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Diversity and habitat segregation of mangrove grapsoid crabs along the west coast of the Malay Peninsula

Laura Ribero[A,B,D], *Phaik Eem Lim*[A,B,D], *Rosli Ramli*[A] *and Gianluca Polgar*[C]

[A]Institute of Biological Sciences, University of Malaya, 50603, Kuala Lumpur, Malaysia.

[B]Institute of Ocean and Earth Sciences, University of Malaya, 50603, Kuala Lumpur, Malaysia.

[C]Department of Biology, Western Kentucky University, Bowling Green, KY 42101, United States of America..

[D]Corresponding authors. Email: lau.ribero@gmail.com; phaikeem@um.edu.my

South-east Asia is a biodiversity hot spot for several different animal and plant taxa, and grapsoid crabs are dominant components of its mangrove macrofauna. However, autecological traits of the species and assemblage structures are still largely undescribed. During the period 2012–14, we surveyed six mainland and insular mangrove sites along the west coast of the Malay Peninsula, four of which had not been investigated previously. Species composition differed among sites with different types of substrate and forest area. Small islands, characterised by coarser intertidal substrates, hosted remarkably different assemblages from mainland systems. Most of the species occurred in a small number of sites, suggesting stenotypic ecological traits or patchy distributions, and a marked variation in species composition and environmental conditions among sites was observed. This suggests that management actions assuming that this region’s coastal wetlands have comparable community compositions may likely lead to species local extinctions, possibly affecting the regional biodiversity of these systems.

Grapsoid assemblages were surveyed in six mangrove sites in the Malay Peninsula. Species composition differed among sites with different types of substrate and forest area. Most species appear to be stenotypic or have patchy distribution. Management actions should consider the marked variability in species composition and environmental factors, to prevent local species extinction and sustainably manage these ecosystems ecological diversity.

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L. Ribero *et al.*

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Introduction

Mangrove ecosystems are transitional ecosystems providing ecosystem services critical to both land and marine systems, and can be particularly affected by shifts in biological diversity (‘critical transition zones' (CTZs); Levin *et al*. 2001). Their conservational importance has been widely recognised (Duke *et al*. 2007).

The Malay Peninsula is part of both the Sundaland biodiversity hot spot ecoregion (Myers *et al*. 2000) and the East Indies Triangle, or Indo-Australian Archipelago (Briggs 1999; Renema *et al*. 2008). Despite its conservation interest (Myers *et al*. 2000), knowledge on the faunal assemblages of this region remains fragmentary. Spatial coverage is also often inadequate, and biodiversity data are typically inferred from surveys of relatively small areas (Wafar *et al*. 2011).

Grapsoid crabs (Crustacea: Brachyura: Grapsoidea), especially those of the family Sesarmidae, include dominant macrofaunal components of Indo-West Pacific mangrove ecosystems (Lee 1998). Because of their ecological role in mangrove food webs and soil dynamics, these crabs have been considered as keystone species (Smith *et al*. 1991) and ecosystem engineers (Kristensen 2008). Little is known of the autecology of mangrove grapsoid crabs (Lee 2008). Local assemblages are a subset of the species regional pool, which is affected by macroecological factors, such as geomorphic and physiographic patterns, climatic regimes and available habitat area (Ellison 2002). Within individual mangrove ecosystems, the structure of macrofaunal assemblages is affected by several environmental parameters acting at the habitat level, such as water availability, edaphic conditions, mangrove stand age and species composition, as well as substrate elevation (e.g. Frusher *et al*. 1994; Lui *et al*. 2002; Ashton *et al*. 2003*a*; Morrisey *et al*. 2003). Therefore, environmental factors appear to affect assemblage composition at different spatial scales (Ellison 2002).

The Malay Peninsula hosts extensive mangrove forests that are primarily distributed along its west coast (Yahaya and Ramu 2003). The largest mangrove systems occur on the mainland, fringing coastal mudflats and mud banks along the lower tracts and mouths of several large rivers with high suspended loads (e.g. the Klang, Selangor and Merbok rivers). Smaller and naturally fragmented insular mangrove systems (e.g. Pulau [island] Langkawi, Pulau Kukup, Pulau Merambong) are instead characterised by lower terrigenous sedimentary inputs and coarser intertidal deposits. In the Malay Peninsula, the higher intertidal zone of mangrove forests has been extensively destroyed, altering the topography of the original high intertidal zone. Therefore, forests with higher area often spread along longer tracts of coast, but cover a distance perpendicular to the coast that is one to two orders of magnitude less than the original intertidal gradients (Coleman *et al*. 1970; L. Ribero, pers. obs.). Because the maximum physicochemical and biological variation in mangrove ecosystems occurs along the intertidal gradient (Polgar and Bartolino 2010), forests with greater area and shorter intertidal gradients may have lower habitat diversity and simpler communities than forests with lower area and longer intertidal gradients.

Although several studies have investigated the diversity and community structure of mangrove grapsoid crabs in this region (e.g. Sasekumar 1974; Ashton *et al.* 2003*b*; Sasekumar and Ooi 2005), the assemblages of several mangrove sites remain undescribed.

Our preliminary surveys suggested that the mangrove crab assemblage composition of these mangrove systems is highly heterogeneous, exhibiting striking patterns of variation among different forests, as well as between insular and mainland systems. To test this hypothesis, we surveyed six mangrove sites along the west coast of the Malay Peninsula, namely two mainland sites in the central tract of the Straits of Malacca (Kuala [estuary] Selangor and Tanjung [Cape] Tuan) and four islands in their northern (Pulau Langkawi), central (Pulau Besar) and southern (Pulau Kukup and Pulau Merambong) tracts, along ~750 km of coastline. These sites differed in insularity, forest area and dominant substrate conditions. The aims of this study were to describe: (1) the patterns of variation in assemblage structure and diversity of the six study sites; and (2) multivariate association between species, sites and selected environmental variables.

Materials and methods

Study sites

From 2012 to 2014, six sites distributed along the West coast of the Malay Peninsula (Fig. 1) were surveyed: Langkawi (6°24′39.81″N, 99°51′35.91″E), Kuala Selangor (3°20′12.22″N, 101°14′7.40″E), Tanjung Tuan (2°24′52.57″N, 101°51′28.24″E), Pulau Besar (2°6′44.39″N, 102°19′37.11″E), Pulau Kukup (1°19′18.69″N, 103°25′30.61″E) and Pulau Merambong (1°18′55.53″N, 103°36′35.71″E).

The regional climate is tropical, with a mean annual temperature of ~27°C and mean annual rainfall of ~2300 mm, with two peaks corresponding to the transition to the south-west monsoon (March–April) and the north-east monsoon (October; Tangang *et al.* 2007; Suhaila and Jemain 2009; Wong *et al.* 2009). Sediment dynamics and intertidal systems along the coast are affected by both tidal and fluvial action. Several large rivers with high suspended load (e.g. the Klang-Langat, Selangor, Merbok, Kedah, Rokan and Kampar rivers) discharge into the small basin of the Straits of Malacca, which is a semidiurnal mesomacrotidal system with tidal ranges of ~1–3 m during neap tides and 3–5 m during spring tides (Coleman *et al.* 1970).

Sampling and measurements

In each site, several 1-day surveys were made in different mangrove forests in order to consider intrasite environmental heterogeneity. Within each mangrove forest, one or more 1-h sampling sessions were made in global positioning system (GPS)-delimited 30- × 30-m plots, positioned in different habitat types along the intertidal gradient. Sampling sessions were conducted ±2 h around the predicted low tide, on the exposed substrate, by the same researcher (LR). Six sampling sessions were conducted in each site (Table 1). However, eight sampling sessions were conducted in Kuala

Selangor in order to represent the higher environmental heterogeneity observed in this site (primarily due to the effects of the Selangor River estuary). In Pulau Merambong, only four sampling sessions were conducted because the overall forest size and environmental heterogeneity of this site are considerably smaller than those of other sites. In each plot, samples were collected by hand or excavation in potential microhabitats of grapsoid crabs, including leaf litter, mangrove aerial root systems, flotsam and debris, tide pools, burrows and dead wood (Smith *et al*. 1991; Frusher *et al*. 1994; Cannicci *et al*. 1996; Sivasothi 2000; Lee and Kwok 2002; Ashton *et al*. 2003*a*, 2003*b*; Emmerson and Ndenze 2007). The type of substrate was characterised in the field by visually estimating the percentage of sand particles (grains visible to the naked eye) relative to the amount of silt and mud (grains not visible to the naked eye; Fetter 1988; Seuffert and Martín 2013; Table 2). Four substrate types were defined: mud; mud and sand; sand; and gravel plus boulders. The forest area and the linear extension of the forest along the intertidal gradient were obtained by integrating field GPS data and satellite images (Google Earth; https://www.google.com/earth, accessed on 23 September 2013). The forest area of Site 1 (Langkawi) was obtained from Jusoff and Taha (2008).

The collected specimens were killed by cooling at 2–4°C or freezing at –25°C, fixed and preserved in 70% ethanol. Tissue subsamples were preserved in 99% undenatured ethanol for future molecular studies. Taxonomic collections were deposited in the Museum of Zoology of the University of Malaya (Kuala Lumpur, Malaysia) and in the Lee Kong Chian Natural History Museum (Singapore). Taxonomic discrimination was conducted to the genus or species level (Tesch 1917; Tweedie 1936, 1940, 1950*a*, 1950*b*; Banerjee 1960; Serène and Soh 1967*a*, 1967*b*, 1970; Davie 1992, 1994; Rahayu and Davie 2002, 2006; Rahayu and Ng 2005, 2009, 2010; Ng 2007; Schubart *et al*. 2009; Davie 2010; Lee *et al*. 2013; Shahdadi and Schubart 2017). Plant species of mangroves and mangrove associates were identified following Tomlinson (1986).

