

Article

Mangrove Rehabilitation and Brachyuran Crab Biodiversity in Ranong, Thailand

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Abstract: Mangroves rehabilitated after deforestation by commercial exploitation must be monitored to confirm that key ecosystem functions are being restored. Brachyuran crabs are conspicuous mangrove macrofauna and were selected as potential indicators of ecosystem recovery. A deforested former mangrove charcoal concession area in Ranong was rehabilitated by planting *Rhizophora* (1994), *Bruguiera* and *Ceriops* (1995) seedlings in single-species blocks. A second area, deforested and heavily degraded by tin mining, was rehabilitated with *R. mucronata* in 1985. Crabs at these sites were compared with those in a mixed-species conservation forest. Timed collections were made in 1999, 2008 and 2019 to compare crab diversity and relative abundance between sites and years. Thirty-three brachyuran crab species were recorded. Fiddler crabs (*Austruca triangularis*, *Tabuca rosea*) and the signal crab, *Metaplax elegans*, were most abundant, followed by sesarmid crabs (15 species). Species composition differed significantly between sites but not between the four planted tree species blocks. We propose *Metaplax elegans* as an indicator of ecological development in low-lying/newly formed sediments; fiddler crabs as equivalent indicators in young mangrove plantations/open forest habitats; and a diverse sesarmid community to indicate ecological functioning in older plantations/dense forests.

Keywords: mangroves; biodiversity; macrofauna; Brachyura; Ocypodidae; Sesarmidae; *Rhizophora*; *Bruguiera*; *Ceriops*; indicators



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1. Introduction

Mangrove ecosystems in Southeast Asia have been severely impacted by habitat degradation, deforestation and coastal land use changes, particularly during the second half of the 20th century, when large areas of mangrove were converted for agriculture and aquaculture [1]. Although the rate of loss has slowed more recently, aquaculture alone accounted for a 30% loss of mangroves in Southeast Asia from 2000 to 2012 [2]. In Thailand, mangrove forests were exploited heavily for charcoal production, tin extraction, shrimp farming, and industrial and urban development [3–5]. From recent global data on mangrove extent [6], it has been estimated that around 23% of Thailand's mangroves were lost on both the Andaman Sea and Gulf of Thailand coastlines between 1970 and 2020 [7,8], with the most significant mangrove area losses occurring before 2000. In response to this situation, since the 1990s, Thailand has given priority to mangrove conservation and rehabilitation, including the designation in 1997 of the Ranong Biosphere Reserve (RBR) in southern Thailand to protect more than 30,000 ha within the largest single mangrove ecosystem in the country [9]. Formerly under the Royal Forest Department of Thailand, the RBR has been managed by the Department of Marine and Coastal Resources (DMCR) since 2002.

The on-going efforts in Thailand and other Southeast Asian countries to rehabilitate former mangrove habitats by planting propagules or seedlings have brought into focus the

need for indicators to show that, in addition to vegetation growth, the ecological functions of mangroves are also being restored at the ecosystem level. Because brachyuran crabs are widely reported to be a dominant group in terms of species and abundance within the mangrove macrofauna (e.g., [10–12]), they are obvious candidates to indicate positive ecological recovery in deforested or degraded areas following mangrove rehabilitation compared to near-pristine mangroves [13]. The recruitment of juvenile fish and crustaceans was reported to be an early indicator of wetland restoration in Australian mangroves [14].

The mangrove crab fauna includes herbivores, detritivores and omnivores, with some species preying on other crabs [15–17]. Brachyurans play a key role in the mangrove detritus food web, involving other macrofauna detritivores, meiofauna, benthic algae, and micro-organisms [18–20], while crabs and their larvae provide valuable food sources to higher-trophic-level consumers, including mud crabs, fish, reptiles, birds, and mammals [21,22]. In addition, the burrowing activities of mangrove crabs modify the physical habitat, including soil topography and texture [23]. Crab burrows also enable oxygen and water penetration in the substratum, increase soil-water nutrient exchange, and provide refuge for other animals.

It is well established from previous research that mangrove-associated crustaceans are widely distributed and abundant along the Andaman Sea coast, including in the Ranong mangroves [24,25]. However, little is known regarding the long-term responses of the crab fauna to mangrove habitat change resulting from rehabilitation activities, including how crab-habitat relationships are affected by the mangrove tree species selected for planting.

The present study was undertaken to monitor long-term changes in the brachyuran crab fauna in two rehabilitated areas of the RBR that were rehabilitated after they had been deforested by tin mining and wood extraction for charcoal production. In the case of the former tin mining site, the mangrove soil had also been removed by tin dredging down to the underlying sand layer. To test the assumption that crab diversity, abundance and community structure can serve as indicators of mangrove habitat recovery and ecological function, the brachyuran crabs in these two rehabilitated sites were compared with the crab fauna in a mature, undisturbed conservation forest area in the RBR. The two rehabilitated sites were first monitored in 1999, which was almost 14 years after mangrove replanting started at the former tin mining area and five years after the former charcoal concession site was replanted [26]. The present study includes unpublished data from these sites and from the conservation forest area in 2008, plus some additional site observations made in 2019 and 2023.

2. Materials and Methods

The Ranong mangroves are located on the border between southern Thailand and Myanmar. This study was carried out in mangroves along the Ngao Estuary, or Klong Ngao (9°52' N and 98°35' E), in the RBR at three sites with different management histories (Figure 1).

Site 1 is a natural, mixed-mature mangrove forest used as a reference control. Site 2 is a former tin mining site that was replanted in 1985 with partial success using *Rhizophora mucronata*. Site 3 is a former mangrove forest concession site clear-felled in 1994 and replanted with nursery-reared seedlings of four mangrove species: *R. apiculata* (Ra), *R. mucronata* (Rm), *Bruguiera cylindrica* (Bc), and *Ceriops tagal* (Ct) planted as monocultures in adjacent blocks with a spacing of 1.5 m × 1.5 m between seedlings. The first Bc and Ct seedlings did not survive due to smothering by weeds, so replacement seedlings were planted in November 1995. The four mangrove plantation blocks in site 3 are notated as 3Ra, 3Rm, 3Bc and 3Ct. A shore profile of each site was prepared in 1999 [26] to estimate shore height and the number of days per year of inundation by high tides.

