

POPULATION ECOLOGY OF THE LAND HERMIT CRAB *COENOBITA RUGOSUS* (ANOMURA, COENOBITIDAE) AT CAPE PANWA, PHUKET ISLAND, ANDAMAN COAST OF THAILAND

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ABSTRACT

The population structure, density, dispersion, sex ratio, diet and reproductive activity of *Coenobita rugosus* at Cape Panwa, Phuket Island, Andaman Coast of Thailand were investigated from April 2011 to March 2012. Crabs were collected monthly by hand by multiple quadrat sampling. Tendency of unimodality of annual size frequency distributions were observed for males, non-ovigerous females, and ovigerous females. Major chela length was determined quantitatively as a secondary sexual character (larger in males) for the first time in terrestrial hermit crabs. The average density of *C. rugosus* during the study period was 6.98 ± 0.36 crabs/m². Dispersion of males and non-ovigerous females of *C. rugosus* was clumped, whereas ovigerous females were distributed uniformly in most sampling months. The overall sex ratio was male-biased (1:0.86 male:female). Nevertheless, the monthly and size class sex ratios were close to the expected 1:1 ratio. Individuals of *C. rugosus* were observed to consume 16 plant species, mostly decomposing leaves and flowers, but three species of animal carcasses including one case of cannibalism were noted. Reproduction of *C. rugosus* occurred throughout the year with the highest percentage of ovigerous females in April and September (31.2% and 31.6%, respectively). The characteristics of *C. rugosus* living Cape Panwa, Phuket Island are consistent with those of hermit crabs inhabiting other constant tropical environments.

Key words: terrestrial hermit crab, population structure, secondary sexual characters, density, dispersion, sex ratio, diet, reproduction

INTRODUCTION

Terrestrial hermit crabs play an important role as scavengers in coastal ecosystems, accelerating the rate of recycling of nutrients and energy in the food chain. All land hermit crab species use discarded empty shells as mobile shelters to protect their soft abdomen from environmental stresses (HAZLETT, 1981; BURGGREN & McMAHON, 1988). In some tropical islands, terrestrial hermit crabs are the most common decapod crustaceans (PAGE & WILLASON, 1982; MORRISON, 2005). In addition, land hermit crabs represent an important component in insular and coastal habitats (MORRISON & SPILLER, 2006).

At least 1,106 valid species of hermit crabs are currently recognized and are classified in superfamily Paguroidea (McLAUGHLIN *ET AL.*, 2010). However, only sixteen species of

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land hermit crabs are known, and the genus has a worldwide distribution (DE GRAVE *ET AL.*, 2009). *Coenobita rugosus* is widely distributed in the Indo-Pacific region (McLAUGHLIN *ET AL.*, 2007), and the most common coenobitid species among three species recorded from Thailand (McLAUGHLIN, 2002). This species is usually found living in the supralittoral zones of sandy beaches and beach forests (BONEKA *ET AL.*, 1995; BARNES, 2002).

Knowledge on population characteristics, including size structure, sex ratios, and reproductive patterns, are important to understand the adaptive mechanisms of establishment of populations in different habitats and the biological constraints shaping population structure, and to evaluate disparities among populations (SALLAM & MANTELATTO, 2010). Investigations of population ecology have been made in certain species (e.g. *C. brevimanus*, *C. perlatus* and *C. rugosus* in Fiji by PAGE & WILLASON (1982, 1983); *C. cavipes* and *C. rugosus* in Mozambique by BARNES (1997a, b); *C. rugosus* in Okinawa, Japan, by NAKASONE (2001); *C. clypeatus* in Bahamas by MORRISON & SPILLER (2006); *C. scaevola* in Egypt, Red Sea, by SALLAM & MANTELATTO (2010), SALLAM (2012)). Nevertheless, data on populations in the east coast of Indian Ocean, especially the Andaman Sea, are scant.

Previous studies on hermit crabs in Thailand have concerned mainly the identification and inventory of species (e.g. RAHAYU & KOMAI, 2000; McLAUGHLIN, 2002). Investigations of other aspects, particularly population ecology are scarce. Therefore, this study aims to investigate population features including size structure, density, dispersion, sex ratio, diet and reproduction of *C. rugosus* at Cape Panwa, Phuket Island, on the Andaman Coast of Thailand. Furthermore, ecological data on the population of *C. rugosus* from this study will provide comparative knowledge on life histories of *C. rugosus* and other coenobitid species as well as initiate a database for the conservation of hermit crabs in this region.

MATERIALS AND METHODS

Study Area

Cape Panwa (7°48'26"N, 98°24'35"E) is situated on the southeast side of Phuket Island in the central part of the Andaman Sea coast of Thailand, about 10 km south of Phuket town. The climate is wet tropical and is influenced by the wet southwesterly monsoon from May to October and the dry northeasterly monsoon from November to April (KHOKIATTIWONG *ET AL.*, 1991).

This study was carried out at the beach in the supralittoral zone in the area of Phuket Marine Biological Center (PMBC) at Cape Panwa, Phuket (Figure 1). The beach of Cape Panwa is an open sand scrub beach, comprising rather coarse sand patches of shale (phylite) (NIELSEN, 1976). The inland edge is covered with sparse vegetation alternating with dense vegetation before cliffs. The study beach is located behind the office of PMBC. This beach is about 50 m wide and the distance between the mean sea level of the study site and the office of PMBC is about 45 m. The study area is exposed to the semidiurnal tide with an amplitude ranging from 2.15–2.27 m at spring tide to 0.85–1.15 m at neap tide (LIMPSAICHOL, 1981). The PMBC is under the Ministry of Natural Resources and Environment of Thailand, and has responsibility for research and investigations concerning marine resources of the Andaman coast of Thailand.

