compared to large islands where shores were more heterogeneous and had more diverse hermit crab assemblage. The species diversity in the structurally complex habitat is greater due to the presence of more niches and ways of exploiting the resources (Bazzaz 1975). The present study recorded five species of hermit crabs in the heterogeneous habitat of Sepangar's rocky shore whereas only two species were found at the homogeneous habitat of Sulaman's bare mangrove zone. Such a difference in the hermit crab assemblage attributed to habitat complexity has also been reported in southern Thailand where corals and rocky shores had 16 and 9 species, respectively, compared to two and four species on the bare shore of mangroves and mudflats, respectively (McLaughlin 2002). Similarly, more species were also associated with structurally complex coral reefs (24 species) and rocky shore (19 species), as compared to the structurally simple mudflats (seven species) in the South China Sea region (Rahayu 2000).

The difference in hermit crab assemblages among habitats is likely to result from the variety (type), availability and suitability of gastropod shells. This is because occupancy of optimum (size and shape) shells is fundamental for the survival of hermit crabs (Elwood et al. 1995). Complex habitats with variety of substrate types are known to support a greater variety of gastropod populations (Mantelatto and Garcia 2002). Such habitats are likely to offer greater assortment of shells to hermit crabs. In this study, the influence of habitat heterogeneity on the shell use of hermit crabs is apparent such that the shells that were used by the hermit crabs were more diverse at Sepangar shore (30 shell species) than Sulaman shore (two shell species). Therefore, the more diverse shells available at Sepangar shore support greater diversity of hermit crabs whereas the low diversity of available shells at Sulaman shore limits the diversity of hermit crabs.

The spatial segregation related to habitat heterogeneity is demonstrated by hermit crab populations at the intertidal zone in Sepangar shore. The presence of clear substrate zonation either by a type or mixture of substrates at the site may have resulted in the spatial confinement of hermit crab species at different zone along the intertidal area (see Turra and Denadai 2002; Fransozo et al.

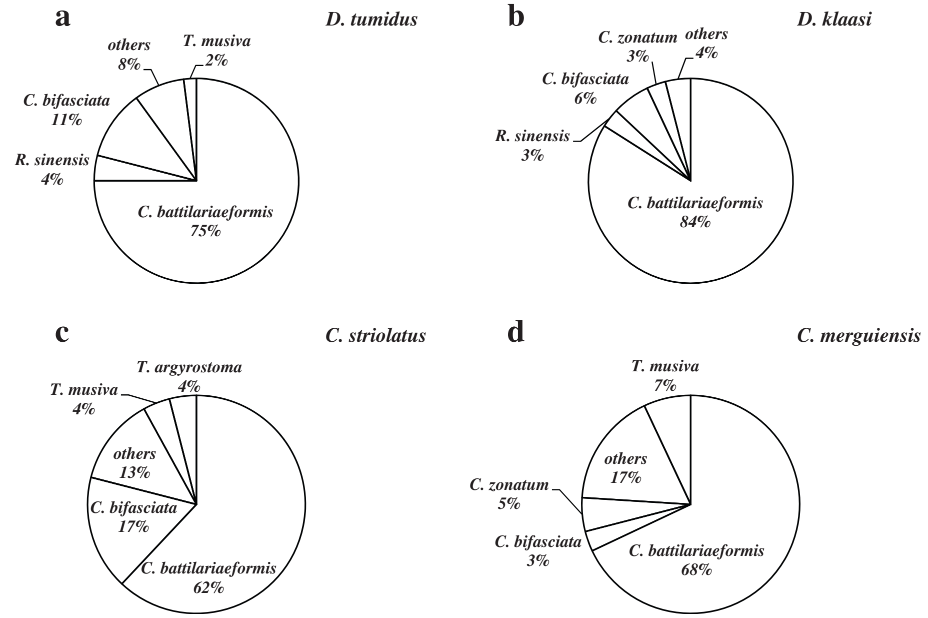

Figure 4 Composition of shells commonly occupied by different hermit crab species (a-d) at Sepangar shore.