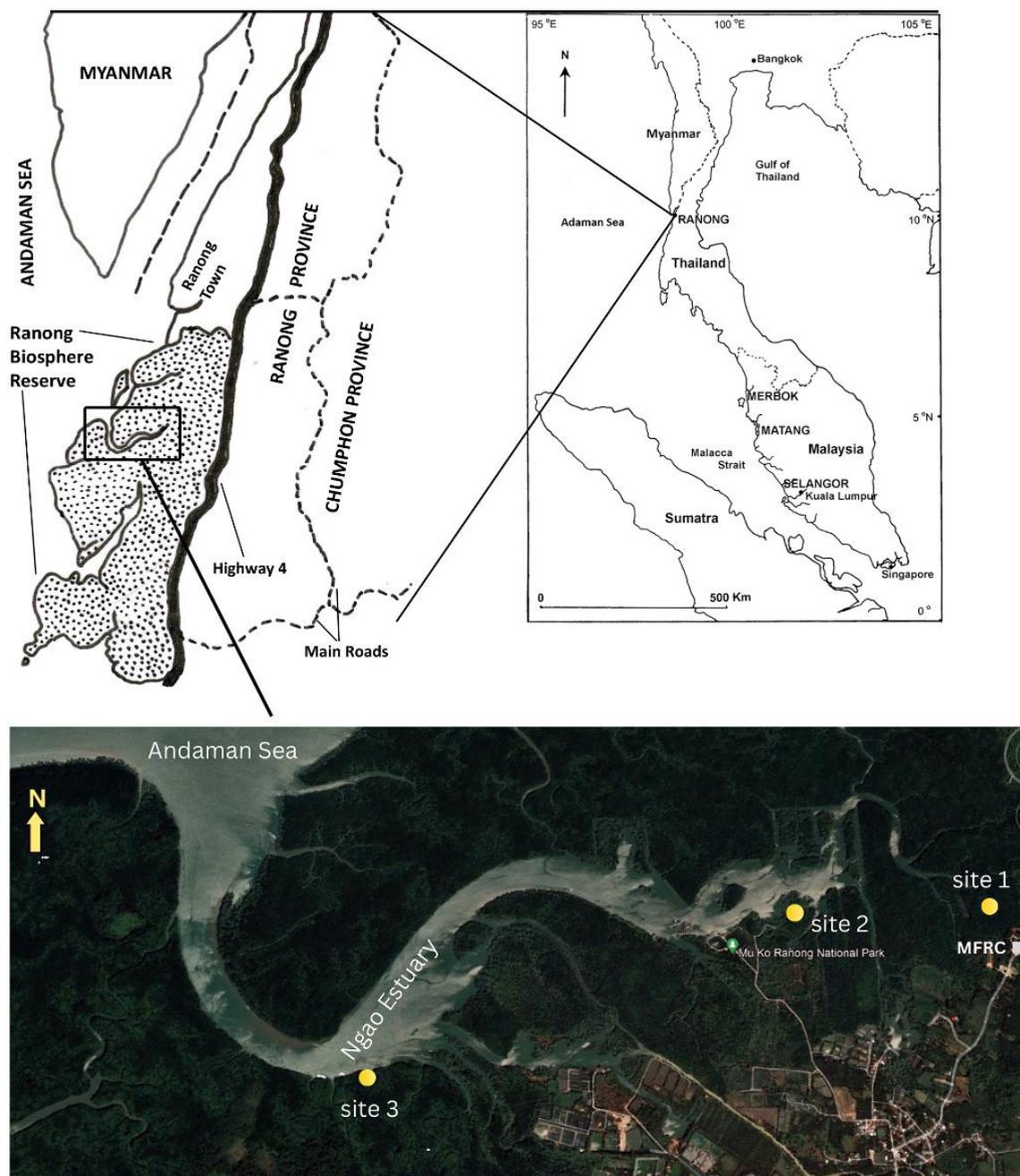


Figure 1. The location of the study sites in the Ranong Biosphere Reserve, Ranong Province, southern Thailand. Site 1: mixed mature species conservation forest ($9^{\circ}52'36''$ N, $98^{\circ}36'08''$ E), site 2: former tin mining ($9^{\circ}52'37''$ N, $98^{\circ}35'27''$ E), and site 3: former charcoal concession forest planted with four species as monocultures *Rhizophora apiculata*, *R. mucronata*, *Bruguiera cylindrica* and *Ceriops tagal* ($9^{\circ}52'02''$ N, $98^{\circ}33'54''$ E).

The sites were sampled in August 1999, November 2008, and September 2019 during the protracted wet season in Ranong. The trees (girth > 4 cm) and saplings (height > 1.5 m) were recorded in a 100 m² vegetation plot (10 m × 10 m quadrat) selected randomly in study sites 1 and 2, and in each species plot in site 3. Tree height was measured using a measuring pole extendable to 8 m; the height of taller trees was estimated by eye by an experienced member of the DMCR field team. Tree girth at breast height (1.3 m), or at 20 cm above the tallest prop root in the case of *Rhizophora* trees, was recorded using a tape

measure. The measurements were used to calculate the diameter at breast height (DBH) and basal area (BA).

Mangrove-associated crustaceans were sampled at the three sites in 1999 and 2008, and again at site 3 in 2019, by making four independent time-based collections in each 100 m² vegetation plot. Each sample represented one person collecting as many crabs as possible in 15 min within the vegetation plots. This was performed at low tide using a hand trowel and a plastic beaker for sample collection. All the crabs collected were placed in separate, labeled plastic jars and carefully transported to the laboratory. They were chilled in the fridge before being preserved in 70–80% ethyl alcohol and identified using keys (e.g., [27–30]). This simple sampling method generates an index of crab abundance that can be compared between locations, but it does not give an estimate of crab density. It has been used previously to provide a representative assessment of species composition [11,13,26]. The method is easy to employ and is not as intrusive and labor-intensive as extracting crabs by excavating them from the mangrove soil [31]. It is also more accurate than trying to identify and count crabs by visual means in dense mangrove forest habitat, as in sites 1 and 3.

Univariate measures, such as Shannon diversity [32], were calculated for the sites by year for both the vegetation and crab data, which were then analyzed using non-parametric multivariate techniques contained in PRIMER version 6.1.16 [33,34]. Bray–Curtis resemblances calculated from non-standardized square-root transformed data were constructed, and the mean data ordinated using non-metric multi-dimensional scaling (nMDS) to visualize the patterns between sites and years. A two-way crossed Analysis of Similarities (ANOSIM) permutation test using 999 randomly selected permutations was performed on the vegetation and crab data similarity matrix to test for significant differences between years and sites [35]. The crab species contributing to the dissimilarities between the sites were investigated using the Similarities Percentage Routine (SIMPER) [36]. Similarity matrices of the averaged crab data and vegetation were compared using RELATE [37].