Sites and sampling sessions

Site 1: Langkawi

The Langkawi Archipelago (Fig. 1) includes 104 islands, mostly consisting of peaks of karstified sandstone and limestone and granitic rocks, crossed by numerous streams and waterfalls. Unconsolidated recent sand and clay deposits characterised the narrow valleys and coastal plains, which were partly colonised by mangroves (Jusoff and Taha 2008).

Intertidal deposits ranged from muddy to sandy, and were primarily covered by *Rhizophora* and *Bruguiera* mangroves. Three surveys and a total of six sampling sessions were conducted in two riverine mangrove forests along the banks of Sungai [river] Ayer Hangat (6°26′46.43″N, 099°48′49.76″E; Forest A) and Sungai Kilim (6°24′00.09″N, 099°51′31.17″E; Forest B; Table 1).

Page 4 of 28

Site 2: Kuala Selangor

The estuarine mangrove site of Kuala [estuary] Selangor fringes the mouth of the Sungai Selangor, ~360 km south of Pulau Langkawi and approximately half-way along the west coast of the Malay Peninsula (Fig. 1). The forest fringe covered >10 km along the coast and extended 100–1700 m from sea to land; the widest formations are mangrove plantations of *Rhizophora apiculata* along the northern coast.

The substrate was muddy, and the site was dominated by *Bruguiera parviflora*, with scattered trees of the genera *Avicennia*, *Sonneratia* and *Rhizophora*, the latter three being more abundant along the forest marine fringe and on the banks of the creek network. In this site, eight surveys and with eight sampling sessions in total were conducted in three different forests, one on the northern side of the estuary (3°20′38.15″N, 101°12′50.29″E; Forest A), and two on the southern side (3°20′07.74″N, 101°14′04.30″E (Forest B) and 03°19′34.81″N, 101°14′16.68″E (Forest C); Table 1).

Site 3: Tanjung Tuan

Tanjung Tuan is a promontory whose coast is colonised by dense but small mangrove forests. The northern coast was fringed by a mangrove fringe ~150 m long and ~20 m wide, dominated by *R. apiculata* and *Sonneratia alba*, which grew on a sandy substrate at the foot of a steep rocky outcrop. In front of its marine edge, a sandy deposit and reef flat were found. A larger forest, ~300 m long and ~100–200 m wide, fringed the southern coast. The *Sonneratia* marine fringe was adjacent to a wider formation dominated by *Rhizophora* species and *Bruguiera gymnorrhiza*. In the back forest, *Pandanus* palms and nibong palms (*Oncosperma tigillaria*) were found. The substrate here was muddy to sandy; in the *Sonneratia* zone, the root system and forest floor were colonised by dense algal mats. Three surveys with a total of six sampling sessions were conducted on both sides of the promontory in two forests (2°24′52.07″N, 101°51′13.49″E (Forest A) and 02°24′43.27″N, 101°51′32.99″E (Forest B)).

Site 4: Pulau Besar

Pulau Besar is a rocky island ~1 km long (Fig. 1) and ~4 km off the coast of Malacca. The island hosts small mangrove patches, 10–30 m wide from sea to land, on sandy to sandy–muddy deposits. Most of these forests are dominated by *Rhizophora* species. Artificial or natural sand berms and eroding banks separate the mangrove systems from the inland forests. Three surveys with a total of six sampling sessions were conducted in three mangrove forests, located on the northern (2°06′58.53″N, 102°19′38.44″E; Forest A), north-western (2°06′49.64″N, 102°19′17.13″E; Forest B) and south-eastern (2°06′18.07″N, 102°19′40.32″E; Forest C) sides of the island.

Site 5: Pulau Kukup

Pulau Kukup is a mangrove island ~2 km long (Fig. 1). Several creeks and small inlets crossed the island (e.g. Sungai Solok). In all survey forests, the soil was muddy and the forests were dominated by *Rhizophora* and *Bruguiera* species, with patches of *Sonneratia* species at the mouth of Sungai Solok. Three surveys for a total of six sampling sessions were conducted along the island's eastern (1°19′34.87″N, 103°26′04.19″E; Forest A) and north-eastern (1°20′07.29″N, 103°25′26.19″E; Forest B) coasts.

Site 6: Pulau Merambong

Pulau Merambong is a small islet in the Johor Strait, ~260 m long (Fig. 1). A narrow mangrove fringe, ~250 m long and 10–30 m wide, dominated by *Rhizophora stylosa* and *B. gymnorrhiza*, fringed its western coast. Several scattered trees of *Ceriops* sp., *Sonneratia alba*, *Avicennia rumphiana* and *Xylocarpus granatum* were also found. The substrate was either sandy or rocky. One survey, with a total of four sampling sessions, was conducted in three mangrove forests along the north-western (1°18′57.55″N, 103°36′33.33″E; Forest A), western (1°18′54.06″N, 103°36′35.08″E; Forest B) and south-western (1°18′52.26″N, 103°36′38.18″E; Forest C) coasts.

Statistical analyses and environmental variables

The Jaccard similarity index (*J*; Jaccard 1901; Schroeder and Jenkins 2018) was used to explore how the sites differed in taxonomic composition within the whole area surveyed (β-diversity). To investigate whether differences in taxonomic composition among sites follow geographic patterns, pairwise *J* dissimilarities between sites were plotted against pairwise geographic distances (km). Linear regression analysis was conducted to test whether *J* dissimilarities were correlated with geographic distances using the Robust algorithm in Past version 3.2 (downloadable at https://folk.uio.no/ohammer/past/, date of last access: 31 August 2019; Hammer *et al*. 2001; Hammer and Harper 2005).

To investigate the association among species and between species and study sites, their presence–absence distribution was investigated by cluster analysis in Past version 3.2 (Hammer *et al*. 2001; Hammer and Harper 2005), using the Jaccard similarity index and the strong linkage aggregation method (Johnson and Wichern 1992).

Four ordinal variables were used to describe the environmental conditions in each study site: (1) substrate type (ST); (2) insularity (IN); (3) forest area (AF); and (4) linear extension of the forested intertidal gradient (IG; Table 2). Several authors have suggested that sediment grain size, here measured by ST, can affect the structure of mangrove macrofaunal assemblages (e.g. Frusher *et al.* 1994; Ashton *et al*. 2003*a*). The relative effect of marine and continental waters, here measured by IN, is one of the key factors affecting the structure and composition of mangrove forests (Ewel *et al.* 1998). AF was measured to account for species–area relationships (SARs), known to occur in mangrove communities (Ellison 2002; Polgar 2009). Both IG and AF were measured to account for differences related to both forest area and its intertidal extension.

The multivariate correspondence between the measured environmental variables and the presence of the studied species in each site was assessed with canonical correspondence analysis (CCA) (ter Braak 1986; Legendre and Legendre 1998) in Past version 3.2 (Hammer *et al*. 2001; Hammer and Harper 2005).

Results

Twenty-eight species and one morphospecies (i.e. specimens morphologically distinct from described species; *Episesarma* sp.1) belonging to 11 grapsoid genera were found, including 21 sesarmids, 4 grapsids and 3 varunids (Table 3). New distribution records were reported for *Nanosesarma edamense*, previously known only from Borneo, Indonesia and New Caledonia (De Man 1887*a*, 1888; Tweedie 1950*a*; Ng and Richer de Forges 2007), and *Metaplax* cf. *distincta*, previously known only from India and Thailand (Ng 2007). According to Tan and Ng (1994), *Metopograpsus quadridentatus* and *Metopograpsus oceanicus* have not been previously recorded in the Malay Peninsula, although the latter species may be present in other 'non-mangrove' coastal ecosystems in this region (PKL Ng, pers. comm.).

Four of six sites hosted a comparable number (8–12) of species; Kuala Selangor contained 19 species and Pulau Merambong contained 4 species. Most of the species were recorded in one to three sites, and only three species occurred in four or more sites (Fig. 2*b*; Table 3). The most widespread species (Table 3) were *Parasesarma eumolpe* (collected in five of six surveyed sites), *Clistocoeloma merguiense* and *Metaplax elegans* (both collected in four of six surveyed sites).

The values of *J* between pairs of sites (Fig. 3) showed that similarity in composition between assemblages was not related to the geographic distance between sites. The linear regression analysis obtained a value of $r^2 = 0.00027$, and a p value = 0.9535, rejecting the hypothesis that *J* values are correlated with the geographic distance between sites. Therefore, the assemblages are apparently not affected by geographic patterns at the scale of the area investigated.

Cluster analysis identified eight groups of species (CS1–CS8) associated with different sites (Fig. 4; Table 3). A few groups (CS2, CS6 and CS7) include species found in one study site (Tanjung Tuan, Kuala Selangor and Langkawi respectively). Group CS4 includes more widely distributed species (*C. merguiense*, *Episesarma versicolor*, *P. eumolpe*, *Parasesarma onychophorum*, *M. elegans*), reported from three to five sites, including large forests on fine or mixed substrate (Kuala Selangor, Pulau Kukup, Langkawi) and smaller mangrove stands on mixed and coarse substrate (Tanjung Tuan, Pulau Besar; except *E. versicolor*), suggesting that these species can be found in different environmental conditions. Group CS8 includes species primarily collected in small islands (Pulau Besar and Pulau Merambong; *N. edamense*, *Nanosesarma minutum*, *Selatium brockii*, *M. oceanicus*). *Episesarma palawanense*, *Nanosesarma batavicum*, *Nanosesarma pontianacense* and *Sarmatium germaini* were not included in any group, indicating that these species have idiosyncratic distribution patterns (Fig. 4; Table 3).