2008). Habitat zonation among sympatric hermit crab species was also observed by Bertness (1981b) on three species of hermit crabs: *Calcinus obscures*, *C. albidigitus* and *Pagurus* sp. on a rocky shore whereby *C. obscures* was distributed from a middle to low intertidal zone and *C. albidigitus* was distributed from a middle to high intertidal zone whereas *Pagurus* sp. was confined at a lower intertidal zone.

The spatial separation of *D. klaasi* with other species particularly at a high-tide mark (0 m) indicates that this

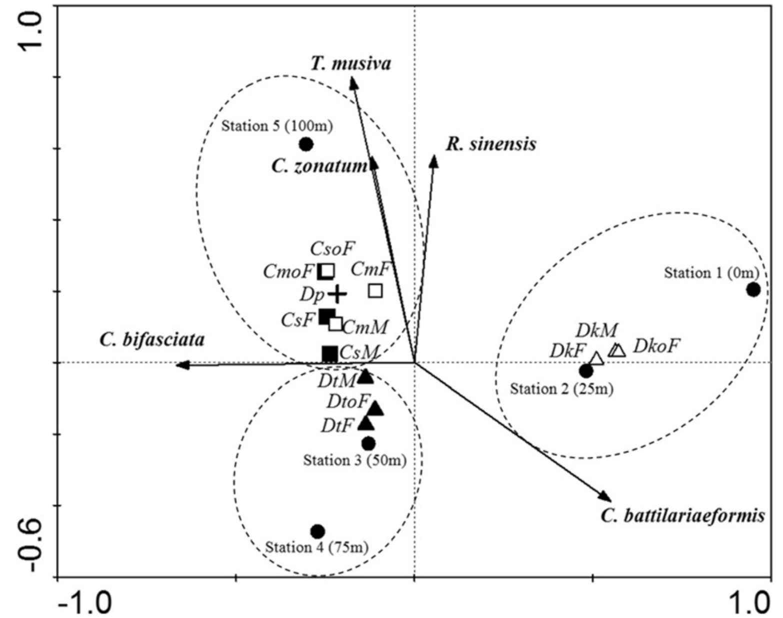

Figure 5 CCA triplots of the relationships between hermit crab species and their shells at Sepangar shore. Direction of arrow indicates the proportional increase in shell species used by hermit crabs. Solid circles indicate sampling stations/zones along transect. Filled and hollow triangles indicate hermit crabs *D. tumidus* (*Dt*) and *D. klaasi* (*Dk*), respectively. Filled and hollow squares indicate hermit crabs *C. striolatus* (*Cs*) and *C. merguiensis* (*Cm*), respectively. Cross indicates hermit crab *D. pallescens* (*Dp*). '*M*', '*F*' and '*oF*' indicate male, non-ovigerous female and ovigerous female, respectively. Ellipsoid envelops the dominant hermit crab species at the indicated sampling stations.

species is more adapted to sand-mud conditions which characterized station 1 (0 m) and station 2 (25 m) whereas its sympatric congener, *D. tumidus*, is dominant at station 3 (50 m) and station 4 (75 m) where the substrate comprised of loose rubbles like gravel, rocks and coral remnants. Both *Clibanarius* species are more adapted to zones that are structurally more complex based on their increasing abundance from 50 to 100 m and their low presence at the high-tide mark where the substrate is more homogenous. The distribution and coexistence of hermit crab species as modulated by substrate type have been shown by Turra and Denadai (2002). They demonstrated experimentally the substrate preference of hermit crabs, under allopatric (single species) and sympatric (three species) (*C. antillensis*, *C. sclopetarius* and *C. vittatus*) conditions, for four substrate types: rocky, pebble, sand and mud. Both *C. antillensis* and *C. sclopetarius* showed more similarity in the pattern of substrate selection under sympatric than allopatric condition, suggesting the mutual influence of coexisting species on substrate selection, whereas substrate selection by *C. vittatus* differed subtly between allopatric and sympatric conditions.