3. Results

3.1. Vegetation

Table 1 gives a summary of the study sites and vegetation characteristics over time. The plant diversity was highest in the conservation forest area (site 1), with a Shannon diversity of 1.36 and six tree species. The other two sites were planted with monocultures, so, as expected, their Shannon diversity values are close to zero, except for site 2 (0.93 in 1999) due to natural colonization by other mangrove species (*Avicennia* spp. and *Sonneratia alba* saplings), but these did not all survive to 2008.

Vegetation height and basal area increased from 1999 to 2008 in all sites except in the former tin mining area (site 2). The density of tall trees also decreased at this site, from 22 trees in 1999 to 14 in 2008. The basal area was largest in the conservation forest (site 1: 60 m² ha⁻¹ in 2008); however, by 2019, the basal area of planted Rm trees in site 3 was only 20% lower (50 m² ha⁻¹).

The nMDS ordination of the vegetation density data (Figure 2) shows that the sites are clustered by species and the stress is low at 0.03. The mangrove basal area data are similar, but stress is 0.06. Two-way crossed ANOSIM with no replication revealed that there were no differences in years across all sites for density ($R = -0.14$; $p = 0.6$), but there were for basal area ($R = 1$; $p = 0.007$). There were significant differences between sites across all years for density ($R = 0.60$; $p = 0.003$), but not for basal area ($R = 0.42$; $p = 0.06$). There were no significant Spearman correlations between the vegetation resemblance matrices and crab data using the procedure RELATE.

Table 1. Vegetation and site characteristics of the study sites in Ranong.

Site	1	2	3Ra	3Rm	3Bc	3Ct
History	Mixed conservation forest (<i>Rhizophora</i> -dominated)	Tin mining until 1985	Charcoal concession forest clear felled in 1994			
Replanted	natural	1985	1994	1994	1995	1995
TH (cm)	342 ± 0	260 ± 0	319 ± 9	327 ± 2	322 ± 10	299 ± 10
XF (days)	295	365	334	323	325	352
H' (99)	1.36	0.93	0	0	0.15	0
H' (08)	1.19	0.49	0.93	0	0.13	0.44
H' (19)	-	-	0.11	0	0	0
H (99)	8.9 ± 4.7	6.9 ± 1.7	3.2 ± 0.3	4.0 ± 0.8	1.3 ± 0.4	1.5 ± 0.2
H (08)	11.9 ± 7.7	3.5 ± 1.4	10.7 ± 2.9	12.9 ± 1.6	5.0 ± 0.02	4.9 ± 0.5
H (19)	-	-	12.1 ± 3.8	19.6 ± 2.3	12.9 ± 0.9	12.2 ± 0.6
DBH (99)	9.0 ± 9.3	6.1 ± 3.2	2.7 ± 0.6	3.4 ± 0.8	1.4 ± 0.7	1.8 ± 0.8
DBH (08)	12.7 ± 11.2	4.7 ± 1.9	7.6 ± 1.9	10.1 ± 2.6	5.2 ± 1.8	6.4 ± 2.4
DBH (19)	-	-	7.9 ± 2.7	9.1 ± 6.7	7.5 ± 3.4	8.6 ± 3.4
A (99)	33	22	38	32	29	55
A (08)	25	14	39	32	35	53
A (19)	-	-	39	32	40	44
BA (99)	43	8.1	2.6	3.8	0.9	2.4
BA (08)	60	5.7	20	33	15	29
BA (19)	-	-	32	50	33	38

Note: TH = topographical height above ELWM in 1999, H' = Shannon Diversity, Means show ± standard deviations or totals. A = tree and sapling abundance. H = height (m), DBH = diameter at breast height (cm), BA = total tree basal area (m² ha⁻¹), - = not available.

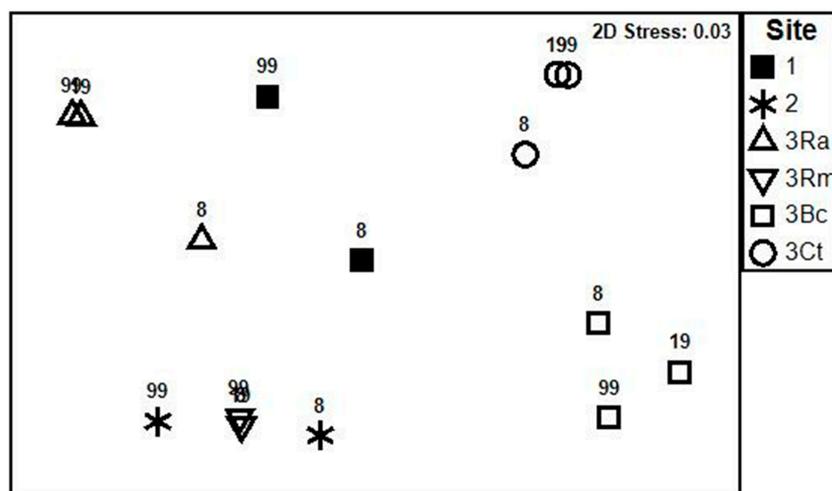


Figure 2. Non-metric MDS ordination of Bray–Curtis similarities derived from square-root transformed vegetation species abundance by site (1 is mixed mature control site, 2 is tin mining site and 3 is former charcoal concession forest planted with four monoculture species Ra = *Rhizophora apiculata*, Rm = *R. mucronata*, Bc = *Bruguiera cylindrica* and Ct = *Ceriops tagal* and year 1999 (99), 2008 (8) and 2019 (19).

3.2. Brachyuran Crabs

Thirty-seven crustacean species were recorded from the study sites sampled in 1999, 2008 and 2019. Twenty-eight species were obtained from the sites in 1999, a further eight species in 2008 and only one additional species in 2019. Table 2 lists the species by site and year. The small sesarmid crab, *Cleistocoeloma merguiensis*, was found in all six sampled vegetation plots in 1999, 2008 and 2019, while at least one fiddler crab species was also recorded in all the plots, but not on every sampling date. Three other sesarmid species, *Parasesarma lenzi*, *Perisesarma onychophorum* and *Episesarma versicolor*, were also widely distributed and abundant, as were the fiddler crabs *Austruca triangularis* and *Tabuca rosea*.

Table 2. Decapoda species collected at each study site in 1999, 2008 and 2019. Presence denoted by +.