The first two ordination axes of the CCA explained 77.3% of the total variance (Fig. 5). The linear extension of the forest along the intertidal gradient (IG) was correlated with the forest area (AF), and these two variables were inversely correlated with the substrate type (ST), showing that sites with finer substrates were generally covered by larger forests, and that sites with coarser substrates were covered by smaller forests. Insularity (IN) was not correlated with the other variables, showing that islands do not differ from the mainland in terms of forest size and substrate conditions (Fig. 5), likely due to the variable distance from terrigenous sources. The study sites are distributed along the first ordination axis, following a gradient of forest extension and substrate composition, from smaller sites with coarser substrate (Pulau Merambong, Pulau Besar, Tanjung Tuan), to sites hosting large forests with finer substrates (Kuala Selangor, Pulau Kukup, Langkawi). Kuala Selangor and Pulau Kukup (first quadrant) have the same substrate type (ST1: mud) and are both large forests (AF3: 25-100 km2, IG3: 1,000-10,000 m). Pulau Besar and Pulau Merambong (third quadrant) are both small insular mangrove sites with coarser substrates (AF1: 0-1 km2, IG1: 0-100 m, ST3: sand, gravel and boulders). Tanjung Tuan and Langkawi (second and fourth quadrants respectively) have the same substrate type (ST2: mud and sand), but differ in forest size and insularity (Tanjung Tuan: AF1: 0-1 km2, IG2: 100-1,000 m, IN1: mainland; Langkawi: AF3: 25-100 km2, IG3: 1,000-10,000 m, IN2: island). The study sites can be categorised into four groups: Group 1, large mangrove forests with fine substrate (Kuala Selangor and Pulau Kukup); Group 2, mainland forests of intermediate size (forest area) and mixed substrates (Tanjung Tuan); Group 3, large insular forests with mixed substrates (Langkawi); and Group 4, small insular forests with coarse substrate (Pulau Besar and Pulau Merambong). At lower values of the first canonical axis, several *Metopograpsus* species (*M. frontalis*, found in Tanjung Tuan, Group CS2 of the cluster analysis; *M. oceanicus*, found in Pulau Besar and Pulau Merambong, Group CS8; *M. quadridentatus*, found in Tanjung Tuan and Pulau Besar, Group CS1) and *M.* cf. *distincta* (found in Tanjung Tuan, Group CS2) are associated with coarser substrate and fringe mangroves (low IG and AE). At higher values of the first canonical axis, several species are associated with finer substrates and larger forests (high IG and AE) and insular systems (high IN), such as *Parasesarma indiarum* and *Parasesarma* melissa (found in Langkawi; Group CS7 of the cluster analysis), *Fasciarma fasciatum*, *Episesarma* sp.1 and *Metaplax* crenulata (Kuala Selangor, Langkawi; Group CS3), *P. onychophorum* and *E. versicolor* (Kuala Selangor, Langkawi, Pulau Kukup; Group CS4) and *N. batavicum* (Langkawi, Pulau Kukup). *P. eumolpe* (found in Langkawi, Kuala Selangor, Tanjung Tuan, Pulau Besar, Pulau Kukup; Group CS4), *Metopograpsus latifrons* (Langkawi, Kuala Selangor, Pulau Besar; Group CS3) and *Parasesarma plicatum* (Kuala Selangor, Tanjung Tuan, Pulau Kukup; Group CS5) plot near the origin, indicating that these species occur in a wide range of the measured conditions.

Discussion

Species richness

The presence of 28 recorded species and 1 morphospecies confirms this region as a 'biodiversity hotspot' for these taxa (Jones 1984; Lee 1998). Similar studies on mangrove grapsoid assemblages made in other geographic regions reported lower numbers of species, ranging from 14 (Vannini and Valmori 1981), to 8 (Manning and Holthuis 1981) to 6 (Naderloo and Türkay 2012). At site level, species richness varies considerably, ranging from 4 to 19 species per site, consistent with other mangrove systems in this region (e.g. Sasekumar 1974; Frith *et al*. 1976; Ashton *et al*. 2003*a*; Diele *et al*. 2013; n = 12–17). Previous studies conducted in Kuala Selangor (Ashton *et al*. 2003*b*) and Langkawi (Sasekumar and Ooi 2005) reported lower numbers of grapsoid species in these sites (four species in three genera and five species in five genera respectively). These findings suggest that the diversity of this region is underestimated, and sites already investigated may host a higher number of species than reported. Such inconsistencies may be related to differences in sampling design, sites surveyed and sampling time (Salgado Kent and McGuinness 2006). For example, in Kuala Selangor, Ashton *et al*. (2003*b*) investigated two 100-m^2 plots, conducting three sampling surveys in ~1 month, whereas in the present study this site was surveyed over a period of 2 years (eight 1-h sampling sessions) and different habitats within the site were investigated (three forests on the northern and southern sides of the estuary, different intertidal zones). In Langkawi, Sasekumar and Ooi (2005) conducted their surveys over 3 days, in three locations (Sungai Kilim, Sungai Kisap, Sungai Ayer Hangat; subdivided into six sampling sites) and collected specimens from 20- × 20-cm quadrat samples (in two sites only, two quadrats per site) by haphazardly walking for 30 min in each site. Therefore, the lower richness recorded by Sasekumar and Ooi (2005) may be related to different sampling techniques and the area of the sites surveyed. Mangrove ecosystems present challenging conditions for field research, including difficulty of movement on the soft substrate, the presence of dangerous fauna and high habitat complexity, which can hamper sampling efficiency and accuracy, thus underestimating actual richness (Lee 2008; Lee *et al*. 2017).

Community structure and diversity of the sites investigated

The species richness of most sites is comparable (Langkawi, Tanjung Tuan, Pulau Kukup and Pulau Besar; 8–12 species), whereas the species richness of Kuala Selangor (n = 19) and Pulau Merambong (n = 4) differs remarkably. In Kuala Selangor, the input of freshwater from the Selangor River may provide additional spatial niches for freshwater and brackish water species, as well as euryhaline species, thus increasing the species richness of the assemblages. In Pulau Merambong, the small number of reported species may be linked to the small size of the mangrove forest, and its low heterogeneity, because the site hosts a continuous and narrow mangrove fringe that borders the west coast of the island. In fact, Pulau Besar and Pulau Merambong have a similar forest extension, but in the former the mangrove fringe is scattered on three different sides of the island, and thus exposed to different hydrodynamic regimes, which likely increases environmental heterogeneity and habitat diversity.

Although species richness is similar among sites, the taxonomic composition of the assemblages varies considerably, being associated with different environmental conditions. Twenty-six of 29 recorded taxa were found in three or fewer of six sites. This suggests that habitats are patchily distributed, and that several species are either stenotypic or have a restricted or patchy geographic distribution. This pattern has been observed for plants, intertidal invertebrates, terrestrial arthropods and terrestrial vertebrates (Gaston *et al*. 2000), as well as in other grapsoid crab communities (e.g. Tweedie 1954; Ashton *et al*. 2003*a*; Salgado Kent and McGuinness 2010). This pattern may be related either to adaptation to specific habitat conditions (niche specialization) or to competitive interactions between species that share the same ecological niche (competitive exclusion; e.g. Verberk 2011). In contrast, *C. merguiense*, *P. eumolpe* and *M. elegans* were found in more than half the study sites, and in different types of sites (in terms of substrate, forest extension and insularity), suggesting that these species are widely distributed and eurytypic. These species are widespread and abundant in the region (e.g. Tweedie 1936; Sasekumar 1974; Ashton *et al*. 2003*b*), occurring in different environmental conditions throughout South-east Asia (*P. eumolpe*; e.g. Frith *et al*. 1976; Ashton *et al*. 2003*a*; Pratiwi and Widyastuti 2013) or the whole Indo-West Pacific region (*C. merguiense* and *M. elegans*; e.g. Saba 1972; Frusher *et al*. 1994; Ng 2007; Nordhaus *et al*. 2009; Diele *et al*. 2013).

The similarities among the assemblages investigated do not appear to be affected by the geographic distance between sites; instead, their taxonomic composition appears to be related to variables acting at the habitat scale, such as substrate type and forest area. Although every site hosts distinct grapsoid assemblages, assemblages of Group 4 sites ('small insular forests with coarse substrate'; Pulau Besar and Pulau Merambong) are characterised by the absence of large burrowing species (e.g. *Episesarma* spp., *Neosarmatium smithi*, *P. onychophorum*), which were found in Groups 1 ('large mangrove forests with fine substrate'; Kuala Selangor and Pulau Kukup) and 3 ('large insular forests with mixed substrates'; Langkawi). The burrowing activity of these species likely requires fine and cohesive substrates. For example, *E. versicolor* typically digs deep burrows in fine substrates, and the burrow structure is affected by substrate type (Thongtham and Kristensen 2003).

In mangrove fringes of small islands (Group 4; Pulau Besar and Pulau Merambong), the grapsoid community is primarily composed of algivorous and predatory species (i.e. *Metopograpsus* spp., *Metaplax* spp., *S. brockii*; e.g. Fratini *et al*. 2000; Sivasothi 2000; Ng 2007). The absence of large folivore and detritivore species (i.e. those feeding on mangrove leaves and litter respectively; e.g. *P. onychophorum*, *Episesarma* spp.; Malley 1978; Sivasothi 2000) is consistent with the small forest area of these sites, which may not provide enough food resources to sustain large populations.

Page 10 of 28

Nanosesarma species were found in sites with a range of different substrate types and forest areas. These species were often found inside crevices in rotting wood (L. Ribero, pers. obs.), consistent with previous studies (e.g. Komai *et al*. 2004). Their small body size allows them to occupy crevices and tunnels build by wood borers (e.g. teredinid bivalves, sphaeromatid isopods), which can provide both shelter from predators and favourable microhabitat conditions (e.g. lower water evaporation rates and temperature fluctuations). This microhabitat was found in all the mangrove sites surveyed, thus explaining the presence of species of this genus in different environmental conditions. However, different species were found in different sites, suggesting the presence of competition for the same spatial niche.