Except at the highest station (0 m), there was considerable overlap in habitat use particularly between *D. tumidus* and the *Clibanarius* species. Among all species, *D. tumidus* appears to be more adaptable to a mixed substrate type based on its higher abundance from 25 to 100 m. Hermit crabs are able to employ different feeding modes depending on the available food sources (Schembri 1982). The mobility and versatility of feeding habits of hermit crabs increase their capability of foraging large areas for food and, thus, bringing them into contact with a variety of substratum. Such ability to cope with the multiplicity of substratum and utilize the variety of food demonstrates the adaptive value of hermit crabs (Schembri 1982). Hermit crab adaptability was also observed in three common intertidal hermit crabs: *Pagurus geminus*, *Pagurus lanuginosus* and *Clibanarius virescens* on a rocky shore in Japan which exhibited apparent but not distinct habitat partitions due to spatial overlaps (Imazu and Asakura 1994).

The high standard deviation of the density and high coefficient of variation between 84% and 207% suggest patchy distribution due to the clustering of the hermit crabs. Clusters of particularly *Diogenes* species in this study were observed on substrates ranging from sand-mud to rocks and gravels. Forming clusters may be advantageous in minimizing risk of desiccation during emersion at low tide (Gherardi and Vannini 1991). This is indicated by less mobility of hermit crabs in a cluster compared to individuals found in tide pools. It is also commonly suggested that clustering serves as a platform for shell exchange among hermit crabs to acquire optimum shell from their conspecifics through elaborate communication mechanisms (Gherardi et al 1994).

Shells of 30 species were occupied by hermit crabs at Sepangar shore; however, *C. batillariaeformis* being the most common snail comprised the majority (75.6%) of the occupied shells. The availability of gastropod shells is an important factor in determining the shell selection pattern of hermit crabs (Bertness 1982). In a Brazilian inlet, hermit crabs *Clibanarius antillensis* and *Calcinus tibicen* were observed to frequently use shells of *Tegula viridula* which was the most abundant gastropod in the area (Floeter et al 2000). In this study, the number of shell species occupied by hermit crabs was high, considering the small sampling area covered (about 1 ha in total). In comparison, Nakin and Somers (2007) recorded 21 species of gastropod shells used by *C. virescens* at three separate sites of a South African coast, while Benvenuto and Gherardi (2001) recorded 20 species of gastropod shells occupied by *C. erythropus* in a rocky Mediterranean shore.

Besides its greater availability, *C. batillariaeformis* shell is characterized by deep spiralisation which allows greater water retention, advantageous to hermit crabs to overcome thermal stress during emersion (Bertness 1982). Although other shells may offer a similar advantage, their use by hermit crabs may be limited by the rare occurrence of the shells and/or incompatible size. Occupying shells smaller than the optimal size, such as shells of *Pyrene* sp., may expose the hermit crab to predators while occupying heavier shells such as shells of *Canarium* sp. and *Angaria* sp. would incur high energetic cost on the hermit crab, slowing its growth and reproduction ability (Osorno et al. 2005).

Despite *C. batillariaeformis* being the most common shells used by all hermit crab species, *D. klaasi* appears to be more exclusive in its use of this shell. Being the sole species at the high shore (0 m) and dominant at midshore (25 m), *D. klaasi* has less competition from other hermit crab species to acquire *C. batillariaeformis* shells, and hence, there is less need to occupy other shells. The high abundance of the *Clibanarius* species from 50 to 100 m put them in a direct competition with *D. tumidus*. This may have caused the slight shift in shell use in favour of *C. bifasciata* by *D. tumidus* and *C. striolatus*. Shells used by hermit crabs were most diverse at the low shore (100 m) where *Clibanarius* species were dominant. *Clibanarius* is able to use more variety of shells due to their larger size compared to the *Diogenes* species. In addition, some large *Clibanarius* may not be able to occupy the small *C. batillariaeformis* shells and, thus, are more dependent on other shell types.