Site	1	1	2	2	3	3	3	3	3	3	3	3	3	3	3	
Main Plant Species Year	Mix 99	Mix 08	Rm 99	Rm 08	Ra 99	Ra 08	Ra 19	Ra 99	Ra 08	Ra 19	Bc 99	Bc 08	Bc 19	Ct 99	Ct 08	Ct 19
Superfamily Grapsoidea																
Family Grapsidae																
<i>Metograpsus latifrons</i> (White, 1847)			+	+												
Family Sesarmidae																
<i>Clistocoeloma merguense</i> De Man, 1888	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Episesarma versicolor</i> (Tweedie, 1940)	+				+			+	+		+			+		+
<i>Nanosesarma batavicum</i> (Moreira, 1903)	+	+												+		
<i>Neosarmatium</i> sp. (Serène and Soh, 1970)														+		
<i>Parasesarma lenzii</i> (De Man, 1895)	+	+			+	+		+	+	+			+	+		+
<i>Parasesarma melissa</i> (De Man, 1888)			+		+			+			+			+		
<i>Parasesarma rutilimanum</i> (Tweedie, 1936)	+	+			+						+	+		+		
<i>Parasesarma</i> sp 1	+			+	+	+				+	+	+		+	+	
<i>Parasesarma</i> sp 2	+															
<i>Perisesarma darwinense</i> (Campbell, 1967)	+				+				+		+				+	
<i>Perisesarma eumolpe</i> (De Man, 1895)						+	+		+	+		+		+		+
<i>Perisesarma onychophorum</i> (De Man, 1895)	+	+			+	+	+	+			+			+		
<i>Perisesarma</i> sp.												+				
<i>Sarmatium</i> sp.									+			+				
<i>Sesarnoides kraussi</i> (De Man, 1888)	+	+			+			+	+					+	+	
Family Varunidae																
<i>Metaplox elegans</i> (De Man, 1888)			+	+		+		+		+		+		+		+
<i>Metaplox sheni</i> (Gordon, 1930)	+				+			+			+			+	+	
Super Family Ocypodoidea																
Family Camptandriidae																
<i>Paracleistostoma depressum</i> (De Man, 1895)					+						+					
<i>Tylodiplax tetratylophora</i> (De Man, 1895)			+	+											+	
Family Dotiliidae																
<i>Ilyoplax delsmanni</i> (De Man, 1926)				+												
<i>Ilyoplax obliqua</i> (Tweedie, 1935)				+												
<i>Ilyoplax punctata</i> (Tweedie, 1935)					+										+	+
<i>Ilyoplax</i> sp.												+				
Family Ocypodidae																
<i>Austruca lactea</i> (De Haan, 1835)				+			+	+		+	+			+		
<i>Austruca triangularis</i> (A. Milne-Edwards, 1873)	+			+	+	+		+	+	+	+	+	+	+	+	+
<i>Tubuca coarctata</i> (H Milne Edwards, 1852)								+								
<i>Tubuca dussumieri</i> (H Milne Edwards, 1852)				+												
<i>Tubuca forcipata</i> (Adams and White, 1849)			+													
<i>Tubuca rosea</i> (Tweedie, 1937)			+	+	+	+		+	+	+	+	+	+	+	+	+
Family Macrophthalmidae																
<i>Ilyograpsus paludicola</i> (Rathbun, 1909)																+
Super Family Pilumnoidea																
Family Pilumnidae																
<i>Heteropanope glabra</i> (Stimpson, 1858)				+	+	+		+		+	+	+		+	+	
<i>Heteropanope</i> sp.			+													
Super Family Paguroidea																
Family Diogenidae																
<i>Clibanarius padavensis</i> De Man, 1888					+		+			+	+		+	+		
<i>Clibanarius</i> sp.					+			+								
Family Thalassinidae																
<i>Thalassina</i> sp.																+
Family Upogebiidae																
<i>Upogebia</i> sp.				+												

There were 18 species in the Superfamily Grapsoidea and 13 species in the Superfamily Ocypodoidea. Crabs in the families Sesarmidae (15 species) and Ocypodidae (six species) accounted for two-thirds of the total diversity, but several other brachyuran families: Camptandriidae, Dotillidae, Grapsidae, Macrophthalmidae, Pilumnidae and Varunidae were also represented (Table 2). Figure 3 shows the number of species by site and year in the main families Sesarmidae, Ocypodidae and Varunidae. The other category includes species in other brachyuran families, hermit crabs, mud lobsters and mud shrimps.