Autecological traits of the species

Previous studies have pointed out that information on autecological traits of several mangrove grapsoid species is still scarce (Lee 2008). The present study conveys first information on the autecology of *N. edamense*, *N. nunongi*, *Parasesarma batavianum* and *P. lanchesteri*, which were previously reported only from taxonomic studies or as distribution records (De Man 1887*a*, 1888, 1890, 1895; Tweedie 1936, 1950*a*; Ng and Richer de Forges 2007; Pratiwi and Rahmat 2015). For other species, this study expanded the knowledge of their autecology, or confirmed previous reports. Although *F. fasciatum* was found previously mainly on sandy substrate in disturbed habitats (Sasekumar 1974, Guerao *et al*. 2004), in this study, the species was found on both muddy and sandy substrates in Langkawi, and on muddy substrate in Kuala Selangor, suggesting that this species can occur on different types of substrate. *Nanosesarma andersonii* was previously recorded in a riverine mangrove forest (De Man 1887*b*) and in variable salinity conditions (Ravichandran *et al*. 2007), although no information on substrate conditions was previously reported. In this study, this species was found in the estuary of Kuala Selangor, on muddy substrate. *N. minutum* has been found in different types of coastal ecosystems and on different substrates (i.e. both mangrove forests on fine substrate and unvegetated rocky shores; e.g. Lundoer 1974; Ravichandran *et al*. 2007). Consistent with these previous reports, we found this species both on mud substrates in a large muddy mangrove forest (Kuala Selangor) and in small mangrove fringes on coarser substrate (Pulau Besar and Pulau Merambong), confirming that this species is capable of adapting to different environmental conditions. *N. pontianacense* has been previously reported from an anthropogenically disturbed estuarine lagoon on muddy substrate (Indonesia; Nordhaus *et al*. 2009), whereas others have reported it from several locations but did not provide information on the environmental conditions (e.g. De Man 1895; Tweedie 1940; Lundoer 1974). In this study, this species was found in Kuala Selangor and Pulau Besar, thus suggesting that the species can be found on different substrates and in different forest types. *N. smithi* has previously been found on sandy substrates with high salinity (Bosire *et al*. 2004). In this study, this species was found on muddy substrates in an estuarine mangrove forest with large freshwater inputs (Kuala Selangor), suggesting that this species can cope with different substrate types and salinity conditions. However, a previous study by Gillikin *et al.* (2004) found that this species cannot survive well when salinity conditions are experimentally altered and that it may be potentially negatively affected by long-term changes in mangrove salinity regimes. *P. indiarum* has been considered one of the dominant species in the mangrove assemblages of Singapore (Huang *et al*. 2008), and has been also reported from Thailand (e.g. Frith et al. 1976) and from the northern part of the Malay Peninsula (Penang and Pahang states; Tweedie 1940). However, we found this species only in Langkawi, and it was absent from other sites. This suggests a patchy distribution of this species in this region, which may be attributed to the specific habitat requirements of this species. This species was recently split by Shahdadi *et al*. (2018), who described a new species (*Parasesarma peninsulare*) for samples reported from the Malay Peninsula and Singapore. Therefore, our specimens may be *P. peninsulare*. However, because a re-examination of the samples was not possible, we maintained the name '*P. indiarum*'.

Conclusions

The present study investigated the composition and structure of several grapsoid assemblages along the coasts of the Strait of Malacca, providing field data for four previously unexplored sites. Different mangrove systems host distinct communities that differ considerably among each other and are associated with changes in sediment type and forest area. Several Malayan wetlands have been converted to human use without a prior assessment of their ecological diversity (e.g. Malacca city land reclamation projects, Pengarang Iskandar Johor; Kanniah *et al*. 2015, Mohamed and Razman 2018). The present study suggests that these projects likely led to the local extinction of several species. Future management plans in this region must take into consideration the remarkable variety of coastal wetland communities if the regional biodiversity is to be sustainably managed.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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References

Yjrn<jrnY1N00Y> _doi="10.1017/S0266467403003158" _id="b1" _issn="0266-4674"Yjrn<jrnY1N00Y>Ashton, E. C., Macintosh, D. J., and Hogarth, P. J. (2003*a*). A baseline study of the diversity and community ecology of crab and molluscan macrofauna in the Sematan mangrove forest, Sarawak, Malaysia. *Journal of Tropical Ecology* **19**, 127–142. doi:10.1017/S0266467403003158Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1007/BF02803654" _id="b2" _issn="0160-8347"Yjrn<jrnY1N00Y>Ashton, E. C., Hogarth, P. J., and Macintosh, D. J. (2003*b*). A comparison of brachyuran crab community structure at four mangrove locations under different management systems along the Melaka Straits–Andaman Sea Coast of Malaysia and Thailand. *Estuaries* **26**(6), 1461–1471. doi:10.1007/BF02803654Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b3"Yjrn<jrnY1N00Y>Banerjee, S. K. (1960). Biological results of the Snellius Expedition. XVIII. The Genera *Grapsus, Geograpsus,* and *Metopograpsus* (Crustacea Brachyura). *Temminckia* **10**, 132–199.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1023/B:BIOC.0000018149.88212.2d" _id="b4" _issn="0960-3115"Yjrn<jrnY1N00Y>Bosire, J. O., Dahdouh-Guebas, F., Kairo, J. G., Cannicci, S., and Koedam, N. (2004). Spatial variations in macrobenthic fauna recolonisation in a tropical mangrove bay. *Biodiversity and Conservation* **13**(6), 1059–1074. doi:10.1023/B:BIOC.0000018149.88212.2dYjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1111/j.1558-5646.1999.tb03769.x" _id="b5" _issn="0014-3820"Yjrn<jrnY1N00Y>Briggs, J. C. (1999). Coincident biogeographic patterns: Indo-West Pacific Ocean. *Evolution* **53**(2), 326–335. doi:10.1111/j.1558-5646.1999.tb03769.xYjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1016/0022-0981(95)00136-0" _id="b7" _issn="0022-0981"Yjrn<jrnY1N00Y>Cannicci, S., Ritossa, S., Ruwa, R. K., and Vannini, M. (1996). Tree fidelity and hole fidelity in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). *Journal of Experimental Marine Biology and Ecology* **196**, 299–311. doi:10.1016/0022-0981(95)00136-0Yjrn</jrnY>Yjrn</jrnY>

Yedb<edbY1N00Y> _id="b8"Yedb<edbY1N00Y>Coleman, J. M., Gagliano, S. M., and Smith, W. G. (1970). Sedimentation in a Malaysian high tide tropical delta. In ‘Deltaic Sedimentation, Modern and Ancient’. (Ed. J. P. Morgan.) Special Publication number 15, pp. 185–197. Tulsa, Oklahoma, U.S.A. (Society of Economic Paleontologists and Mineralogists.)Yedb</edbY>Yedb</edbY>

Yjrn<jrnY1N00Y> _id="b9" _issn="0079-8835"Yjrn<jrnY1N00Y>Davie, P. J. F. (1992). Revision of *Sarmatium* Dana (Crustacea: Brachyura: Sesarminae) with descriptions of three new species. *Memoirs of the Queensland Museum* **32**, 79–97.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b10" _issn="0079-8835"Yjrn<jrnY1N00Y>Davie, P. J. F. (1994). Revision of *Neosarmatium* Serène and Soh (Crustacea: Brachyura: Sesarminae) with descriptions of two new species. *Memoirs of the Queensland Museum* **35**, 35–74.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1163/9789047427759_012" _id="b11"Yjrn<jrnY1N00Y>Davie, P. J. F. (2010). A new species of *Perisesarma* (Brachyura, Sesarmidae) from Western Australia. *Studies on Malacostraca: Lipke Bijdeley Holthuis Memorial Volume* **14**, 195–207. doi:10.1163/9789047427759_012Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b12" _issn="0323-7087"Yjrn<jrnY1N00Y>De Man, J. G. (1887*a*). Uebersicht der Indo-pacifischen arten der gattung *Sesarma* Say, nebst einer kritik der von W. Hess und E. Nauck in den jahren 1865 und 1880 beschriebenen Decapoden. *Zoologische Jahrbucher. Abteilung fur Systematik, Geographie und Biologie der Tiere* **2**(3–4), 639–722.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1111/j.1096-3642.1887.tb00027.x" _id="b13" _issn="0944-2006"Yjrn<jrnY1N00Y>De Man, J. G. (1887*b*). Report on the Podophthalmous Crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr John Anderson, FRS, Superintendent of the Museum. *Journal of the Linnean Society of London, Zoology* **22**, 1–312. doi:10.1111/j.1096-3642.1887.tb00027.xYjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.5962/bhl.part.4747" _id="b14" _issn="0365-6136"Yjrn<jrnY1N00Y>De Man, J. G. (1888). Bericht über die von Herrn Dr J. Brock im indischen Archipel gesammelten Decapoden und Stomatopoden. *Archiv für Naturgeschichte* **53**, 215–600. doi:10.5962/bhl.part.4747Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b15"Yjrn<jrnY1N00Y>De Man, J. G. (1890). Carcinological studies in the Leyden Museum. *Notes from the Leyden Museum* **12**(1–2), 49–126.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b16" _issn="0323-7087"Yjrn<jrnY1N00Y>De Man, J. G. (1895). Bericht uber die von Herrn Schiffscapitan Storm zu Atjeh, an den westlichen Kusten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. Zweiter Theil. *Zoologische Jahrbucher. Abteilung fur Systematik, Geographie und Biologie der Tiere* **9**, 75–218.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1016/j.gloplacha.2012.09.003" _id="b17" _issn="0921-8181"Yjrn<jrnY1N00Y>Diele, K., Ngoc, D. T., Geist, S. J., Meyer, F. W., Pham, Q. H., Saint-Paul, U., Tran, T., and Berger, U. (2013). Impact of typhoon disturbance on the diversity of key ecosystem engineers in a