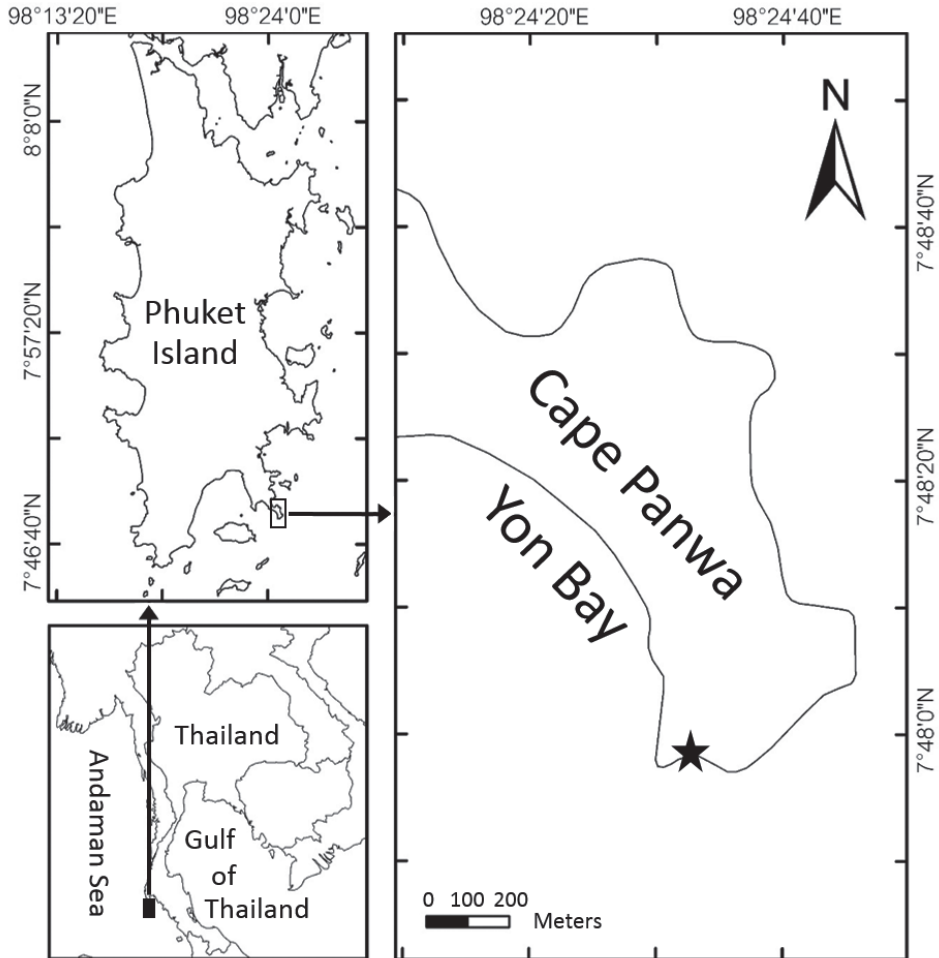


Figure 1. Map of study site. The study site (marked with a star) is located at Cape Panwa, Phuket Island, Andaman Coast of Thailand.

From April 2011 to March 2012, the air temperature at the study site ranged between 24–28 °C, the relative humidity 76–96%, the salinity of seawater 30–33 ppt and the monthly rainfall 50–503 mm.

Specimen Sampling and Analysis

At Cape Panwa, Phuket Island, *C. rugosus*, *C. violascens* and *C. brevipanus* coexisted throughout the study period. As for species identification, the obvious diagnosis separating both adult and juvenile *C. rugosus* from the other two sympatric coenobitid species is the presence of oblique laminar tubercles on the upper outer surface of the palm of the left chela,

which is believed to be the stridulatory structure (NAKASONE, 1988; McLAUGHLIN, 2002; McLAUGHLIN *ET AL.*, 2007).

Individuals of *C. rugosus* were collected monthly between April 2011 and March 2012. The hermit crabs were collected by hand at low tide from the supralittoral zone in the early morning by the same person (the first author) (SALLAM *ET AL.*, 2008). The sampling was carried out three days per month. The weather during sampling was mild and without storms. The multiple sampling quadrat technique (BARNES, 1999) was used to collect *C. rugosus*. Four temporary line transects at 15-m intervals were randomly drawn perpendicular to the shoreline from the supralittoral zone to the inland area. Sixteen temporary quadrats of area 1 m² were placed every 5 m on transects between 5 m and 45 m above the mean sea level. The number of quadrats on each transect was unequal, because the distances from the starting quadrat to the cliffs were different on each transect. Five to six quadrats were sampled on each sampling day. The quadrats had walls 10 cm high to prevent crabs from escaping, as land hermit crabs are agile and can move quickly.

After collection, all crabs sampled were brought to the laboratory in the office of PMBC. To investigate crab characters, each crab was carefully pulled out of its shell while holding the crab in the air and waiting until most of its body extended from the shell. If the crab's uropods were still held on inside the shell, especially those inhabiting shells with a long spire, a metal wire was used to tickle the crab's abdomen to induce it to vacate the shell.

Removal of crabs from the population at the study site was not permitted according to the policy of the PMBC to avoid negative impacts on native animals. In addition, all authors agreed to the current sampling method without crab removal in order to maintain and preserve this population of *C. rugosus*, because the study site is the last beach of Cape Panwa, Phuket Island, which is not disturbed by tourist accommodations and activities. Therefore, after the investigation, all crabs were allowed to reinhabit their previously occupied shells and were maintained in several aquaria with food and water until the end of the investigations in each sampling month before being released into the natural habitat at the same point they were collected.

Crab size was measured as the cephalothoracic shield length (CSL, from the tip of the rostrum to the midpoint of the posterior edge of the cervical groove) to the nearest 0.01 mm using digital vernier calipers. The measurements of each character of each individual were carried out three times and then the values were averaged before using for data analysis. They were categorized into 0.5 mm size classes for each sex to reveal the size structure of the population, as previously reported (NAKASONE, 2001; SALLAM *ET AL.*, 2008). In addition, the major chela length (MCL, from the articulation between carpus and propodus to the tip of fixed finger of the left cheliped) was measured to the nearest 0.01 mm. Sexes of *C. rugosus* were separated by gonopore position; male gonopores and sexual tubes were situated at the base of the fifth pereopods, while female gonopores were located at the base of the third pereopods (FOREST *ET AL.*, 2000).

Population characteristics of *C. rugosus* in this study were evaluated in terms of population structure, density, dispersion, sex ratio, diet and reproduction. The total distribution of individuals in each size class, based on the CSL, was constructed to reveal the population structure. The numbers of crabs in each quadrat were counted and used to calculate the population density. Dispersion was determined by quadrat sampling using Green's coefficient (GC) (LUDWIG & REYNOLDS, 1988; KREBS, 1999) in each month of sampling. Positive, negative and zero GC values suggest clumped, uniform and random dispersion, respectively. This index

of dispersion was adopted to determine dispersion of *C. rugosus* in this study rather than the traditional variance-to-mean ratio because GC is nearly independent of population density and sample size (KREBS, 1999). The sex ratio (male:female) was calculated for the yearly and monthly samples as well as for each size class (SALLAM & MANTELATTO, 2010). All food items observed to be consumed by *C. rugosus* in the study area were identified and recorded, although for the plant portion of the diet we included only those items with a minimum of five observations in the results. The reproductive activity of the population was evaluated as the proportion of ovigerous (egg-carrying) females to the total number of females collected in each month and the total study period. Recruitment into the population was characterized by the occurrence of juveniles, defined as individuals of either sex smaller than the smallest ovigerous female (SALLAM & MANTELATTO, 2010).

Environmental factors

The air temperature (°C), relative humidity (%; measured by hygrometer), salinity of seawater (parts per thousand (ppt); evaluated by an optical refractometer), and rainfall data (mm; provided by Southern Meteorological Center (West Coast), Thai Meteorological Department) were recorded during the study year at this site.

Statistical analysis

All collected crabs were classified into the following reproductive groups: males, all females, non-ovigerous females, and ovigerous females. The normality and homoscedacity of data were examined using Kolmogorov-Smirnov and Levene tests, respectively. The median size of adult crabs (larger than or equal to the smallest ovigerous female; SALLAM & MANTELATTO, 2010) of both sexes was compared using the non-parametric Mann-Whitney *U*-test. To detect secondary sexual characters, a comparison of the MCL of adult crabs between sexes was carried out using analysis of covariance (ANCOVA) (KOGA *ET AL.*, 2010). The sex ratio (male:female (M:F)) of the population was assessed using a Chi-square test. Differences in densities between sampling months were checked by analysis of variance (ANOVA). The relationship between crab density and environmental factors and the relationship between reproductive activity and physical parameters were tested using Spearman's rank-order correlation (ZAR, 2010). Statistical significance was accepted at $p < 0.05$. SPSS Statistics 17.0 (SPSS INC., 2008) was used for all statistical analyses.