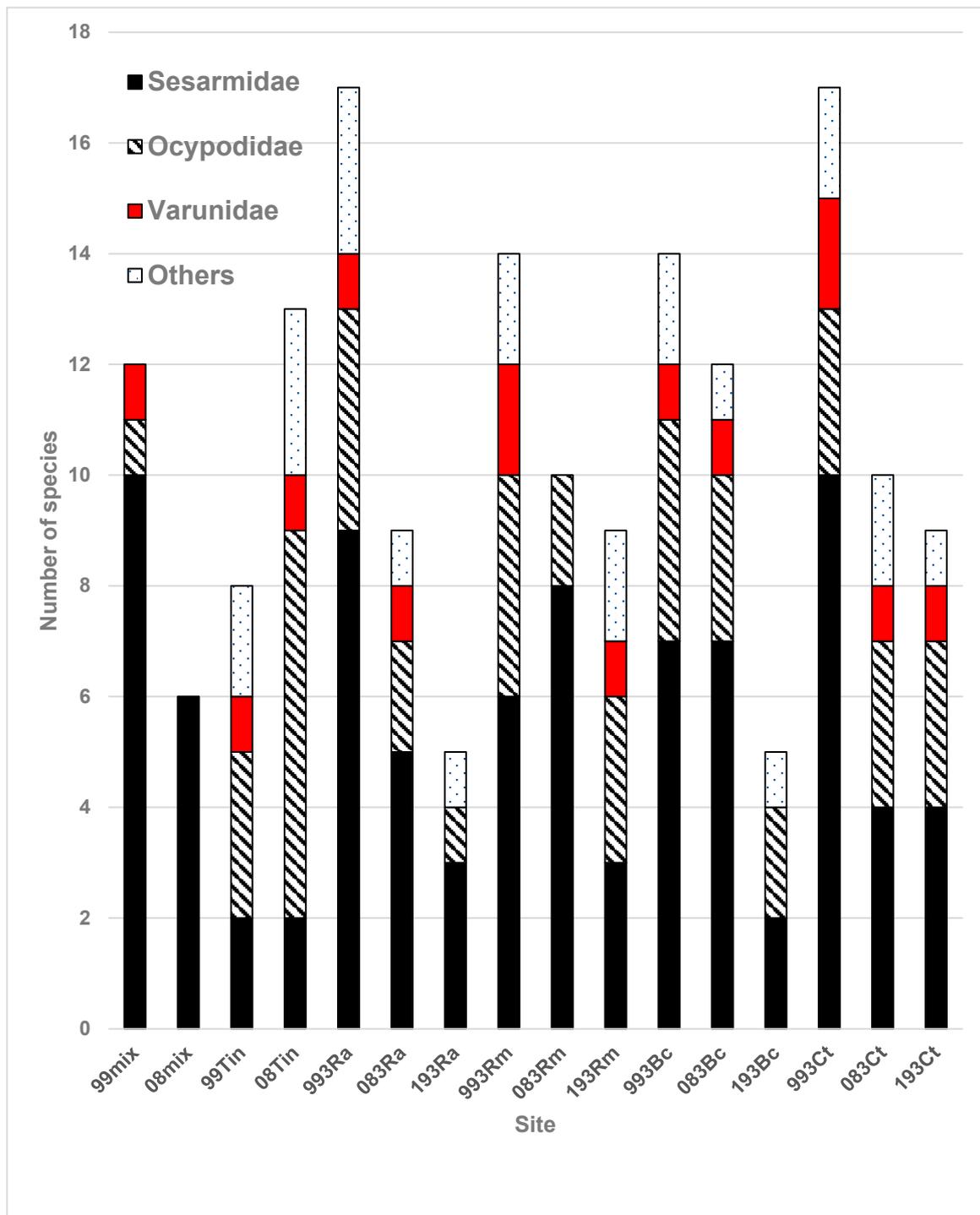


Figure 3. Number of species of crabs by site, year and family. Year: 99 = 1999; 08 = 2008; 19 = 2019. Site: mix = site 1 mature control; Tin = site 2 former tin mining, 3Ra, 3Rm, 3Bc, 3Ct = site 3 former charcoal concession forest with monoculture of *Rhizophora apiculata*, *R. mucronata*, *Bruguiera cylindrica* and *Ceriops tagal*, respectively.

Shannon diversity for the sites by year is shown in Figure 4. The conservation forest with mixed mangrove tree species (site 1) had the highest crab diversity (2.1 in 1999), followed by the 3Ct forest block at site 3 (2.07 in 2019).

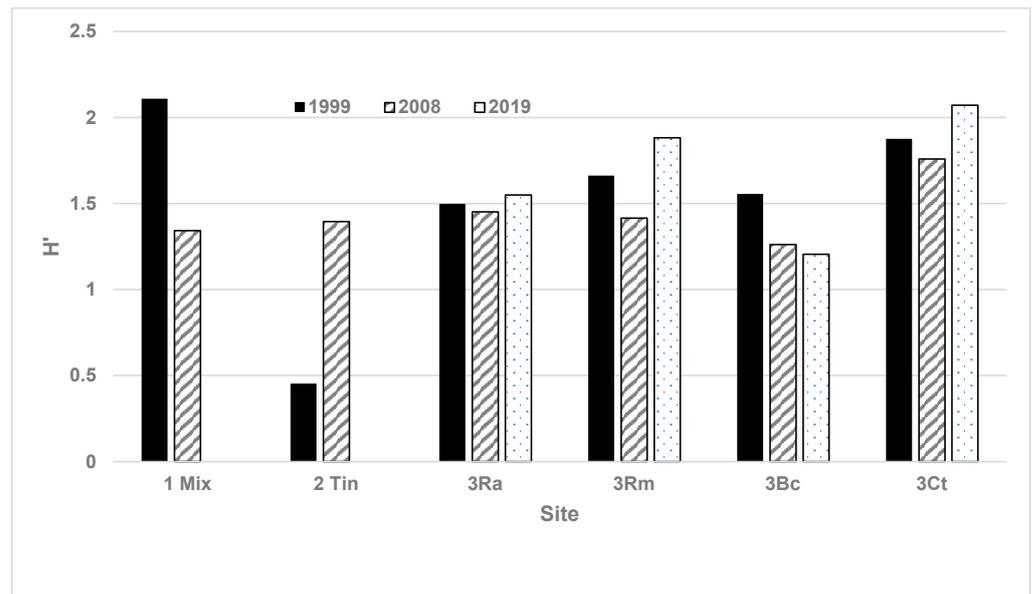


Figure 4. Shannon diversity of crabs by site and year: site 1 mix is mature control site, 2 Tin is former tin mining area, site 3 is former charcoal concession forest planted with Ra = *Rhizophora apiculata*, Rm = *R. mucronata*, Bc = *Bruguiera cylindrica*, Ct = *Ceriops tagal*.

The nMDS ordination of mean crab abundance data is shown in Figure 5. The tin mining site is clustered to the left of the plot, the mature forest site to the right, and site 3 is in the center, with 1999 at the bottom, 2008 in the middle, and 2019 at the top. A two-way crossed ANOSIM with replication for the crab replicates abundance data resemblance matrix shows significant differences between years across all sites ($R = 0.51$; $p = 0.001$), with year 1999 significantly different to 2008 and 2019 ($R = 0.51$ and 0.64 , respectively, $p = 0.001$), but year 2008 was not significantly different to 2019 ($R = 0.23$ $p = 0.2$). The sites were significantly different for crab abundance across sample years ($R = 0.51$; $p = 0.001$), but the pairwise differences (Table 3) show that 3Ra, 3Rm, 3Bc and 3Ct species forest blocks were not significantly different from each other. However, site 3 was significantly different from sites 1 and 2.

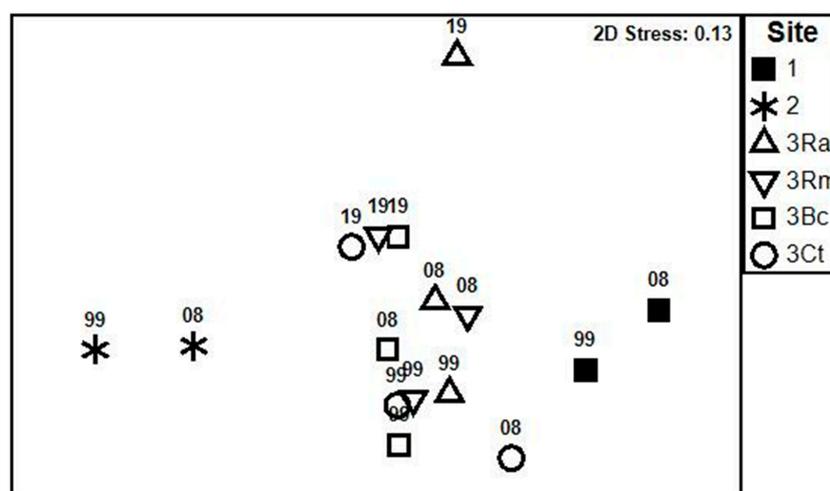


Figure 5. Non-metric MDS ordination of Bray–Curtis similarities derived from square-root transformed crab species abundance by site (1 is mixed mature control site, 2 is tin mining site and 3 is former charcoal concession forest planted with four monoculture species Ra = *Rhizophora apiculata*, Rm = *R. mucronata*, Bc = *Bruguiera cylindrica* and Ct = *Ceriops tagal* and year 1999 (99), 2008 (8) and 2019 (19).