Page 14 of 28

monoculture mangrove forest plantation, Can Gio Biosphere Reserve, Vietnam. *Global and Planetary Change* **110**, 236–248. doi:10.1016/j.gloplacha.2012.09.003Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1126/science.317.5834.41b" _id="b18" _issn="0036-8075"Yjrn<jrnY1N00Y>Duke, N. C., Meynecke, J.-O., Dittmann, S., Ellison, A. M., Anger, K., Berger, U., Cannicci, S., Diele, K., Ewel, K. C., Field, C. D., Koedam, N., Lee, S. Y., Marchand, C., Nordhaus, I., and Dahdouh-Guebas, F. (2007). A world without mangroves? *Science* **317**, 41–42. doi:10.1126/science.317.5834.41bYjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1007/s00468-001-0133-7" _id="b19" _issn="0931-1890"Yjrn<jrnY1N00Y>Ellison, A. M. (2002). Macroecology of mangroves: large-scale patterns and processes in tropical coastal forests. *Trees* **16**(2–3), 181–194. doi:10.1007/s00468-001-0133-7Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1007/s11273-006-9008-4" _id="b20" _issn="0923-4861"Yjrn<jrnY1N00Y>Emmerson, W. D., and Ndenze, T. T. (2007). Mangrove tree specificity and conservation implications of the arboreal crab *Parasesarma leptosoma* at Mngazana, a mangrove estuary in the Eastern Cape, South Africa. *Wetlands Ecology and Management* **15**, 13–25. doi:10.1007/s11273-006-9008-4Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.2307/2997700" _id="b21" _issn="0960-7447"Yjrn<jrnY1N00Y>Ewel, K. C., Twilley, R. R., and Ong, J. E. (1998). Different kinds of mangrove forests provide different goods and services. *Global Ecology and Biogeography Letters* **7**, 83–94. doi:10.2307/2997700Yjrn</jrnY>Yjrn</jrnY>

Ybok<bokY1N00Y> _id="b22"Ybok<bokY1N00Y>Fetter, C. W. Jr (1988). 'Applied Hydrogeology', 2nd edn. (Charles E. Merrill and Co.: Columbus, NY, USA.)Ybok</bokY>Ybok</bokY>

Yjrn<jrnY1N00Y> _doi="10.1163/20021975-99990044" _id="b23" _issn="0278-0372"Yjrn<jrnY1N00Y>Fratini, S., Cannicci, S., Abincha, L. M., and Vannini, M. (2000). Feeding, temporal, and spatial preferences of Metopograpsus *thukuhar* (Decapoda; Grapsidae): an opportunistic mangrove dweller. *Journal of Crustacean Biology* **20**(2), 326–333. doi:10.1163/20021975-99990044Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b24" _issn="0858-1088"Yjrn<jrnY1N00Y>Frith, D. W., Tantanasiriwong, R., and Bhatia, O. (1976). Zonation of macrofauna on a mangrove shore, Phuket Island. *Research Bulletin – Phuket Marine Biological Center* **10**, 1–37.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.2307/1352412" _id="b25" _issn="0160-8347"Yjrn<jrnY1N00Y>Frusher, S. D., Giddins, R. L., and Smith, T. J. III (1994). Distribution and abundance of grapsid crabs (Grapsidae) in a mangrove estuary: effects of sediment characteristics, salinity tolerances, and osmoregulatory ability. *Estuaries* **17**(3), 647–654. doi:10.2307/1352412Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1046/j.1365-2664.2000.00485.x" _id="b26" _issn="0021-8901"Yjrn<jrnY1N00Y>Gaston, K. J., Blackburn, T. M., Greenwood, J. J. D., Gregory, R. D., Quinn, R. M., and Lawton, J. H. (2000). Abundance–occupancy relationships. *Journal of Applied Ecology* **37**, 39–59. doi:10.1046/j.1365-2664.2000.00485.xYjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1016/j.jembe.2003.09.024" _id="b27" _issn="0022-0981"Yjrn<jrnY1N00Y>Gillikin, D. P., De Wachter, B., and Tack, J. F. (2004). Physiological responses of two ecologically important Kenyan mangrove crabs exposed to altered salinity regimes. *Journal of Experimental Marine Biology and Ecology* **301**(1), 93–109. doi:10.1016/j.jembe.2003.09.024Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1093/plankt/fbh127" _id="b28" _issn="0142-7873"Yjrn<jrnY1N00Y>Guerao, G., Anger, K., Nettelmann, U. W. E., and Schubart, C. D. (2004). Complete larval and early juvenile development of the mangrove crab *Perisesarma fasciatum* (Crustacea: Brachyura: Sesarmidae) from Singapore, with a larval comparison of *Parasesarma* and *Perisesarma. Journal of Plankton Research* **26**(12), 1389–1408. doi:10.1093/plankt/fbh127Yjrn</jrnY>Yjrn</jrnY>

Ybok<bokY1N00Y> _id="b29"Ybok<bokY1N00Y>Hammer, Ø., and Harper, D. A. T. (2005). ‘Palaeontological Data Analysis.’ (Blackwell Publishing: Oxford, UK.)Ybok</bokY>Ybok</bokY>

Yjrn<jrnY1N00Y> _id="b30" _issn="1935-3952"Yjrn<jrnY1N00Y>Hammer, Ø., Harper, D. A. T., and Ryan, P. D. (2001). PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1), art. 4: 1–9..Yjrn</jrnY>Yjrn</jrnY>

Huang, H., Todd, P. A., and Yeo, D. C. J. (2008). Inter-and intra-specific variation in the facial colours of Perisesarma eumolpe and Perisesarma indiarum (Crustacea: Brachyura: Sesarmidae). Hydrobiologia, 598(1), 361–371.

Yjrn<jrnY1N00Y> _id="b32" _issn="0037-9603"Yjrn<jrnY1N00Y>Jaccard, P. (1901). Distribution de la flore alpine dans le Bassin des Dranes et dans quelques regions voisines. *Bulletin de la Société Vaudoise des Sciences Naturelles* **37**, 241–272.Yjrn</jrnY>Yjrn</jrnY>

Ybok<bokY1N00Y> _id="b33"Ybok<bokY1N00Y>Johnson, R. A., and Wichern, D. W. (1992). ‘Applied Multivariate Statistical Analysis.’ (Prentice-Hall: Englewood Cliffs, NJ, USA.)Ybok</bokY>Ybok</bokY>

Yedb<edbY1N00Y> _id="b34"Yedb<edbY1N00Y>Jones, D. A. (1984). Crabs of the mangal ecosystem. In ‘Hydrobiology of the Mangal’. (Eds F. D. Por and I. Dor.) pp. 89–109. (W. Junk: The Hague, Netherlands.)Yedb</edbY>Yedb</edbY>

Yjrn<jrnY1N00Y> _id="b35" _issn="1913-9063"Yjrn<jrnY1N00Y>Jusoff, K., and Taha, D. (2008). Managing sustainable mangrove forests in Peninsular Malaysia. *Journal of Sustainable Development* **1**(1), 88–96.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.3390/rs71114360" _id="b36" _issn="1032-9714"Yjrn<jrnY1N00Y>Kanniah, K. D., Sheikhi, A., Cracknell, A. P., Goh, H. C., Tan, K. P., Ho, C. S., and Rasli, F. N. (2015). Satellite images for monitoring mangrove cover changes in a fast growing economic region in Southern Peninsular Malaysia. *Remote Sensing* **7**, 14360–14385. doi:10.3390/rs71114360Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b37" _issn="0915-9444"Yjrn<jrnY1N00Y>Komai, T., Nagai, T., Yogi, A., Naruse, T., Fujita, Y., and Shokita, S. (2004). New records of four grapsoid crabs (Crustacea: Decapoda: Brachyura) from Japan, with notes on four rare species. *Natural History Research* **8**, 33–63.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1016/j.seares.2007.05.004" _id="b38" _issn="1385-1101"Yjrn<jrnY1N00Y>Kristensen, E. (2008). Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *Journal of Sea Research* **59**, 30–43. doi:10.1016/j.seares.2007.05.004Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1071/MF97179" _id="b39" _issn="1323-1650"Yjrn<jrnY1N00Y>Lee, S. Y. (1998). Ecological role of grapsid crabs in mangrove ecosystems: a review. *Marine and Freshwater Research* **49**, 335–343. doi:10.1071/MF97179Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1016/j.seares.2007.05.002" _id="b40" _issn="1385-1101"Yjrn<jrnY1N00Y>Lee, S. Y. (2008). Mangrove macrobenthos: assemblages, services, and linkages. *Journal of Sea Research* **59**, 16–29. doi:10.1016/j.seares.2007.05.002Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1023/A:1020175729972" _id="b41" _issn="0923-4861"Yjrn<jrnY1N00Y>Lee, S. Y., and Kwok, P. W. (2002). The importance of mangrove species association to the population biology of the sesarmine crabs *Parasesarma affinis* and *Perisesarma bidens. Wetlands Ecology and Management* **10**, 215–226. doi:10.1023/A:1020175729972Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.11646/zootaxa.3641.4.8" _id="b42" _issn="1175-5326"Yjrn<jrnY1N00Y>Lee, B. Y., Ng, N. K., and Ng, P. K. L. (2013). On the identity of *Clistocoeloma balansae* A. Milne-Edwards, 1873, and *C. tectum* (Rathbun, 1914), with description of a new species from the West Pacific (Crustacea: Decapoda: Sesarmidae). *Zootaxa* **3641**(4), 420–432. doi:10.11646/zootaxa.3641.4.8Yjrn</jrnY>Yjrn</jrnY>

Yedb<edbY1N00Y> _id="b43"Yedb<edbY1N00Y>Lee, S. Y., Jones, E. B. G., Diele, K., Castellanos-Galindo, G. A., and Nordhaus, I. (2017). Biodiversity. In 'Mangrove Ecosystems: a Global Biogeographic Perspective'. (Eds V. H. Rivera-Monroy, S. Lee, Y. E. Kristensen, R. R. Twilley) pp. 55–86. (Springer: New York, U.S.A.)Yedb</edbY>Yedb</edbY>