RESULTS

Hermit Crab Assemblages

Three species of land hermit crabs, *C. rugosus*, *C. violascens* and *C. brevipanus*, were found sympatrically throughout the study period. In addition, two marine hermit crabs, *Clibanarius virescens* and *Cl. merguensis*, were found in the rocky pools in the intertidal area adjacent to the sampling site.

Population Structure of *Coenobita rugosus*

A total of 1,339 individuals of *C. rugosus* were sampled, 719 males (53.7%), 620 females (46.3%), including 515 non-ovigerous females (38.5%) and 105 ovigerous females (7.8%) (Tables 1 and 2). The mean size \pm SD and size range (minimum–maximum) of *C. rugosus* based on the CSL was 6.32 ± 2.20 (2.53–15.74) mm for all individuals, 6.46 ± 2.40 (2.53–15.74) mm for males, 6.15 ± 1.95 (2.80–15.12) mm for all females, 5.82 ± 1.83 (2.80–13.67) mm

Table 1. Size frequency distribution of individuals of *Coenobita rugosus* at Cape Panwa, Phuket Island, Thailand from April 2011 to March 2012.

Size class (mm)	Number of individuals			
	Males	Non-ovigerous females	Ovigerous females	Total
2.5–3	14	4	0	18
3–3.5	35	29	0	64
3.5–4	59	52	0	111
4–4.5	54	51	0	105
4.5–5	67	58	0	125
5–5.5	64	55	3	122
5.5–6	52	49	9	110
6–6.5	53	67	9	129
6.5–7	59	30	16	105
7–7.5	40	24	19	83
7.5–8	50	34	11	95
8–8.5	38	20	9	67
8.5–9	33	14	8	55
9–9.5	23	12	8	43
9.5–10	15	3	3	21
10–10.5	15	2	3	20
10.5–11	16	3	1	20
11–11.5	9	4	4	17
11.5–12	4	0	0	4
12–12.5	4	2	0	6
12.5–13	5	1	0	6
13–13.5	2	0	0	2
13.5–14	1	1	1	3
14–14.5	2	0	0	2
14.5–15	2	0	0	2
15–15.5	1	0	1	2
15.5–16	2	0	0	2
Total	719	515	105	1339

Table 2. Number, percentage and sex ratio of individuals of *Coenobita rugosus* sampled monthly at Cape Panwa, Phuket Island, Thailand from April 2011 to March 2012.

Month	Number of individuals				Sex ratio	χ^2 test (<i>p</i> -value)
	Males*	Non-ovigerous females*	Ovigerous females*	Total		
Apr. 2011	58 (48.7)	42 (35.3)	19 (16.0)	119	1:1.05	0.783
May 2011	59 (53.2)	42 (37.8)	10 (9.0)	111	1:0.88	0.506
Jun. 2011	74 (54.8)	51 (37.8)	10 (7.4)	135	1:0.82	0.263
Jul. 2011	61 (56.5)	43 (39.8)	4 (3.7)	108	1:0.77	0.178
Aug. 2011	58 (53.7)	40 (37.0)	10 (9.3)	108	1:0.86	0.441
Sep. 2011	71 (55.5)	39 (30.5)	18 (14.1)	128	1:0.80	0.216
Oct. 2011	70 (62.5)	35 (31.3)	7 (6.3)	112	1:0.60	0.008**
Nov. 2011	52 (50.0)	49 (47.1)	3 (2.9)	104	1:1	-
Dec. 2011	66 (57.4)	40 (34.8)	9 (7.8)	115	1:0.74	0.113
Jan. 2012	63 (52.5)	54 (45.0)	3 (2.5)	120	1:0.90	0.584
Feb. 2012	35 (53.8)	27 (41.5)	3 (4.6)	65	1:0.86	0.535
Mar. 2012	52 (45.6)	53 (46.5)	9 (7.9)	114	1:1.19	0.349
Total	719	515	105	1339	1:0.86	0.007**

* Numbers in parentheses indicate the percentage of proportion of all sampled individuals in the indicated month.

** Significantly different ($p < 0.05$) from a 1:1 male: female sex ratio

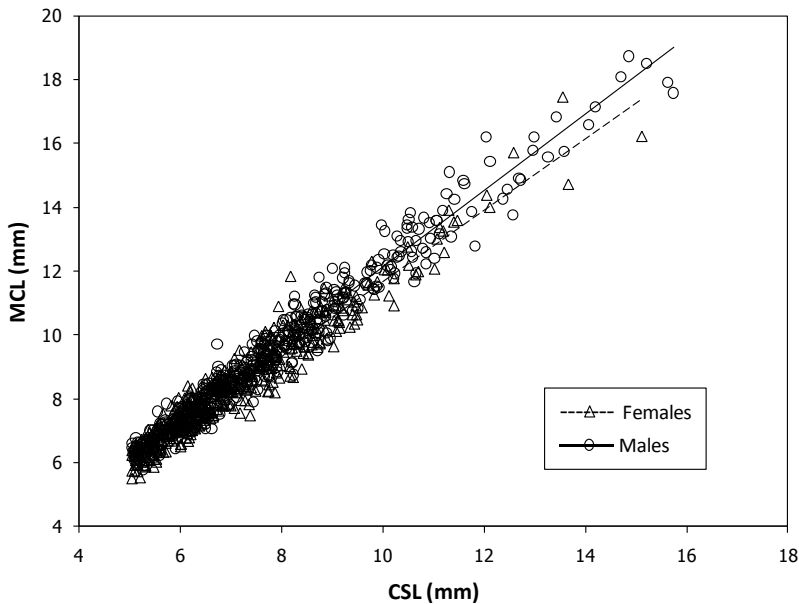


Figure 2. Relationship between the cephalothoracic shield length (CSL) and major chela length (MCL) in *Coenobita rugosus*. Data are shown for the 893 adult male and female *Coenobita rugosus* (CSL larger than or equal to 5.06 mm), sampled over the study year.

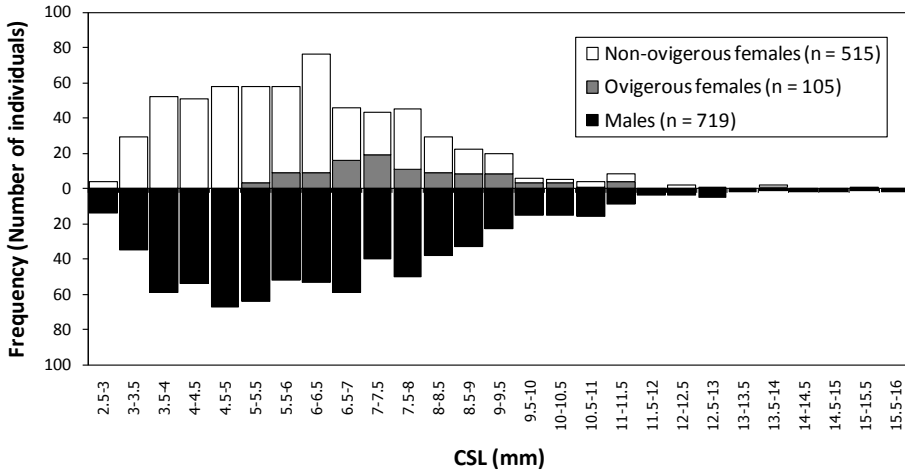


Figure 3. Annual size frequency distribution based on the cephalothoracic shield length (CSL) of *Coenobita rugosus*. Data are from the 1,339 individuals of *Coenobita rugosus* sampled over the study year.

for non-ovigerous females and 7.78 ± 1.68 (5.06–15.12) mm for ovigerous females. The number of crabs sampled in each monthly collection varied from 65 (February 2012) to 135 (June 2011) (Table 2).