Conclusions

This study shows that structurally more complex habitats will host a greater diversity and abundance of hermit crabs. This is similarly shown in their shell use where hermit crabs occurring in the more heterogeneous habitat used a greater variety of shell species. Substrate heterogeneity along the intertidal shore results in hermit crab zonation but with some overlap in habitat use that appears to influence the shell use pattern.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

THW and CVC wrote the manuscript. THW carried out the sampling and laboratory works. The idea of this study was first conceived by MA who had also participated in some of the field works with THW. The final manuscript was read and approved by all authors.

Acknowledgements

The authors would like to thank Borneo Marine Research Institute, Universiti Malaysia Sabah for provision of laboratory space, equipment, chemicals and other necessary tools for this study. Special thanks are due to Dr. Dwi Listyo Rahayu from Indonesian Institute of Science (LIPI) for identification and confirmation of hermit crab species.

Author details

[1]Borneo Marine Research Institute, Universiti Malaysia Sabah, Sabah, Malaysia. [2]Present address: Institute of Biological Sciences, Faculty of Science, University of Malaya, Kuala Lumpur, Malaysia. [3]Institute of Ocean & Earth Sciences, Faculty of Science, University of Malaya, Kuala Lumpur, Malaysia.

Received: 4 April 2014 Accepted: 9 September 2014
[redacted]

References

Abele LG (1974) Species diversity of decapods crustaceans in marine habitats. Ecology 55(1):156–161

Bach CB, Hazlett B, Rittschof D (1976) Effects of interspecific competition on fitness of the hermit crab *Clibanarius tricolor*. Ecology 57:579–586

Bazzaz FA (1975) Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology 56:485–488

Benvenuto C, Gherardi F (2001) Population structure and shell use in the hermit crab, *Clibanarius erythropus*: a comparison between Mediterranean and Atlantic shores. J Mar Biol Assoc UK 81:77–84

Bertness MD (1981a) Pattern and plasticity in tropical hermit crab growth and reproduction. Am Nat 117:2295–2313

Bertness MD (1981b) Competitive dynamics of a tropical hermit crab assemblage. Ecology 62:751–761

Bertness MD (1982) Shell utilization, predation pressure, and thermal stress in Panamanian hermit crabs: an interoceanic comparison. J Exp Mar Biol Ecol 64:159–187

Bertness MD, Cunnigham C (1981) Crab shell-crushing predation and gastropod architectural defence. J Exp Mar Biol Ecol 50:213–230

Connell JH (1972) Community interactions on marine rocky intertidal shores. Annu Rev Ecol Syst 3:169–192

De Grave SD, Barnes DKA (2001) Ecology of tropical hermit crabs (Crustacea Decapoda) at Quirimba Island, Mozambique: a multivariate assemblage perspective. Trop Zool 14:197–209

Druehl LD (1967) Vertical distributions of some benthic marine algae in a British Columbia inlet, as related to some environmental factors. J Fish Res Board Can 24:33–46

Elwood RW, Marks N, Dick JTA (1995) Consequences of shell-species preferences for female reproductive success in the hermit crab *Pagurus bernhardus*. Mar Biol 123(3):431–434

Floeter SR, Nalesso RC, Rodrigues MMP, Turra A (2000) Patterns of shell utilization and selection in two sympatric hermit crabs (Anomura: Diogenidae) in south-eastern Brazil. J Exp Mar Biol Ecol 80:1053–1059

Fotheringham N (1976) Hermit crab shells as limiting resource (Decapoda: Paguridae). Crustaceana 31(2):193–199

Fransozo A, Bertini G, Braga AA, Negreiros-Fransozo ML (2008) Ecological aspects of hermit crabs (Crustacea, Anomura, Paguroidea) off the northern coast of Sao Paulo State, Brazil. Aquat Ecol 42:437–448

Gherardi F, Vannini M (1991) Hermit crabs in a mangrove swamp: clustering dynamics in *Clibanarius laevimanus*. Mar Behav Physiol 21:85–104

Gherardi F, Zatteri F, Vannini M (1994) Hermit crabs in a mangrove swamp: the structure of *Clibanarius laevimanus* clusters. Mar Biol 121:41–52

Harley CDG (2003) Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. Limnol Oceanogr 48(4):1498–1508