Ybok<bokY1N00Y> _id="b44"Ybok<bokY1N00Y>Legendre, P., and Legendre, L. (1998). 'Numerical Ecology.' (Elsevier: Amsterdam, Netherlands.)Ybok</bokY>Ybok</bokY>

Yjrn<jrnY1N00Y> _doi="10.1007/s10021-001-0021-4" _id="b45" _issn="1432-9840"Yjrn<jrnY1N00Y>Levin, L. A., Boesch, D. F., Covich, A., Dahm, C., Erséus, C., Ewel, K. C., Kneib, R. T., Moldenke, A., Palmer, M. A., Snelgrove, P., Strayer, D., and Weslawski, J. M. (2001). The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems* **4**, 430–451. doi:10.1007/s10021-001-0021-4Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1023/A:1015281114542" _id="b46" _issn="0018-8158"Yjrn<jrnY1N00Y>Lui, T. H., Lee, S. Y., and Sadovy, Y. (2002). Macrobenthos of a tidal impoundment at the Mai Po marshes nature reserve, Hong Kong. *Hydrobiologia* **468**(1–3), 193–211. doi:10.1023/A:1015281114542Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b47" _issn="0858-1088"Yjrn<jrnY1N00Y>Lundoer, S. (1974). A checklist of the marine Brachyura in the reference collection at PMBC, Thailand. *Research Bulletin – Phuket Marine Biological Center* **4**, 1–11.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1007/BF00455032" _id="b48" _issn="0025-3162"Yjrn<jrnY1N00Y>Malley, D. F. (1978). Degradation of mangrove leaf litter by the tropical sesarmid crab *Chiromanthes onychophorum. Marine Biology* **49**, 377–386. doi:10.1007/BF00455032Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.5479/si.00810282.306" _id="b49" _issn="0081-0282"Yjrn<jrnY1N00Y>Manning, R. B., and Holthuis, L. B. (1981). West African brachyuran crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology* **306**, 1–379. doi:10.5479/si.00810282.306Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b50"Yjrn<jrnY1N00Y>Mohamed, J., and Razman, M. R. (2018). Management and initiatives towards sustainable coastal development in Malaysia: experience from reclamation activities in Malacca. *Asian Journal of Environment, History and Heritage* **2**(1), 23–32.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1016/S0272-7714(02)00208-1" _id="b51" _issn="0272-7714"Yjrn<jrnY1N00Y>Morrisey, D. J., Skilleter, G. A., Ellis, J. I., Burns, B. R., Kemp, C. E., and Burt, K. (2003). Differences in benthic fauna and sediment among mangrove (*Avicennia marina* var. *australasica*) stands of different ages in New Zealand. *Estuarine, Coastal and Shelf Science* **56**(3–4), 581–592. doi:10.1016/S0272-7714(02)00208-1Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1038/35002501" _id="b52" _issn="0028-0836"Yjrn<jrnY1N00Y>Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**(6772), 853–858. doi:10.1038/35002501Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.11646/zootaxa.3374.1.1" _id="b53" _issn="1175-5326"Yjrn<jrnY1N00Y>Naderloo, R., and Türkay, M. (2012). Decapod crustaceans of the littoral and shallow sublittoral Iranian coast of the Persian Gulf: faunistics, biodiversity and zoogeography. *Zootaxa* **3374**, 1–67. doi:10.11646/zootaxa.3374.1.1Yjrn</jrnY>Yjrn</jrnY>

Yths<thsY1N00Y> _id="b54"Yths<thsY1N00Y>Ng, N. K. (2007). The systematics of the crabs of the family Varunidae (Brachyura, Decapoda). Ph.D. Thesis, National University of Singapore, Singapore.Yths</thsY>Yths</thsY>

Yedb<edbY1N00Y> _id="b55"Yedb<edbY1N00Y>Ng, P. K. L., and Richer de Forges, B. (2007). The Brachyura of New Caledonia. In ‘Compendium of Marine Species of New Caledonia’, 2 edn. (Eds C. E. Payri and B. Richer de Forges.) Documents Scientifiques et Techniques 111, pp. 315–331. (IRD: Nouméa, New Caledonia.)Yedb</edbY>Yedb</edbY>