The median CSL size of adult male *C. rugosus* was significantly larger than that of the adult females collected (Mann-Whitney *U*-test, $Z = 3.824$, $p < 0.001$). Additionally, the median size of adult males was significantly larger than that of adult non-ovigerous females (Mann-Whitney *U*-test, $Z = 5.373$, $p < 0.001$), but not significantly different from that of ovigerous females (Mann-Whitney *U*-test, $Z = 1.338$, $p = 0.181$). Ovigerous females were significantly larger than adult non-ovigerous females (Mann-Whitney *U*-test, $Z = 5.395$, $p < 0.001$).

Significant variation in the MCL, a secondary sexual character, was detected between males and females by ANCOVA (Figure 2), where a significant difference in both the slopes and intercepts of the regressions between sexes was noted. The linear regression equations of adult male and female *C. rugosus* were $MCL = 1.199 \text{ CSL} + 0.128$ ($r^2 = 0.966$, $p < 0.001$, $n = 476$) and $MCL = 1.119 \text{ CSL} + 0.483$ ($r^2 = 0.934$, $p < 0.001$, $n = 417$), respectively. The slope for the male regression was steeper than that for females ($F = 20.639$, d.f. = 1, $p < 0.001$), but nevertheless the intercept of the male regression was smaller than that for female ($F = 54.475$, d.f. = 1, $p < 0.001$).

When the yearly size (CSL) frequency (number of specimens) distribution of all *C. rugosus* sampled during the study period (Table 1) was plotted (Figure 3), sexual size dimorphism was evident; males only occurred in three out of the four largest size classes, although the numbers in each size category (1–2 crabs) were low (seven of the largest crabs were males). Tendency of unimodality of size distributions was observed for males, non-ovigerous females, and ovigerous females with a non-normal distribution for males (Kolmogorov-Smirnov test, $K = 1.998$, $p = 0.001$) and non-ovigerous females (Kolmogorov-Smirnov test, $K = 1.626$, $p = 0.010$), but with a normal distribution for ovigerous females (Kolmogorov-Smirnov test, K

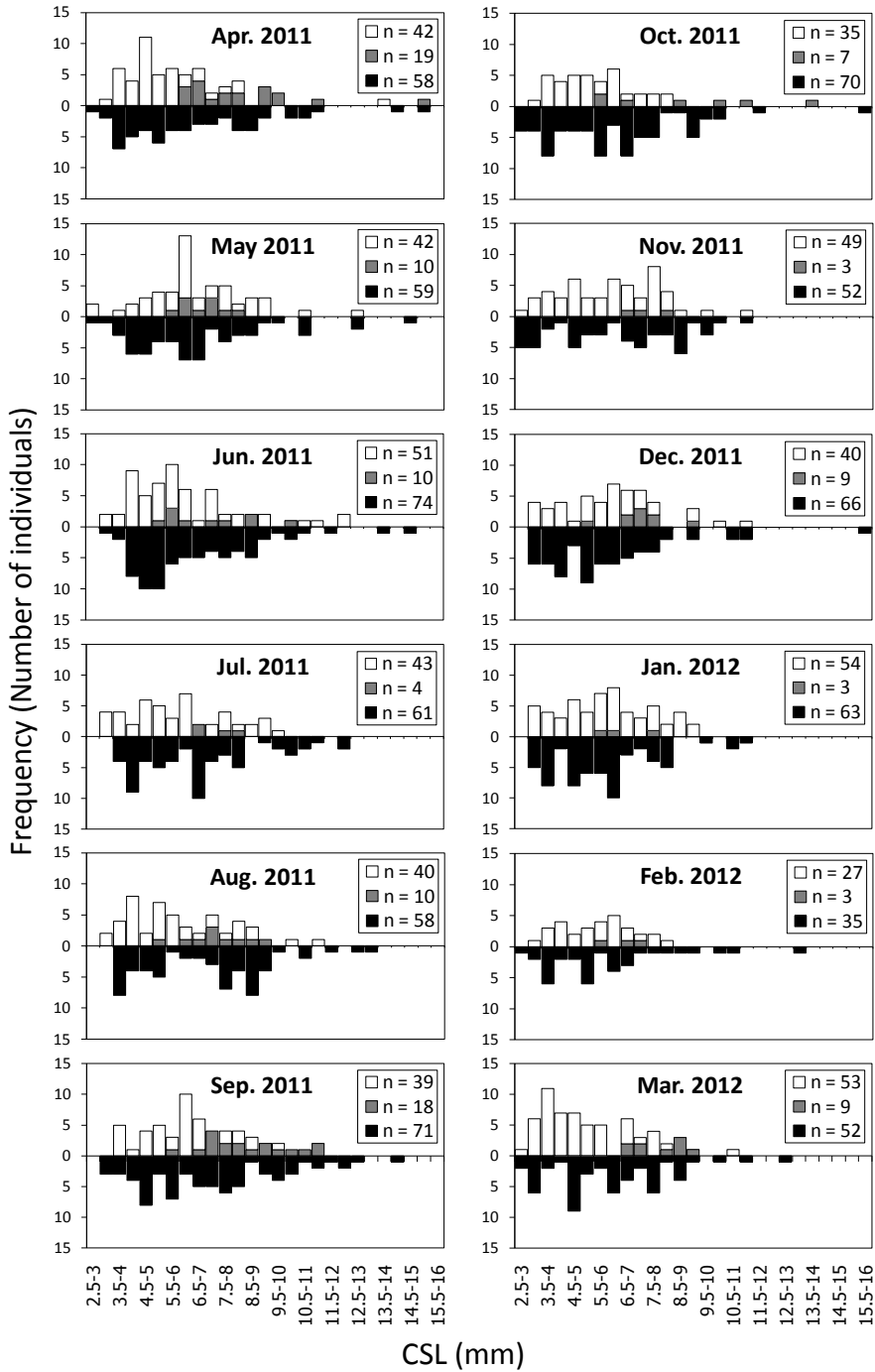


Figure 4. Monthly size frequency distribution of *Coenobita rugosus*.

■ = Males; □ = Non-ovigerous females; ▒ = Ovigerous females.

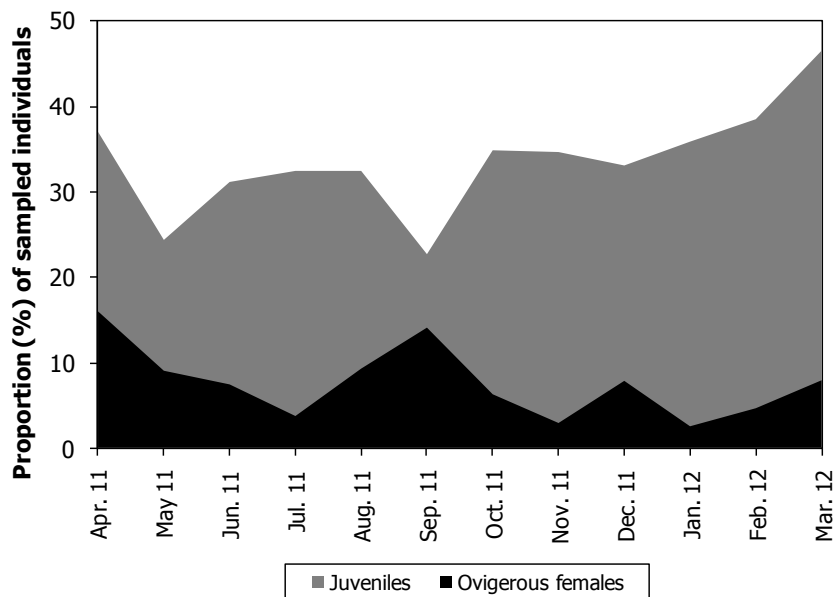


Figure 5. The relative proportion (%) of juvenile and ovigerous female *Coenobita rugosus*. Data are from the 446 juvenile (both male and female with CSL smaller than 5.06 mm) and 105 ovigerous female (CSL larger than or equal to 5.06 mm) *Coenobita rugosus*, sampled over the study year.