Table 3. Two-way crossed ANOSIM results for differences between sites across sample years for the crab abundance square root transformed Bray–Curtis similarity matrix.

Pairwise Comparisons between Sites	Global R	Significance P%
1, 2	1.0	0.3
1, 3Ra	0.54	0.2
1, 3Rm	0.68	0.1
1, 3Bc	0.93	0.1
1, 3Ct	0.85	0.1
2, 3Ra	0.97	0.1
2, 3Rm	0.98	0.2
2, 3Bc	0.99	0.1
2, 3Ct	0.98	0.1
3Ra, 3Rm	0.08	21.1
3Ra, 3Bc	0.29	0.5
3Ra, 3Ct	0.24	1.8
3Rm, 3Bc	0.05	29.1
3Rm, 3Ct	0.06	23.0
3Bc, 3Ct	0.05	25.9

Results from a two-way SIMPER analysis by years and sites revealed that site 2 had the greatest similarity of crab species across years (61.1), followed by site 1 (50.4) and site 3 (46.8). The mixed species conservation forest (site 1) was distinguished from sites 2 and 3 by the presence of a diverse and abundant sesarmid population, including *Clistocoeloma merguiensis*, *Parasesarma lenzii*, *P. rutilimanum*, *Sesarmoides kraussi* and *Nanosesarmium batavium*. The former tin mining site had a high abundance of *Metaplax elegans*; this site also included *Metopograpsus latifrons*, a species not found at the other sites, and *Tyloidiplax tetralphora*, which was only recorded here and in the 3Ct forest block. Fiddler crabs (Family Ocypodidae) were well represented in all four mangrove species blocks at site 3 but were scarce in the conservation forest (site 1). By 2008, fiddler crabs had become common at site 2 in the former tin mining area (Table 4).

Table 4. Mean crab species abundance (individuals caught in 15 min) by site (1 is mixed mature control site, 2 is tin mining site and 3 is former charcoal concession forest planted with four monoculture species Ra = *Rhizophora apiculata*, Rm = *R. mucronata*, Bc = *Bruguiera cylindrica* and Ct = *Cerriops tagal* and year 1999 (99), 2008 (08) and 2019 (19).

Year	99	08	99	08	99	08	19	99	08	19	99	08	19	99	08	19
Site	1	1	2	2	3Ra	3Ra	3Ra	3 Rm	3 Rm	3 Rm	3Bc	3Bc	3Bc	3Ct	3Ct	3Ct
<i>Cm</i>	4.67	5.25	0.67	0.25	3	2.5	0.25	2.67	0.25	0.25	0.5	1.25	0.25	1.17	2.25	0.5
<i>Pl</i>	2.67	3.33			0.67	0.25		0.67	1	0.25		0.25	0.5			0.5
<i>Pr</i>	0.67	1.25			0.17						0.67	0.25		0.17		
<i>Nb</i>	0.33	0.25												0.17		
<i>Sk</i>	0.67	1			0.17			0.17	0.25					0.33	0.5	
<i>Me</i>			37.3	18		0.5		0.33	0.25		0.25			0.33		0.5
<i>Tt</i>			1.33	1.25											0.25	
<i>Ml</i>			0.33	0.5												
<i>Tr</i>			0.33	3	3.17	0.25		8.17	1.5	1.25	8	5.25	2.75	8		1.25
<i>At</i>	1			0.25	24.2	5.75		20.7	8	1.5	32.3	17	2	16.2	4	1
<i>Pe</i>						0.25	0.5		0.5	0.25		0.5	0	0.33		0.25
<i>Po</i>	1	0.25			2.83	0.25	0.25	5.17			3.67			4.17		
<i>Hg</i>				0.25	0.33	0.5		0.5		0.25	0.17	0.25		0.17	0.75	

Species abbreviations: *Cm* = *Clistocoeloma merguiense*, *Pl* = *Parasesarma lenzii*, *Pr* = *Parasesarma rutilimanum*, *Nb* = *Nanosesarma batavicum*, *Sk* = *Sesarmoides kraussi*, *Me* = *Metaplax elegans*, *Tt* = *Tyloidiplax tetralphora*, *Ml* = *Metopograpsus latifrons*, *Tr* = *Tubuca rosea*, *At* = *Austruca triangularis*, *Pe* = *Perisesarma eumolpe*, *Po* = *Perisesarma onychophorum*, *Hg* = *Heteranope glabra*.

4. Discussion

The diversity of 33 brachyuran crab species in the Ranong mangroves and the dominance of sesarmids and ocypodids is consistent with similar mangrove faunal studies conducted in Phuket [24] and Sematan in Sarawak [13], which also recorded more than 30 brachyuran species. However, a small number of crabs could not be identified to species level. The taxonomy of the brachyuran fauna has been reviewed within the study period [27–29]. With the aid of DNA barcoding, there may well be further species identified in the Ranong mangroves, as in Vietnam [30]. Establishing a specimen reference collection of brachyuran species types in DMCR would greatly assist future monitoring of the ecological changes associated with mangrove rehabilitation in Thailand.

The range in the number of brachyuran crab species collected in the conservation forest varied from 12 in 1999 to eight in 2008 (Figure 3). The variation in species diversity between the sites and years may have been due to seasonal, weather or tidal factors at the time the crabs were sampled rather than habitat differences. Ranong is the wettest province in Thailand, with 4000 to 5000 mm of rainfall annually [25]. Although the crab collections were carried out within the May to November wet season in Ranong (in August 1999, November 2008 and September 2019), weather and tidal conditions were certainly a factor, particularly in 2019 at site 3: rain and an incoming high tide greatly reduced the number of surface-active crabs during the 15 min timed collection periods, which is a weakness of this sampling method for mangrove crabs. Similarly, crab assemblage composition in mangrove sites in Penang, Malaysia, differed across time and may have been influenced by different combinations of seasonal environmental variables [38].