Imazu M, Asakura A (1994) Distribution, reproduction and shell utilization patterns in three species of intertidal hermit crabs on a rocky shore on the Pacific coast of Japan. J Exp Mar Biol Ecol 184:41–65

Knox GA (2001) The ecology of seashores. CRC Press, Florida

Leite FPP, Turra A, Gandolfi SM (1998) Hermit crabs (Crustacea: Decapoda: Anomura), gastropod shells and environmental structure: their relationship in southern Brazil. J Nat Hist 32:1599–1608

Mantelatto FLM, Garcia RB (2002) Hermit crab fauna from the infralittoral zone of Anchieta Island (Ubatuba, Brazil). Modern Approaches to the Study of Crustacea. Kluwer Academic/Plenum Publishers, New York, pp 137–143

McLaughlin PA (2002) A review of the hermit-crab (Decapoda: Anomura: Paguridea) fauna of Southern Thailand, with particular emphasis on the Andaman Sea, and descriptions of three new species. Phuket Mar Biol Cent Spec Publ 23(2):385–460

Nakin MDV, Somers MJ (2007) Shell availability and use by the hermit crab *Clibanarius virescens* along the eastern Cape coast, South Africa. Acta Zool Acad Sci H 53(2):149–155

Nybakken JW (1982) Marine biology: an ecological approach. Harper and Row Publisher, New York

Osorno JL, Contreras-Garduno J, Macias-Garcia C (2005) Long-term costs of using heavy shells in terrestrial hermit crabs (*Coenobita compressus*) and the limits of shell preference: an experimental study. J Zool (Lond) 266:377–383

Rahayu DL (2000) Hermit crabs from the South China Sea (Crustacea: Decapoda: Anomura: Diogenidae, Paguridae, Parapaguridae). Raffles B Zool 8:377–404

Rai-mondi PT (1988) Rock type affects settlement, recruitment, and zonation of the barnacle *Chthamalus anisopoma* Pilsbury. J Exp Mar Biol Ecol 123:253–267

Rodil IF, Lastra M, Sánchez-Mata AG (2006) Community structure and intertidal zonation of the macroinfauna in intermediate sandy beaches in temperate latitudes: North coast of Spain. Estuar Coast Shelf Sci 67:267–279

Sacrosati R, Heaven C (2007) Spatial trends in community richness, diversity, and evenness across rocky intertidal environmental stress gradients in eastern Canada. Mar Ecol Prog Ser 342:1–14

Schembri PJ (1982) Feeding behavior of fifteen species of hermit crabs (Crustacea: Decapoda: Anomura) from the Otaĝo reĝion, southeastern New Zealand. J Nat Hist 16:859–878

Stephenson TA (1961) Life between tide marks in North America. Iva. Vancouver Island. J Ecol 49:1–29

Teoh HW, Chong VC (2014) Shell use and partitioning of two sympatric species of hermit crabs on a tropical mudflat. J Sea Res 86:13–22

Ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67(5):1167–1179

Ter Braak CJF, Smilauer P (2002) CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power, Ithaca

Turra A, Denadai MR (2002) Substrate use and selection in sympatric intertidal hermit crab species. Braz J Biol 62:107–112

Vance RR (1972) Competition and mechanisms of coexistence in three sympatric species of intertidal hermit crabs. Ecology 53:1062–1074

Veloso VG, Caetano CHS, Cardoso RS (2003) Composition, structure and zonation of intertidal macroinfauna in relation to physical factors in microtidal sandy beaches in Rio de Janeiro, Brazil. Sci Mar 67(4):393–402

Wethey DS (1983) Geographic limits and local zonation: the barnacles *Semibalanus (Balanus)* and *Chthamalus* in New England. Biol Bull 165:330–341

Zar JH (2010) Biostatistical analysis, 5th edn. Prentice Hall, Englewood Cliffs, p 944

doi:10.1186/s40555-014-0067-6
Cite this article as: Teoh *et al.*: **Influence of habitat heterogeneity on the assemblages and shell use of hermit crabs (Anomura: Diogenidae).** *Zoological Studies* 2014 **53**:67.