Yjrn<jrnY1N00Y> _doi="10.1007/s10113-009-0097-5" _id="b57" _issn="1436-3798"Yjrn<jrnY1N00Y>Nordhaus, I., Hadipudjana, F. A., Janssen, R., and Pamungkas, J. (2009). Spatio-temporal variation of macrobenthic communities in the mangrove-fringed Segara Anakan lagoon, Indonesia, affected by anthropogenic activities. *Regional Environmental Change* **9**(4), 291–313. doi:10.1007/s10113-009-0097-5Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1007/s11273-008-9090-x" _id="b58" _issn="0923-4861"Yjrn<jrnY1N00Y>Polgar, G. (2009). Species–area relationship and potential role as a biomonitor of mangrove communities of Malayan mudskippers. *Wetlands Ecology and Management* **17**(2), 157–164. doi:10.1007/s11273-008-9090-xYjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.3354/meps08597" _id="b59" _issn="0171-8630"Yjrn<jrnY1N00Y>Polgar, G., and Bartolino, V. (2010). Size variation of six species of oxudercine gobies along the intertidal zone in a Malayan coastal swamp. *Marine Ecology Progress Series* **409**, 199–212. doi:10.3354/meps08597Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b60"Yjrn<jrnY1N00Y>Pratiwi, R., and Rahmat, R. (2015). Sebaran kepiting mangrove (Crustacea: Decapoda) yang terdaftar di koleksi Rujukan Pusat Penelitian Oseanografi-Lipi 1960–1970. *Berita Biologi* **14**(2), 195–202. [The Mangrove Crabs (Crustacea: Decapoda) recorded in reference collection of Research Centre for Oceanografi-Indonesian Institute of Sciences 1960–1970].Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b61"Yjrn<jrnY1N00Y>Pratiwi, R., and Widyastuti, E. (2013). Pola sebaran dan zonasi krustasea di hutan bakau perairan Teluk Lampung. *Zoo Indonesia* **22**(1), 11–21. [Distributional patterns and zonation of crustaceans mangrove in Lampung Bay].Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1163/156854002760095624" _id="b62" _issn="0011-216X"Yjrn<jrnY1N00Y>Rahayu, D. L., and Davie, P. J. F. (2002). Two new species and a new record of *Perisesarma* (Decapoda, Brachyura, Grapsidae, Sesarminae) from Indonesia. *Crustaceana* **75**(3), 597–607. doi:10.1163/156854002760095624Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b63" _issn="1280-9551"Yjrn<jrnY1N00Y>Rahayu, D. L., and Davie, P. J. F. (2006). Two new species of mangrove crabs of the genus *Neosarmatium* Serène & Soh, 1970 (Decapoda, Brachyura, Sesarmidae) from Papua, Indonesia. *Zoosystema* **28**(2), 573–584.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b64" _issn="0024-0672"Yjrn<jrnY1N00Y>Rahayu, D. L., and Ng, P. K. L. (2005). On two new species of the genera *Haberma* and *Parasesarma* (Crustacea: Decapoda: Brachyura: Sesarmidae) from Papua, Indonesia. *Zoölogische Mededeelingen* **79**, 167–178.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.11646/zootaxa.1980.1.3" _id="b65" _issn="1175-5326"Yjrn<jrnY1N00Y>Rahayu, D. L., and Ng, P. K. L. (2009). Two new species of *Parasesarma* De Man, 1895, from Southeast Asia (Crustacea: Decapoda: Brachyura: Sesarmidae). *Zootaxa* **1980**, 29–40. doi:10.11646/zootaxa.1980.1.3Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.11646/zootaxa.2327.1.1" _id="b66" _issn="1175-5326"Yjrn<jrnY1N00Y>Rahayu, D. L., and Ng, P. K. L. (2010). Revision of the *Parasesarma plicatum* (Latreille, 1803) species-group (Crustacea: Decapoda: Brachyura: Sesarmidae). *Zootaxa* **2327**, 1–22. doi:10.11646/zootaxa.2327.1.1Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b67" _issn="1300-1590"Yjrn<jrnY1N00Y>Ravichandran, S., Anthonisamy, S., Kannupandi, T., and Balasubramanian, T. (2007). Habitat preference of crabs in Pichavaram mangrove environment, Southeast Coast of India. *Su Ürünleri Dergisi* **2**(1), 47–55.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1126/science.1155674" _id="b68" _issn="0036-8075"Yjrn<jrnY1N00Y>Renema, W., Bellwood, D. R., Braga, J. C., Bromfield, K., Hall, R., Johnson, K. G., Lunt, P., Meyer, C. P., McMonagle, L. B., Morley, R. J., and O'dea, A. (2008). Hopping hotspots: global shifts in marine biodiversity. *Science* **321**(5889), 654–657. doi:10.1126/science.1155674Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b69"Yjrn<jrnY1N00Y>Saba, M. (1972). Umore-benkeigani no koukihassei [Studies on the post-embryonic development of *Clisotocoeloma merguiense* de Man]. *Mie-seibutsu* **22**, 25–29.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1007/s11273-004-5075-6" _id="b70" _issn="0923-4861"Yjrn<jrnY1N00Y>Salgado Kent, C. P., and McGuinness, K. A. (2006). A comparison of methods for estimating relative abundance of grapsid crabs. *Wetlands Ecology and Management* **14**, 1–9. doi:10.1007/s11273-004-5075-6Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b71"Yjrn<jrnY1N00Y>Salgado Kent, C. P., and McGuinness, K. A. (2010). Spatial and temporal variation in relative numbers of grapsid crabs (Decapoda: Grapsidae) in northern Australian mangrove forests. *The Beagle: Records of the Museums and Art Galleries of the Northern Territory* **26**, 79–87.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.2307/3157" _id="b72" _issn="0021-8790"Yjrn<jrnY1N00Y>Sasekumar, A. (1974). Distribution of macrofauna on a Malayan mangrove shore. *Journal of Animal Ecology* **43**, 51–69. doi:10.2307/3157Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b73"Yjrn<jrnY1N00Y>Sasekumar, A., and Ooi, A. L. (2005). Fauna of Langkawi mangrove forests. *Malaysian Journal of Science* **24**, 123–132.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1002/ecs2.2100" _id="b74" _issn="2150-8925"Yjrn<jrnY1N00Y>Schroeder, P. J., and Jenkins, D. J. (2018). How robust are popular beta diversity indices to sampling error? *Ecosphere* **9**(2), e02100. doi:10.1002/ecs2.2100Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.11646/zootaxa.2154.1.1" _id="b75" _issn="1175-5326"Yjrn<jrnY1N00Y>Schubart, C. D., Liu, H.-C., and Ng, P. K. L. (2009). Revision of *Selatium* Serène & Soh, 1970 (Crustacea: Brachyura: Sesarmidae), with description of a new genus and two new species. *Zootaxa* **2154**, 1–29. doi:10.11646/zootaxa.2154.1.1Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b76" _issn="0025-1291"Yjrn<jrnY1N00Y>Serène, R., and Soh, C. L. (1967*a*). Note on the five largest species of *Sesarma* crabs in Malaysia and Singapore. *Malayan Nature Journal* **20**(1–2), 27–30.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b77" _issn="1793-4044"Yjrn<jrnY1N00Y>Serène, R., and Soh, C. L. (1967*b*). A new species of *Sesarma* from Singapore. *Bulletin of the National Museum (Singapore)* **33**(16), 107–110.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b78"Yjrn<jrnY1N00Y>Serène, R., and Soh, C. L. (1970). New Indo-Pacific genera allied to *Sesarma* Say 1817 (Brachyura, Decapoda, Crustacea. *Treubia* **27**(4), 387–416.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1016/j.limno.2012.06.002" _id="b79"Yjrn<jrnY1N00Y>Seuffert, M. E., and Martín, P. R. (2013). Distribution of the apple snail *Pomacea canaliculata* in Pampean streams (Argentina) at different spatial scales. *Limnologica* **43**(2), 91–99. doi:10.1016/j.limno.2012.06.002Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1093/zoolinnean/zlx032" _id="b80" _issn="0024-4082"Yjrn<jrnY1N00Y>Shahdadi, A., and Schubart, C. D. (2017). Taxonomic review of *Parasesarma* (Decapoda: Brachyura: Sesarmidae) and closely related genera based on morphology and molecular phylogenetics: new classification, two new genera and the questionable phylogenetic value of the epibranchial tooth. *Zoological Journal of the Linnean Society* **182**(3), 517–548. doi:10.1093/zoolinnean/zlx032Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b81" _issn="0217-2445"Yjrn<jrnY1N00Y>Shahdadi, A., Ng, P. K. L., and Schubart, C. D. (2018). Morphological and phylogenetic evidence for a new species of *Parasesarma* De Man, 1895 (Crustacea: Decapoda: Brachyura: Sesarmidae) previously referred to as *Parasesarma indiarum* (Tweedie, 1940). *The Raffles Bulletin of Zoology* **66**, 739–762.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1163/156854000504093" _id="b82" _issn="0011-216X"Yjrn<jrnY1N00Y>Sivasothi, N. (2000). Niche preferences of tree-climbing crabs in Singapore mangroves. *Crustaceana* **73**(1), 25–38. doi:10.1163/156854000504093Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1016/0272-7714(91)90081-L" _id="b83" _issn="0272-7714"Yjrn<jrnY1N00Y>Smith, T. J., III, Boto, K. G., Frusher, S. D., and Giddins, R. L. (1991). Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuarine, Coastal and Shelf Science* **33**, 419–432. doi:10.1016/0272-7714(91)90081-LYjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1002/met.137" _id="b84" _issn="1350-4827"Yjrn<jrnY1N00Y>Suhaila, J., and Jemain, A. A. (2009). A comparison of the rainfall patterns between stations on the east and the west coasts of Peninsular Malaysia using the smoothing model of rainfall amounts. *Meteorological Applications* **16**(3), 391–401. doi:10.1002/met.137Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1007/BF00005655" _id="b85" _issn="0018-8158"Yjrn<jrnY1N00Y>Tan, C. G. S., and Ng, P. K. L. (1994). An annotated checklist of mangrove brachyuran crabs from Malaysia and Singapore. *Hydrobiologia* **285**, 75–84. doi:10.1007/BF00005655Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1007/s00704-006-0263-3" _id="b86" _issn="0177-798X"Yjrn<jrnY1N00Y>Tangang, F. T., Juneng, L., and Ahmad, S. (2007). Trend and interannual variability of temperature in Malaysia: 1961–2002. *Theoretical and Applied Climatology* **89**(3–4), 127–141. doi:10.1007/s00704-006-0263-3Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.2307/1938672" _id="b87" _issn="0012-9658"Yjrn<jrnY1N00Y>ter Braak, C. J. F. (1986). Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**, 1167–1179. doi:10.2307/1938672Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.5962/bhl.title.10640" _id="b88" _issn="0024-0672"Yjrn<jrnY1N00Y>Tesch, J. J. (1917). Synopsis of the Genera *Sesarma, Metasesarma, Sarmatium* and *Clistocoeloma*, with a key to the determination of the Indo-Pacific species. *Zoölogische Mededeelingen* **3**(2–3), 127–260. doi:10.5962/bhl.title.10640Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b89" _issn="0240-8759"Yjrn<jrnY1N00Y>Thongtham, N., and Kristensen, E. (2003). Physical and chemical characteristics of mangrove crab (*Neoepisesarma versicolor*) burrows in the Bangrong mangrove forest, Phuket, Thailand; with emphasis on behavioural response to changing environmental conditions. *Vie et Milieu* **53**, 141–151.Yjrn</jrnY>Yjrn</jrnY>

Ybok<bokY1N00Y> _id="b90"Ybok<bokY1N00Y>Tomlinson, P. B. (1986). ‘The Botany of Mangroves.’ (Cambridge University Press: London, UK.)Ybok</bokY>Ybok</bokY>

Yjrn<jrnY1N00Y> _id="b91"Yjrn<jrnY1N00Y>Tweedie, M. W. F. (1936). On the crabs of the family Grapsidae in the collection of the Raffles Museum. *Bulletin of the Raffles Museum, Singapore* **12**, 44–70.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b92"Yjrn<jrnY1N00Y>Tweedie, M. W. F. (1940). New and interesting Malaysian species of *Sesarma* and *Utica* (Crustacea, Brachyura). *Bulletin of the Raffles Museum, Singapore* **16**, 88–113.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b93"Yjrn<jrnY1N00Y>Tweedie, M. W. F. (1950*a*). Grapsoid crabs from Labuan and Sarawak. *The Sarawak Museum Journal* **5**(2), 338–369.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b94"Yjrn<jrnY1N00Y>Tweedie, M. W. F. (1950*b*). Notes on grapsoid crabs from the Raffles Museum. I. A new genus and description of a new species of the subfamily Sesarminae. *Bulletin of the Raffles Museum, Singapore* **23**, 310–316.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b95"Yjrn<jrnY1N00Y>Tweedie, M. W. F. (1954). Notes on grapsoid crabs from the Raffles Museum. 4. Auditory and visual signalling. *Bulletin of the Raffles Museum, Singapore* **25**, 121–127.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1080/03749444.1981.10736614" _id="b96"Yjrn<jrnY1N00Y>Vannini, M., and Valmori, P. (1981). Researches on the coast of Somalia. The shore and the dune of Sar Uanle: 30. Grapsidae (Decapoda Brachyura): pubblicazioni del centro di studio per la faunistica ed ecologia tropicali del CNR: CXCIII. *Monitore Zoologico Italiano Supplemento* **14**(1), 57–101. doi:10.1080/03749444.1981.10736614Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _id="b97"Yjrn<jrnY1N00Y>Verberk, W. (2011). Explaining general patterns in species abundance and distributions. *Nature Education Knowledge* **3**(10), 38.Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.1371/journal.pone.0014613" _id="b98" _issn="1932-6203"Yjrn<jrnY1N00Y>Wafar, M., Venkataraman, K., Ingole, B., Khan, S. A., and LokaBharathi, P. (2011).