= 1.163, $p = 0.133$). There was a significant deviation from homoscedacity for males, non-ovigerous females and ovigerous females (Levene test, $p < 0.001$). Most individuals were within the 3.0–11.5 mm CSL size range (1,292/1,339 crabs sampled or 96%). The five most frequent size categories of males were 3.5–4.0, 4.0–4.5, 4.5–5.0, 5.0–5.5 and 6.5–7.0 mm. For female crabs, the most frequent size categories were 3.5–4.0, 4.0–4.5, 4.5–5.0, 5.0–5.5 and 6.0–6.5 mm for non-ovigerous females, and from 5.5–6.0, 6.0–6.5, 6.5–7.0, 7.0–7.5, 7.5–8.0 and 8.0–8.5 mm for ovigerous females, respectively. The monthly size frequency distribution of males, non-ovigerous females, and ovigerous females sampled during the study period is summarized for the study year in Figure 4.

The 446 juveniles (CSL < 5.06 mm, smaller than the smallest ovigerous female) constituted 33.3% of the total crabs collected over the year, whilst the monthly proportion of juveniles in the samples ranged from 22.7% in September 2011 to 46.5% in March 2012 (Figure 5) and the actual number ranged from 25 (February 2012) to 53 (March 2012) juvenile crabs. Nevertheless, crabs in the smallest size class (2.5–3.0 mm) were not found in samples from June to September, December 2011 and January 2012 (Figure 4).

Population Density and Dispersion

The average density of *C. rugosus* between April 2011 to March 2012 was 6.98 ± 0.36 crabs/m², whilst the monthly density ranged from 4.06 ± 3.94 (February 2012) to 8.44 ± 4.34 crabs/m² (June 2011). There was no significant difference in density between sampling months (ANOVA, $F = 0.732$, d.f. = 11, $p = 0.707$). The number of crabs in sampled quadrats ranged from 0 to 28 individuals. Crabs were not found in three quadrats from all 192 quadrats sampled along the study period. The relationships between crab density and the physical factors (temperature, relative humidity, seawater salinity and rainfall amount) were not significant (Spearman's rank-order correlation, $p > 0.05$) (Figure 6).

The GC values were calculated to reveal any potential dispersion patterns in *C. rugosus* at the study site, and are shown in Figure 7. The monthly dispersions of total individuals were aggregated (positive values of GC between 0.003 and 0.048). Male individuals showed clumped dispersions in all months at the study site with positive GC values, ranging from weakly (0.006) in November to strongly (0.052) in August, while aggregated dispersions were also observed in non-ovigerous females (weakly (0.018) in June to strongly in February (0.079) and April (0.066)) during the study period. The dispersions of ovigerous females were clumped in April, May, September and especially in October 2011 (positive values of GC between 0.028 and 0.441) but uniform from June to August 2011 and between November 2011 and March 2012 (GC values from -0.067 to -0.007).

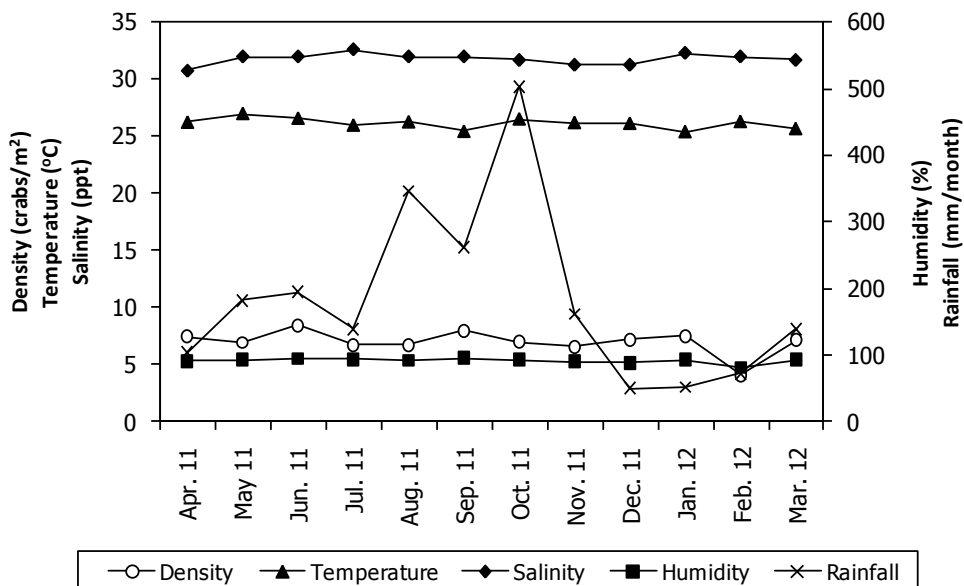


Figure 6. Average population density of *Coenobita rugosus* and various environmental factors.

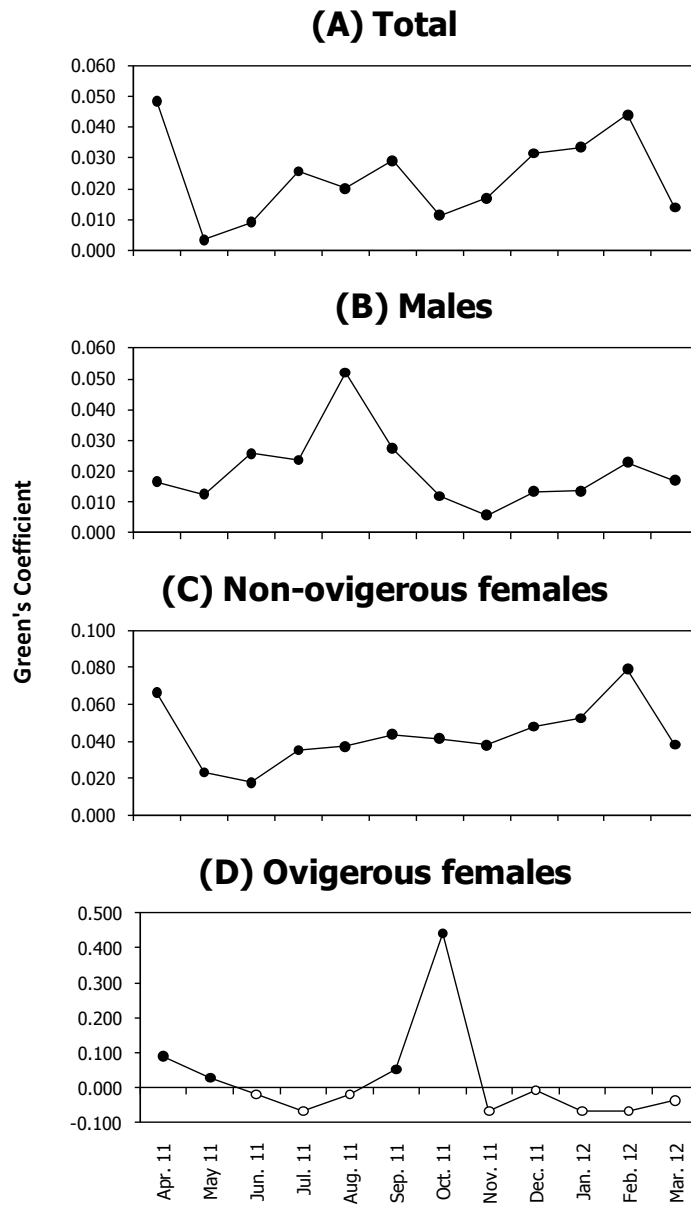


Figure 7. Green's coefficients (GC). Shown are the GC values for the (A) total, (B) male, (C) non-ovigerous female, and (D) ovigerous female *Coenobita rugosus* sampled over the study year.