However, we did detect broad differences in the crab communities between sites and changes in species composition and relative abundance with time at sites 2 and 3, consistent with the observed long-term development of forest habitat in these two rehabilitated areas. The higher relative abundance of brachyurans in site 3 in 1999 compared to 2008 (Figure 3) shows the influence of forest habitat development in the planted single species blocks. Fiddler crabs prefer an open, unshaded habitat that drains quickly after tidal inundation. *Tubuca rosea* and *Austruca triangularis* (the two most common species in this study) were distinctly less abundant in 2008 due to the increased vegetation cover by that year, especially in the *Rhizophora* forest blocks (3Rm, 3Ra: Table 4). Because tropical fiddler crabs construct simple vertical burrows that must be deep enough to protect them from temperature stress and desiccation, as well as from predators, the roots of mangrove vegetation can be a barrier to their burrow-making.

The former tin mining area (site 2 in this study) is an extreme example of deforestation and degradation of mangrove forest habitat. To reach the underlying tin-rich sand deposits, tin dredgers destroyed all the mangrove vegetation and the upper soil layer. Tin mining in the Ranong mangroves ended in 1985 [9], and when first studied in 1988–1989 the impacted area had only a thin layer of recently accumulated fine sediment with a high sulphide content, and below a depth of 15 cm, the substratum consisted of about 80% sand [25]. The 1988–1989 study recorded a very low diversity of soil-dwelling macrofauna in site 2, as few faunal taxa were able to tolerate the exposed, low-lying, and anaerobic conditions. The dominant groups were gastropod snails (up to 99 snails m⁻²) comprising mainly the mud snails *Cerithium patulum* and *Cerithidea* species, and polychaete worms. A small number of crustaceans were also present in 1988–1989, but unfortunately, the species were not reported in [25].

The Royal Forest Department rehabilitated the former tin mining area by planting *Rhizophora mucronata* seedlings in 1985, but mangrove seedling survival and growth were initially poor because of the very exposed nature of the habitat, which was stressful to this mangrove species [39]. By 1999, only eight crab species were recorded in this extremely degraded area, and only *Metaplex elegans* was abundant (Table 4), even 14 years after rehabilitation began. By 2008, the brachyuran fauna had increased to 13 species, including some *Austruca*, *Tubuca*, and *Ilyoplax* species, but *M. elegans* was still the most numerous brachyuran species. Although the replanted mangroves gradually accelerated the accumulation

of fine sediment, this site was still some 60–80 cm below the intertidal height of the main forest areas in 1999 [26], and even by 2008 it remained lower than the preferred intertidal level for most sesarmid species. Thus, ecological recovery following rehabilitation planting in heavily degraded former mangrove habitats may take considerable time and require monitoring for 20 years or more.

The orange signal crab, *Metaplex elegans*, is abundant on the slopes and mudflats below the main mangrove levee along the Ngao Estuary. *Metaplex elegans* was also described as occurring on banks with “plastic-muddy” substrata and not within mangrove stands in Taiwan [40]. Because *Metaplex* crabs are abundant at low intertidal levels on soft mud banks and mudflats below the main mangrove forest zone, we suggest that they can serve as a reliable indicator of ecological activity in newly formed or unconsolidated sediments, including after major habitat disturbances, as in the former tin mining area (site 2). Our general observations confirmed that *M. elegans* is abundant in such habitats throughout the RBR. Because *Metaplex* crabs are detritivores [41] they can process large quantities of surface sediment when feeding. Thus, we conclude that *Metaplex* crabs are an important component of the detritus-based food web in the Ranong mangrove ecosystem.

Based on digging crabs out of their burrows [25], estimated the average density of mixed populations of *Metaplex* spp. and fiddler crabs on low-lying mud banks in the RBR to be 10–15 crabs m⁻². In similar mangrove habitats in Selangor, Malaysia, the highest densities m⁻² recorded [42] were: *Metaplex elegans*—25 (on mudbanks); *Deltuca dussumieri*—18 (foreshore and unshaded areas of the forest fringe); *Tubuca rosea*—62 (seaward forest fringe and open forest habitat); and [43]: *Austruca triangularis*—63 (open forest habitat and landward forest fringe).

Like *Metaplex* species, fiddler crabs are selective deposit feeders [44]. Ingested food items include particulate detrital matter, animal tissue fragments, microheterotrophs (e.g., fungi, nematode worms), and microphytobenthos [12,45]. Feeding experiments have shown that fiddler crabs are highly efficient at assimilating bacteria (>98%) and they select bacteria strongly over microalgae [46], suggesting that an important part of their nutrition comes from the bacteria that form on the surface of detrital particles. The abundance and bioturbation activities of fiddler crabs, in the form of deposit-feeding, the discarding of feeding pellets and feces, burrow construction, and burrow maintenance, clearly demonstrate their importance in both biotic and abiotic processes in mangrove ecosystems [45]. The burrowing activities of fiddler crabs and other mangrove brachyurans create a more oxidized and heterogeneous local environment that can enhance the rate of organic matter decomposition [47,48]. In an experimental study in Florida, the height, trunk diameter, and leaf production of white mangroves (*Laguncularia racemosa*) were positively related to the density of fiddler crab burrows [49]. Fiddler crabs are abundant on higher mud flats and mud banks above mid-tide level, as well as at the edge of the mangrove forest zone and in open or cleared forest habitats [24,42,43].

Crabs of the Sesarmidae family are the most characteristic and dominant brachyurans found in the main mangrove forest areas on the levee bordering Klong Ngao. They are also prominent among the macrofauna in other mangrove forests on the Andaman Sea coast of Thailand and the Melaka Straits in Malaysia [11,25,50]. Sesarmid crabs construct complex burrow systems that alter the topography of the forest floor and provide microhabitats for many other mangrove-associated fauna. Bioturbation by sesarmids also aerates the substratum, decreases its sulphide content, and increases sediment-water exchange, nutrient transfer, and sediment organic carbon [12,51,52]. By increasing soil aeration, the burrowing activities of sesarmid crabs were found to have a positive effect on the productivity and reproductive output of *Rhizophora* trees in Australia [53].

Because of their prominent role in ecosystem functioning [54], further study of sesarmids in the Ranong mangrove ecosystem is clearly merited. However, their ability to move very quickly and to retreat into extensive slanting burrow systems constructed among mangrove tree roots makes it very difficult to quantify their abundance, and they are often underestimated (e.g., [55]), as in the present study. Moreover, some species are

reported to spend as much as 97.5% of the time in their burrows [56] or are nocturnally active [57]. For these reasons, we regard our data on sesarmid species as only indicative of their true abundance.