Page 22 of 28

State of knowledge of coastal and marine biodiversity of Indian Ocean countries. *PLoS One* **6**(1), e14613. doi:10.1371/journal.pone.0014613Yjrn</jrnY>Yjrn</jrnY>

Yjrn<jrnY1N00Y> _doi="10.5194/hessd-6-5471-2009" _id="b99" _issn="1812-2108"Yjrn<jrnY1N00Y>Wong, C. L., Venneker, R., Uhlenbrook, S., Jamil, A. B. M., and Zhou, Y. (2009). Variability of rainfall in Peninsular Malaysia. *Hydrology and Earth System Sciences Discussions* **6**(4), 5471–5503. doi:10.5194/hessd-6-5471-2009Yjrn</jrnY>Yjrn</jrnY>

Yother<otherY1N00Y> _id="b100"Yother<otherY1N00Y>Yahaya, J., and Ramu, S. C. (2003). Coastal resource development in Malaysia: is there a need for sustainable mangrove forest management? Faculty of Economics and Administration (FEA) Working Paper number 2003–2. University of Malaya, Kuala Lumpur, Malaysia.Yother</otherY>Yother</otherY>

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DOI: 10.1071/MF19147; TOC Head:

Table 1. Sampling design: dates for each of the 1-day surveys, the forests surveyed within each site and the number of 1-h sampling sessions conducted in 30- × 30-m plots in each forest

ps, pioneer shore; mf, middle forest; hf, high forest

Site	Number of surveys	Survey dates	Forest	Number per 1-h sampling sessions	Habitat types sampled per forest
Langkawi	3	15, 16 and 17 November 2013	A (6°26′46.43″N, 099°48′49.76″E)	3	ps, mf, hf
			B (6°24′00.09″N, 099°51′31.17″E)	3	ps, mf
Kuala Selangor	8	3 February, 15 March, 5 and 17 May, 12 June, 25 and 27 September 2012, 9 November 2013	A (3°20′38.15″N, 101°12′50.29″E)	2	ps, mf, hf
			B (3°20′07.74″N, 101°14′04.30″E)	3	ps, mf
			C (3°19′34.81″N, 101°14′16.68″E)	3	ps, mf, hf
Tanjung Tuan	3	1 and 9 September, 4 November 2012	A (2°24′52.07″N, 101°51′13.49″E)	3	ps
			B (2°24′43.27″N, 101°51′32.99″E)	3	ps, mf
Pulau Besar	3	23 and 24 June 2012, 28 November 2012	A (2°06′58.53″N, 102°19′38.44″E)	2	ps
			B (2°06′49.64″N, 102°19′17.13″E)	2	ps
			C (2°06′18.07″N, 102°19′40.32″E)	2	ps
Pulau Kukup	3	26 and 27 December 2012, 5 March 2014	A (1°19′34.87″N, 103°26′04.19″E)	3	ps, mf, hf
			B (1°20′07.29″N, 103°25′26.19″E)	3	ps, mf
Pulau Merambong	1	14 November 2012	A (1°18′57.55″N, 103°36′33.33″E)	1	ps
			B (1°18′54.06″N, 103°36′35.08″E)	2	ps
			C (1°18′52.26″N,	1	ps

103°36′38.18″E)

Table 2. Environmental parameters

Substrate type (ST) was divided into the following categories: 1, mud; 2, mud and sand; 3, sand, gravel and boulders (rocky shores). Insularity (IN) was categorised as mainland (1) or island (2). Forest area (AF) was divided into the following categories: 1, 0–1 km^2; 2, 1–25 km^2; 3, 25–100 km^2. Linear extension of the forested intertidal gradient (IG) was divided into the following categories: 1, 0–100 m; 2, 100–1000 m; 3, 1000–10 000 m

	ST	IN	AF	IG
Langkawi	2	2	3	3
Kuala Selangor	1	1	2	3
Tanjung Tuan	2	1	1	2
Pulau Besar	3	2	1	1
Pulau Kukup	1	2	2	3
Pulau Merambong	3	2	1	1

Table 3. Presence–absence matrix (1 = present) of the grapsoid crabs recorded in the sampling sites

Parasesarma indiarum (Tweedie, 1940) could be also *Parasesarma peninsulare*, recently described from samples from this region, previously considered as *P. indiarum* (see Shahdadi *et al*. 2018). However, because re-examination of the samples was not possible, we maintained the name '*P. indiarum*'. 'Total' is the total number of sites in which the species was found (i.e. frequency of occurrence of each species). LK, Langkawi; KS, Kuala Selangor; TT, Tanjung Tuan; PB, Pulau Besar; PK, Pulau Kukup; PM, Pulau Merambong

BRACHYURA: GRAPSOIDEA	LK	KS	TT	PB	PK	PM	Total
Sesarmidae							
Clistocoeloma merguiense De Man, 1888	1	1	1		1		4
Episesarma sp.1	1	1					2
Episesarma palawanense (Rathbun, 1914)					1		1
Episesarma versicolor (Tweedie, 1936)	1	1			1		3
Fasciarma fasciatum (Lanchester, 1900)	1	1					2
Nanosesarma andersonii (De Man, 1895)		1					1
Nanosesarma batavicum (Moreira, 1903)	1				1		2
Nanosesarma edamense (De Man, 1887)				1		1	2
Nanosesarma minutum (De Man, 1887)		1		1		1	3
Nanosesarma nunongi Tweedie, 1950		1			1		2
Nanosesarma pontianacense (De Man, 1895)		1		1			2
Neosarmatium smithi (H. Milne Edwards, 1853)		1					1
Parasesarma batavianum (De Man, 1890)			1	1	1		3
Parasesarma eumolpe (De Man, 1895)	1	1	1	1	1		5
Parasesarma indiarum (Tweedie, 1940)	1						1
Parasesarma lanchesteri (Tweedie, 1936)		1					1
Parasesarma melissa (De Man, 1887)	1						1
Parasesarma onychophorum (De Man, 1895)	1	1			1		3
Parasesarma plicatum (Latreille, 1806)		1	1		1		3
Sarmatium germaini (A. Milne-Edwards, 1869)		1	1				2
Selatium brockii (De Man, 1887)		1		1		1	3
Sesarmoides kraussi (De Man, 1887)		1					1
Grapsidae							
Metopograpsus frontalis Miers, 1880			1				1
Metopograpsus latifrons (White, 1847)	1	1		1			3

Metopograpsus oceanicus (Hombron & Jacquinot, 1846)				1		1	2
Metopograpsus quadridentatus Stimpson, 1858			1	1			2
Varunidae							
Metaplax crenulata (Gerstaecker, 1856)	1	1					2
Metaplax cf. *distincta* H. Milne Edwards, 1852			1				1
Metaplax elegans De Man, 1888	1	1		1	1		4
Total number of records per site of grapsoid crabs	12	19	8	10	10	4	

Fig. 1. Sampling sites. LK, Langkawi; KS, Kuala Selangor; TT, Tanjung Tuan; PB, Pulau Besar; PK, Pulau Kukup; PM, Pulau Merambong.

Fig. 2. (*a*) Species richness per site. Sampling sites have been ordered along a decreasing latitudinal gradient. (*b*) Frequency of occurrence of crab species in a given number of sites (1–6). LK, Langkawi; KS, Kuala Selangor; TT, Tanjung Tuan; PB, Pulau Besar; PK, Pulau Kukup; PM, Pulau Merambong.

Fig. 3. Jaccard similarity indices (*J*) plotted against the geographic distance between pairs of sites (km) and regression line. The linear regression analysis provided a $r^2 = 0.00027$ and $p = 0.9535$. LK, Langkawi; KS, Kuala Selangor; TT, Tanjung Tuan; PB, Pulau Besar; PK, Pulau Kukup; PM, Pulau Merambong.

Fig. 4. Hierarchical cluster analyses of grapsoid species relative to sampling sites. Eight groups including at least two species (CS1–CS8) are associated with different sites. Sampling sites in which every component of the group was found are in brackets; sites where only some of the components of the group were found are given in parentheses. Four species were not included in any group: *Sarmatium germaini* (ger), *Nanosesarma batavicum* (n.bat), *Nanosesarma pontianacense* (pon) and *Episesarma palawanense* (pal). The vertical dashed line is the arbitrary 0.65 similarity cut-off value. LK, Langkawi; KS, Kuala Selangor; TT, Tanjung Tuan; PB, Pulau Besar; PK, Pulau Kukup; PM, Pulau Merambong; and, *Nanosesarma andersonii*; bro, *Selatium brockii*; cre, *Metaplax crenulata*; dis, *Metaplax* cf. *distincta*; eda, *Nanosesarma edamense*; ele, *Metaplax elegans*; epi1, *Episesarma* sp.1; eum, *Parasesarma eumolpe*; fas, *Fasciarma fasciatum*; fro, *Metopograpsus frontalis*; ind, *Parasesarma indiarum*; kra, *Sesarmoides kraussi*; lan, *Parasesarma lanchesteri*; lat, *Metopograpsus latifrons*; mel, *Parasesarma melissa*; mer, *Clistocoeloma merguiense*; min, *Nanosesarma minutum*; nun, *Nanosesarma nunongi*; oce, *Metopograpsus oceanicus*; ony, *Parasesarma onychophorum*; pli, *Parasesarma plicatum*; p.bat, *Parasesarma batavianum*; qua, *Metopograpsus quadridentatus*; smi, *Neosarmatium smithi*; ver, *Episesarma versicolor.*

Fig. 5. Canonical correspondence analysis (CCA). Triplot showing the positions of the species (closed circles) sampled in the different surveys (open squares). Species and surveys are plotted in the multivariate space defined by the environmental variables. The percentage variance explained by the first two ordination axes is indicated in parentheses. Environmental variables are illustrated as vectors. Quadrants are indicated by roman numerals. LK, Langkawi; KS, Kuala Selangor; TT, Tanjung Tuan; PB, Pulau Besar; PK, Pulau Kukup; PM, Pulau Merambong; and, *Nanosesarma andersonii*; bro, *Selatium brockii*; cre, *Metaplax crenulata*; dis, *Metaplax* cf. *distincta*; eda, *Nanosesarma edamense*; ele, *Metaplax elegans*; epi1, *Episesarma* sp.1; eum, *Parasesarma eumolpe*; fas, *Fasciarma fasciatum*; fro, *Metopograpsus frontalis*; ger, *Sarmatium germaini*; ind, *Parasesarma indiarum*; kra, *Sesarmoides kraussi*; lan, *Parasesarma lanchesteri*; lat, *Metopograpsus latifrons*; mel, *Parasesarma melissa*; mer, *Clistocoeloma merguiense*; min, *Nanosesarma minutum*; nun, *Nanosesarma nunongi*; n.bat, *Nanosesarma batavicum*; oce, *Metopograpsus oceanicus*; ony, *Parasesarma onychophorum*;

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pal, *Episesarma palawanense*; pli, *Parasesarma plicatum*; pon, *Nanosesarma pontianacense*; p.bat, *Parasesarma batavianum*; qua, *Metopograpsus quadridentatus*; smi, *Neosarmatium smithi*; ver, *Episesarma versicolor*; ST, substrate type; IN, insularity; AF, forest area; IG, linear extension of the forested intertidal gradient.