Sex Ratio

The overall sex ratio of *C. rugosus* was slightly male-biased (1:0.86 M:F) and significantly different from the expected 1:1 ratio ($\chi^2 = 7.320$, d.f. = 1, $p = 0.007$). However, the monthly sex ratios of *C. rugosus* sampled were close to 1:1 in all the months, except for in October 2011, which was male-biased (Table 2). The monthly sex ratios (as % of males) ranged from 45.6% (March 2012) to 62.5% (October 2011), whilst the proportion of non-ovigerous females ranged between 30.5% (September 2011) and 47.1% (November 2011) and ovigerous females ranged from 2.5% (January 2012) to 16.0% (April 2011).

The sex ratio in most size classes tended to be about 1:1 (Figure 8). Nevertheless, the 2.5–3.0 mm and the three size classes between 9.5–11.0 mm had male-biased sex ratios ($\chi^2 = 5.556, 3.857, 5.000, 7.200$, d.f. = 1, $p = 0.018, 0.050, 0.025, 0.007$, respectively), whilst the 6.0–6.5 mm size was female-biased ($\chi^2 = 4.101$, d.f. = 1, $p = 0.043$). Size classes of 11.5–12.0, 13.0–13.5, 14.0–15.0 and 15.5–16.0 mm were comprised of only males, but the number of individuals was very small (2–4 per size class).

Diet

During this study, 16 species of plants and three species of animal carcass were observed being consumed by *C. rugosus* (Table 3). Decomposed leaves and fresh and decomposed flowers were the most common foods eaten by the crabs. Fallen flowers of *Cordia subcordata* were found throughout the year and were the most frequently consumed food item by *C. rugosus* (personal observations). Two species of brachyuran crabs were consumed (as carrion) by *C. rugosus*, where the decaying articulations between the segments of the pereopods were consumed. In addition, one observation of cannibalistic behavior by a juvenile *C. rugosus*

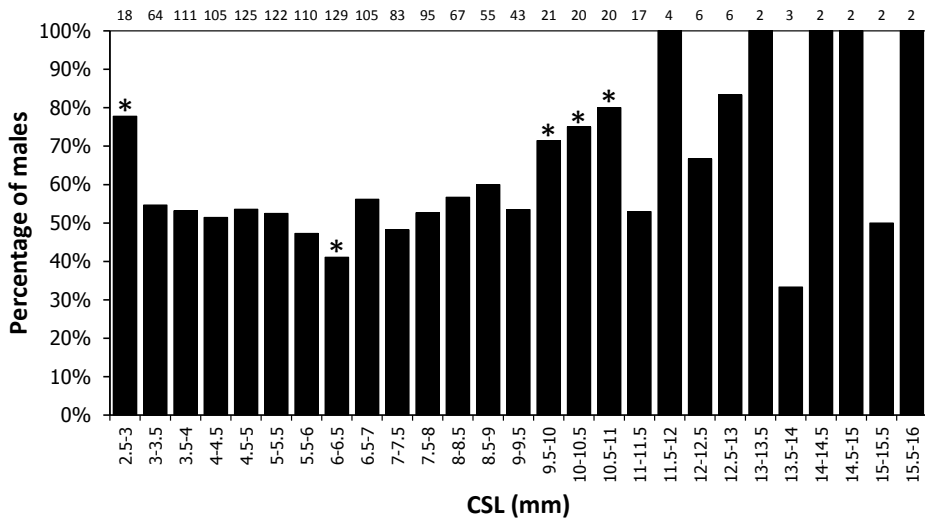


Figure 8. Sex ratio of *Coenobita rugosus*. The sex ratio is shown as the percentage of males based on the CSL size. * = Significant ($p < 0.05$) deviation from the expected 1:1 sex ratio. Value above each column is the total number of individuals in each size class.

Table 3. List of foods eaten by *Coenobita rugosus* at Cape Panwa, Phuket Island, Thailand from April 2011 to March 2012.

Species	Family	Parts of food eaten*
<i>Acacia auriculaeformis</i> A. Cunn. ex Benth.	Leguminosae	Leaves (D)
<i>Clerodendrum inerme</i> (L.) Gaertn.	Lamiaceae	Flowers (F, D), leaves (D)
<i>Cordia subcordata</i> Lam.	Boraginaceae	Flowers (F, D), leaves (D)
<i>Derris scandens</i> (Roxb.) Benth.	Leguminosae	Flowers (F, D)
<i>Diospyros</i> sp.	Ebenaceae	Fruits (D)
<i>Enhalus acoroides</i> (L.f.) Royle	Hydrocharitaceae	Leaves (D)
<i>Guettarda speciosa</i> L.	Rubiaceae	Flowers (F, D), leaves (D)
<i>Ipomoea violacea</i> L.	Convolvulaceae	Flowers (F, D), leaves (D)
<i>Lagerstroemia</i> sp.	Lythraceae	Flowers (F, D), leaves (D)
<i>Lantana camara</i> L.	Verbenaceae	Leaves (D)
<i>Ruellia tuberosa</i> L.	Acanthaceae	Flowers (F, D), leaves (D)
<i>Secamone elliptica</i> R.Br.	Asclepiadaceae	Leaves (D)
<i>Stachytarpheta jamaicensis</i> (L.) Vahl	Verbenaceae	Leaves (D)
<i>Thespesia populnea</i> (L.) Soland. ex Corr.	Malvaceae	Leaves (D)
<i>Urarica crinita</i> (L.) Desv. ex DC.	Leguminosae	Leaves (D)
<i>Wedelia prostrata</i> Hemsl.	Asteraceae	Leaves (D)
<i>Coenobita rugosus</i> H. Milne Edwards	Coenobitidae	Carcass (cannibalism)
<i>Grapsus albolineatus</i> Latreille	Grapsidae	Decaying articulations between segments of pereopods
<i>Thalamita</i> sp.	Portunidae	Decaying articulations between segments of pereopods

*F = fresh and D = decaying

was also recorded, in which a shell-less *C. rugosus* carcass was consumed (11.06 mm CSL adult male with a damaged and slightly decomposed abdomen).

Reproduction

C. rugosus appeared to reproduce throughout the year because ovigerous females were found throughout the study period. The proportion of females that were ovigerous ranged from 5.3% and 5.8% in January and November to 31.6% and 31.2% in September and April (Figure 9).