Despite this limitation, the results show that the mature conservation forest site was dominated by a diverse and abundant population of sesarmid species, as reported from other near-pristine sites in Malaysia [13]. Site 1 was distinguished from the other sites by a high abundance of *Clistocoeloma merguiensis*, *Parasesarma lenzii*, *P. rutilimanum*, *Sesarmoides kraussi* and *Nanosesarmiun batavium*. These species were also found at site 3, but at lower densities. There was no significant difference in crab community composition between the four single tree species blocks in site 3. Although we were unable to identify any clear sesarmid crab-mangrove tree species associations from our analysis, in feeding experiments, some sesarmid species, but not others, have shown preferences for the leaves of certain mangrove tree species [55–59]. Sesarmids feed on leaves close to their burrows, and they may also take leaves into their burrows. This leaf-burying behavior may reduce food competition between crabs or improve the food quality and digestibility of leaf material through microbial activity during burrow-storage [60]. Although research on sesarmid crabs has focused on their feeding biology as herbivores consuming mangrove leaves and leaf litter [56–58,61], some species are more omnivorous, consuming surface sediment and the associated microphytobenthos [62], as well as animal tissue [55,59]. The gut contents of one of the most abundant sesarmids in the present study, *Perisesarma onychophorum*, were reported to contain 95% mangrove leaf material and small quantities of diatoms and invertebrates [50]. Some larger sesarmid crabs are known to prey, at least occasionally, on fiddler crabs [15,21].

In Brazil, the diversity and distribution of brachyuran crabs were reported to be influenced by the species of mangrove trees, but sediment properties were the more important determining factor [63]. The mangrove soil surface in the Ranong study sites has a fine clay-silt texture, but sandier mixed sediments occur commonly in the sub-surface layers within the depths that large sesarmid burrows descend to [25]. Topography and sediment composition are likely to be important environmental factors influencing brachyuran diversity and abundance that merit further investigation in the RBR.

Brachyuran crabs have strong reproductive and larval dispersal capacities, which suggests that the recorded differences in species distribution in the Klong Ngao mangroves were the result of selective settlement, or differential survival, rather than an inability to recruit more widely. Planktonic crab larvae ingress into Klong Ngao from coastal waters on incoming full and new moon spring tides [64]. The pre-settlement larval stage, or megalopa, can also attach to floating mangrove leaves to aid their transportation, a strategy that may also reduce the risk of predation [65,66]. Since it was observed that large numbers of mangrove leaves are carried by tidal movements between the estuary and the mangrove forest, this is a further reason to conclude that recruitment did not limit the distribution of the crab species recorded in this study.

Brachyuran crab larvae are abundant in Klong Ngao, with up to 13 zoeae and 18 megalopae m^{-3} estimated from plankton samples taken during the main wet season months of July to November in Ranong. This period also coincides with the main breeding season of sesarmid and ocypodid crabs [25]. The data reported also included larvae belonging to several marine crab families. When larvae of only mangrove-associated crab species were considered [64], their average numbers in Klong Ngao estimated from both dry and wet season plankton samples were ocypodids $3.0 m^{-3}$, sesarmids $0.8 m^{-3}$ and *Metaplax* $0.5 m^{-3}$. In terms of ecological function, the high reproductive output of brachyuran crabs in the Klong Ngao mangroves provides both an abundant supply of potential recruits into the intertidal mangrove crab population and an important source of planktonic food for aquatic consumers. In a study of 55 marine fish species feeding in mangroves during high tides in Selangor on the west coast of peninsular Malaysia, Ref. [67] reported that benthic fauna, including crabs, contributed 46% of their diet on average, while zooplankton, including brachyuran crab larvae, formed 31%. Other studies in Malaysia [68,69] found a

high proportion of consumed sesarmid and ocypodid crabs in the stomach contents of the eel catfish, *Plotosus canius*, and the remains of *Metaplax* crabs in the marine catfish, *Arius sagor*. Sesarmid crabs were found to be the main food items of the grouper *Epinephelus malabaricus* and the snapper *Lutjanus argentimaculatus* in mangrove-fringed estuaries in northeastern Australia [70]. The eel catfish and snappers are common in Klong Ngao [25], so it is reasonable to assume that brachyuran crabs are also a significant food source for these and other carnivorous estuarine fishes in the Ranong mangrove ecosystem. Thus, it is clearly important to conserve mature mangrove forest ecosystems, as in the RBR, to aid the recruitment of a diverse crab fauna back into deforested/degraded areas to support the recovery of mangrove ecological functions following mangrove rehabilitation.

5. Conclusions

This study confirms that brachyuran crabs are diverse, abundant and ecologically important in the Andaman Sea mangrove ecosystem of Ranong and in similar mangrove habitats in Southeast Asia. There was very slow ecological recovery in a heavily degraded former tin mining site, even many years after mangrove rehabilitation efforts, as evidenced by the low diversity of crabs compared to an undisturbed mangrove forest conservation area. However, the diversity of brachyuran crabs in the deforested former charcoal concession area, which was rehabilitated with four different mangrove species, recovered more quickly, and the crab assemblages were not significantly different in the four forest monocultures.

We conclude that *Metaplax elegans* (Varunidae) can serve as an indicator of ecological recovery in extremely degraded mangrove areas and in low-lying, newly formed, or unconsolidated fine sediments. The fiddler crabs *Tubuca rosea* and *Austruca triangularis* (Ocypodidae), and the sesarmids, *Clistocoeloma merguense*, *Parasesarma lenzii* and *Perisesarma onychorhorum* (Sesarmidae), are proposed as equivalent indicator species of ecological functioning in young mangrove plantations/open forest habitats and older plantations/dense forests, respectively. These brachyuran species are easily identifiable, even from *in situ* visual observation; they are also widely distributed, but each occupies a distinct type of mangrove habitat; and their ecological roles in the mangrove ecosystem are quite well documented.

In view of the protracted breeding seasons of these and other brachyuran species in the Ranong mangroves and the high abundance of their larvae in the Klong Ngao zooplankton, we conclude that the observed differences in distribution and abundance between brachyuran species in the study sites were the result of differential settlement and/or mortality, including from predation. Further research is needed to verify this interpretation of our results, but we highlight the need to protect near natural mangrove forest to maintain faunal recruitment, diversity and ecological functioning in mangrove ecosystems.

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