Ovigerous females ranged from 5.06–15.12 mm CSL, with a mean CSL size of 7.78 ± 1.68 mm ($n = 105$). Although no individuals in the 11.5–13.5 and 14.0–15.0 mm size classes were observed (Figure 10), the sample size in each of these size categories was small, with few females over 11.5 mm CSL. The smallest ovigerous female sampled, and so the potential minimum sexual maturity size, as a morphological criterion to determine juvenile and adult stages, was 5.06 mm CSL.

There was no significant relationship between the proportion of ovigerous females and the environmental factors of temperature, relative humidity, seawater salinity and rainfall (Spearman's rank-order correlation, $p > 0.05$).

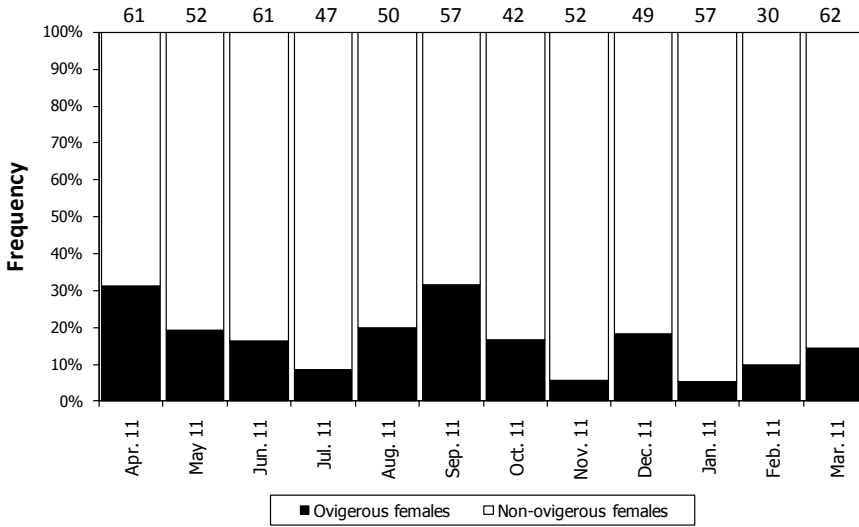


Figure 9. Proportion (%) of non-ovigerous and ovigerous female *Coenobita rugosus*. Data cover the one year sampling period. Value above each column is the total number of individuals sampled in that month.

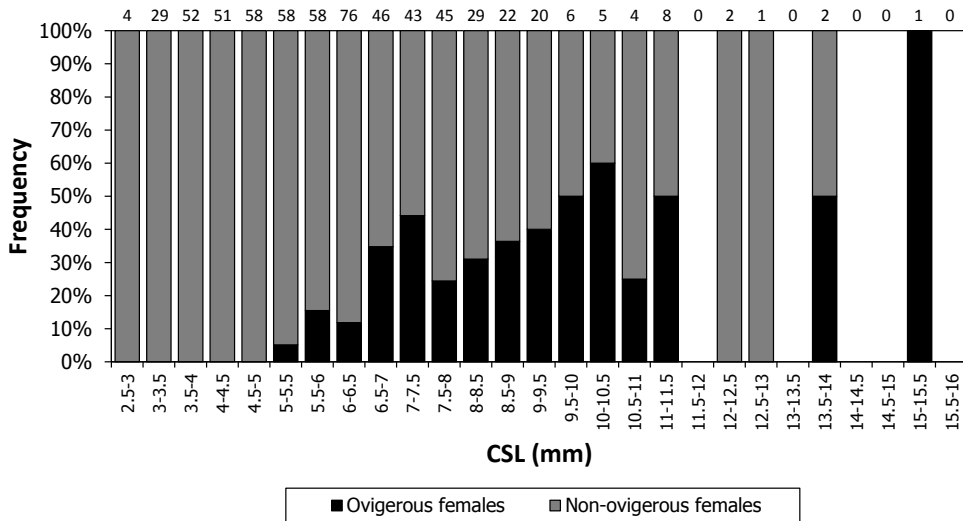


Figure 10. Size-dependent proportion of non-ovigerous female and ovigerous female *Coenobita rugosus*. Crab size classes are shown in terms of the CSL. Value above each column is the total number of individuals in that size class.

DISCUSSION

The characteristics of *C. rugosus* living at Cape Panwa, Phuket Island, may reflect adaptive responses to the constant tropical environment by showing regular densities and sex ratios close to 1:1 during all sampling months as well as the continuous reproduction and recruitment throughout the year.

C. rugosus at the study site showed tendency of unimodality of annual size frequency distribution with slight monthly variations. The unimodality usually reflects the balance between a continuous recruitment without class disruption, and constant mortality rates (DIAZ & CONDE, 1989; MANTELATTO & SOUSA, 2000; SALLAM & MANTELATTO, 2010). The obvious unimodal pattern of size frequency distribution was noted for the congeneric species *C. scaevola* (SALLAM & MANTELATTO, 2010).

Male *C. rugosus* potentially reached a larger (CSL) size than females, as previously recorded in *C. clypeatus* (WILDE, 1973) and *C. scaevola* (SALLAM & MANTELATTO, 2010). This sexual size dimorphism is probably due to male crabs growing more rapidly than females due to differences in their energy consumption and utilization / allocation (ABRAMS, 1988; SALLAM & MANTELATTO, 2010). Furthermore, the MCL was found to be a secondary sexual character of *C. rugosus* at this site, with males having a relatively larger MCL than females. This is the first quantitative evaluation of this trait in terrestrial hermit crabs, although it has been recorded before in marine hermit crabs *Calcinus tibicen* (FRANSOZO ET AL., 2003), *Diogenes nitidimanus* (KOGA ET AL., 2010), *Paguristes erythropros* (BIAGI & MANTELATTO, 2006) and *Loxopagurus loxochelis* (MANTELATTO & MARTINELLI, 2001). This sexual feature presumably infers that larger male crabs are able to fertilize more females than smaller ones, resulting in greater reproductive fitness (ABRAMS, 1988). However, the disparity in MCL for a particular size of CSL of both sexes of adult *C. rugosus* was only less than 1 mm. Therefore, this character may be unsuitable in distinguishing sexes of *C. rugosus*, particularly as measured in the field.

The density of *C. rugosus* did not significantly differ among months. This presumably reflects the almost constant environment in the study area. Three quadrats that crabs were not encountered were exposed directly to sunlight or covered with little shade or vegetation. This observation is relevant to the investigation of BROOK ET AL. (2009) who pointed out that *C. rugosus* depended considerably on vegetation in the supralittoral area as well as MORRISON (2005) who reported that *C. clypeatus* were significantly more abundant on vegetated islands than on bare islands. The average density of *C. rugosus* in the current study area collected by quadrat sampling fell between the range of average densities of *C. clypeatus* in the vegetated areas on three islands (0.013 ± 0.021 and 13.20 ± 14.31 crabs/m²), which were evaluated by baited pitfall traps (MORRISON & SPILLER, 2006). Differences in abundance between these studies may reflect the different sampling methods, times and life histories as well as discrepancies between habitats of the two crab species.

Dispersion of individuals in a population can provide valuable insight into interactions between individuals of a species and their biotic and abiotic environment. The dispersions of all crabs, as well as male and non-ovigerous female *C. rugosus* were aggregated. A clumped pattern is normally associated with an unequal resource distribution (KREBS, 1999). *C. rugosus* at the study site was found to mainly dwell in the supralittoral zones, in areas covered by vegetation, similar to the populations at other localities (PAGE & WILLASON, 1982; NAKASONE, 2001; BARNES, 2002). The vegetation presumably provides shelter, shade and food (PAGE & WILLASON, 1982; BROOK ET AL., 2009). However, such vegetation was unevenly distributed at

this study site and so may well have influenced the dispersion of most of the crabs. Uniform dispersion results from negative interactions between individuals in population, such as competition for food or space (LUDWIG & REYNOLDS, 1988). For the case of ovigerous female *C. rugosus*, it is possible that these females avoided other ovigerous females during their vulnerable period of carrying eggs. However, it is currently unclear as to why they would do this. This may also be the reason why ovigerous females tended to be secretive (BURGGREN & McMAHON, 1988). In addition, it might be because these females are inactive diurnally and active nocturnally and therefore more difficult for researchers to detect (SALLAM *ET AL.*, 2008).

The male-biased overall sex ratio of *C. rugosus* at Cape Panwa may be the result of several factors, including detectability. For example, males may be more active to facilitate finding or defending females / territories or have more active foraging patterns for other unknown reasons. A male-biased sex ratio is uncommon in hermit crab populations studied so far worldwide. In contrast, most hermit crabs show a female-biased sex ratio, including another coenobitid, *C. scaevola* (M:F = 1:1.2) (SALLAM *ET AL.*, 2008). However, the overall male-biased sex ratio of this study resulted from the accumulation of individuals collected during the entire 12-month study period. However, when we examined the sex ratio based on monthly averages then the ratio was close to and not significantly different from the expected 1:1 ratio (FISHER, 1930) (M:F = 1:0.9, $\chi^2 = 0.321$, d.f. = 1, $p = 0.571$).

The sex ratio among CSL size class of *C. rugosus* was similar to a standard pattern described by WENNER (1972) of an approximately equal proportion of males and females in the smaller size classes and a deviation towards a certain sex (in this case males) at the larger size classes. However, for this population, the sex ratio of the smallest size class (2.5–3.0 mm) was also male-biased, although this anomaly was presumably attributed to different habitat use and behavior of small females, probably resulting in a lower probability of detection of these females than males. For example, juvenile females might inhabit more concealed microsites. Conversely, the sex ratios of size classes of *C. scaevola*, living in variable environments in hyper arid regions, showed an anomalous pattern as described by WENNER (1972) (SALLAM & MANTELATTO, 2010).

The observed diet of *C. rugosus* at this site was somewhat diverse although less diverse than the diet reported for *C. compressus* at the Osa Peninsula of Cost Rica (LAIDRE, 2013). The majority of food items for this population of *C. rugosus* came from plants living on the beach. Therefore, it is possible that the main food source for this population may come from terrestrial inputs although quantitative data were not collected in the present study. In contrast, MORRISON (2005) inferred that *C. clypeatus* on bare islands in the central Exumas, Bahamas may feed on resources that are derived from marine inputs. Nevertheless, further quantitative investigations are needed to prove our hypothesis. Fallen *Cordia subcordata* flowers as the most often consumed food item by *C. rugosus* in this study was similar to the results of SMALL & THACKER (1994) and THACKER (1994) where *C. compressus* in Panama commonly consumed fallen flowers of *Bombacopsis sessilis*. However, based on the observations of this study, the living parts of plants were not eaten by *C. rugosus*, as previously reported (PAGE & WILLASON, 1983).

The removal of carrion by *C. rugosus* may help reduce or prevent colonization by flies (PAGE & WILLASON, 1983). The hermit crab carcass without its occupied shell presumably died as a result of fighting for shells or in competition between males to copulate with a female. The odor of the dead hermit crab could have attracted and led other conspecific individuals to locate its empty shell for exchange (SMALL & THACKER, 1994), but the occupied shell of the

dead crab was not seen for confirmation. SMALL & THACKER (1994) reported that *C. perlatus* in Micronesia and *C. compressus* in Panama did not consume dead conspecifics during field experiments. On the contrary, WILDE (1973) recorded the death of *C. clypeatus* caused by cannibalism during a laboratory experiment. Cannibalism may cause reductions in population size (FOX, 1975), but this phenomenon was observed only one time for this population during the study period.

The year-round continuous reproduction of land crabs generally occurs near the tropics (BURGGREN & McMAHON, 1988). Ovigerous females of *C. rugosus* were found throughout the year at this study site. In contrast, the breeding season of *C. rugosus* in Okinawa, Japan was reported to be in late May to November (NAKASONE, 2001). Intraspecific variation in the reproductive period may occur as an adaptive response for reproductive success in different environments (SASTRY, 1983b). The highest reproductive activity in relation to ovigerous female percentage was in April and September 2011 and showed no significant relationship with the investigated environmental variables, although these high ovigerous female proportions occurred at the end of the dry northerly monsoon and the wet southwesterly monsoon of the Indian Ocean, respectively (NICHOLS & WILLIAMS, 2009). Therefore, further investigation of potential factors influencing reproductive activity of *C. rugosus* is required to understand this phenomenon. In addition, because of a lack of information on egg development and observations of mating behavior, these data are also needed to clarify the reproductive season of *C. rugosus*.

The smallest ovigerous female found in this Cape Panwa population (5.06 mm CSL) was larger than that of the population at Okinawa (3.93 mm CSL; NAKASONE, 2001). Differences in the beginning of sexual maturity between these two geographically separated populations of *C. rugosus* might result from disparities between habitats and environments of the two locations, life histories, different sampling methods and sampling periods (GARCIA & MANTELATTO, 2000; MANTELATTO & GARCIA, 2000). Nevertheless, the dissection on the reproductive system of ovigerous females was not carried out in this study. This anatomical examination should be investigated further along with physiological studies to confirm and compare the maturity of *C. rugosus* among sites. Additionally, the traditional criterion of sexual maturity of hermit crabs using the size of the smallest ovigerous female may not a strong indicator compared to following a cohort through time and using their mean / median size at sexual maturity.

Larval dispersal and recruitment of crustaceans with pelagic larvae are related to the duration of larval development, dynamics of water circulation, characteristics of life history, and habitat requirements (SASTRY, 1983a). The larval developmental time of *C. rugosus* zoea is approximately 20–31 days with five stages (SHOKITA & YAMASHIRO, 1986), and the larvae then metamorphose to the glaucothoe stage. Nevertheless, at present, there is no available information on the developmental duration of the glaucothoe stage before metamorphosing to the first crab stage. Juvenile *C. rugosus* (2.5–5.0 mm) were detected in all months, suggesting that recruitment of larvae to the population occurred throughout and to a large extent. However, the number of juveniles dropped dramatically in May and September 2011, which may reflect the effects of random chance of sampling and/or predation by particular predators, such as the rough red-eyed crab, *Eriphia smithii*. Analysis of the stomach contents of this predator may help address the causes of the decrease of juvenile *C. rugosus*.

The present study has revealed some of the important aspects of the population ecology of *C. rugosus* at Cape Panwa, Phuket Island. This information on the ecology of *C. rugosus* can be used as fundamental knowledge for the conservation of this species because the existence

and abundance of land hermit crabs could be used as a potential indicator of the quality and degree of deterioration of the supralittoral zones of the beaches, especially where the establishment of tourist activities and facilities occur (SALLAM *ET AL.*, 2008; BROOK *ET AL.*, 2009). Therefore, the conservation of coastal habitats, specifically for the supralittoral area and its vegetation, is primarily needed for the preservation of these animals.

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