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# SHELL UTILIZATION BY THE LAND HERMIT CRAB *COENOBITA RUGOSUS* (ANOMURA, COENOBITIDAE) WITH NOTES ON THE FIRST RECORD OF BIVALVE SHELL USE

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ABSTRACT

Understanding of the use of shells as an indispensible resource for land hermit crabs increases our understanding of their life history. We investigated shell utilization of the land hermit crab *Coenobita rugosus* from April 2011 to March 2012 on Phuket Island in the Andaman Coast of Thailand. A total of 1,322 individuals of *C. rugosus* were collected (711 males, 507 non-ovigerous females and 104 ovigerous females) using multiple quadrat sampling, and were found to use 63 molluscan shell species, including 62 gastropod shell species from 20 families and one bivalve shell. The diversity of shells used increased with body size from small to medium-sized crabs, but decreased in larger crabs. The most commonly occupied shell species was *N. albicilla* (19.6 % of crabs). However, *N. albicilla* used by *C. rugosus* was not the lightest shell species based on the ratio between internal volume and weight following the "energy saving hypothesis". Globose shells and those with ovate apertures were the most commonly used shell types. The shell utilization patterns of *C. rugosus* at the study site were different among reproductive stages. Furthermore, strong correlations between internal volume and aperture size of occupied shells and hermit crab characters suggest that the shell internal volume and size of aperture are the main determinants for shell utilization of *C. rugosus*. Consequently, the pattern of shell utilization of *C. rugosus* is seemingly similar to those of other coenobitid species based on the frequent occupation of certain shell species and shapes. Additionally, the great shell diversity used by this population of *C. rugosus* compared with other conspecific populations and congeneric species may reflect more plasticity in shell utilization due to the high diversity of shell resources in the tropical habitats in the Indo-Pacific region.

Keywords: Coenobitidae, terrestrial hermit crab, shell use pattern, shell quality, bivalve shell use

## INTRODUCTION

Sixteen species of land hermit crabs of the genus *Coenobita*, family Coenobitidae, among 1,106 currently recognized species of hermit crabs have been reported in tropical and subtropical coastal areas around the world (McLaughlin *et al.*, 2007; De Grave *et al.*, 2009; McLaughlin *et al.*, 2010). Land hermit crabs are also the most common crustaceans in some tropical islands (Page & Willason, 1982; Morrison, 2005). These crabs are also an important component in the marine-land interface of the supralittoral zones of insular and coastal areas

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(Morrison & Spiller, 2006) as generalist scavengers accelerating the rate of recycling of nutrients and energy in food webs (Laidre, 2013).

In order to protect their soft and vulnerable abdomens, all land hermit crab species use empty gastropod shells as portable homes (Burggren & McMahon, 1988). The unique shell-carrying habit of coenobitid crabs provides many types of benefits, including protection against predators and from desiccation (Burggren & McMahon, 1988; Greenaway, 2003). The space inside the occupied shell is available for storing water to maintain crab body moisture, allowing them to forage farther inland (Wilde, 1973). Several shell characteristics have been reported to be correlated with hermit crab morphological characters (i.e., shell size and weight, aperture size, internal volume) (Hazlett, 1981). Shells probably play a role as a limiting resource for certain hermit crab populations (Fotheringham, 1976; Kellogg, 1976; Laidre, 2012). In addition, inhabited shells possibly affect growth, reproduction and risk of predation (Blackstone, 1985; Osorno *et al.*, 2005; Sallam *et al.*, 2008; Contreras-Garduno *et al.*, 2009; Sallam, 2012). Furthermore, shell resources for hermit crabs in different areas have effects on population characteristics such as abundance, maximum size and reproduction (Fotheringham, 1976; Sallam *et al.*, 2008).

The shell utilization pattern of land hermit crabs has been studied in several areas of the world (e.g. Western Atlantic by Morrison & Spiller (2006); Eastern Pacific by Abrams (1978), Guillen & Osorno (1993) and Laidre & Vermeij (2012); North Pacific by Willason & Page (1983) and Szabo (2012); Western Pacific by Boneka *et al.* (1995); Red Sea by Volker (1967), Sallam *et al.* (2008) and Sallam (2012); Western Indian Ocean by Barnes (1999, 2001, 2002)). Nevertheless, information on shell use by land hermit crabs of the Andaman Sea east of the Indian Ocean, an area of high gastropod diversity, (Tantanasiriwong, 1978; Middelfart, 1997), is scant.

*C. rugosus* has been recorded as a widely distributed and common species in the Indo-Pacific region (McLaughlin *et al.*, 2007). Among three species of land hermit crabs recorded in Thailand, *C. rugosus* is the most common (McLaughlin, 2002). This species is usually found living on sandy beaches and beach forests in the supralittoral zone (Frith & Alexander, 1978; Boneka *et al.*, 1995; Nakasone, 2001; Barnes, 2002). At Cape Panwa, Phuket Island, Thailand, *C. rugosus* was recently investigated in relation to population ecology (Bundhitwongrut *et al.*, 2014). The present study is an initial attempt to investigate the life history and shell utilization of *C. rugosus*. The objectives of the present study are to examine shell utilization patterns and the relationship between characters of shells used and crab characteristics of the population of *C. rugosus* at Cape Panwa, Phuket Island, Andaman coast of Thailand.

## MATERIALS AND METHODS

### Study Area

This study was conducted at Cape Panwa (7°48'26"N, 98°24'35"E), which is situated on the southeast side of Phuket Island on the Andaman coast of Thailand approximately 10 km south of the town of Phuket. 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 conducted at the beach in the supralittoral zone in the area of the Phuket Marine Biological Center (PMBC) at Cape

Panwa, Phuket. The beach of Cape Panwa is an open sand scrub beach, comprised of rather coarse sand patches of shale (phylitte) (Nielsen, 1976a). The inland edge is covered with sparse vegetation alternating with dense vegetation in front of steep 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 of 2.15–2.27 m at spring tide to 0.85–1.15 m at neap tide (Limpsaichol, 1981). A map of the study area and environmental conditions during the study period are given in Bundhitwongrut *et al.* (2014).

### Specimen Sampling and Analysis

The study was conducted during April 2011 to March 2012, simultaneously with an investigation of the population ecology of *C. rugosus* (Bundhitwongrut *et al.*, 2014). *C. rugosus* were collected three days per month. The hermit crabs were collected by hand at low tide from the supralittoral zone by the same person (the first author) in the early morning (Sallam *et al.*, 2008). Multiple 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 $m^2$ were placed every 5 m on transects from 5 m above the mean sea level to 45 m further inland. The quadrats had walls 10 cm high to prevent crabs from escaping, as land hermit crabs are agile and can move quickly.

All crabs sampled were brought to the laboratory in the office of PMBC. 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 in order to investigate crab characters. According to the policy of the PMBC, removal of crabs from the population at the study site was not permitted to avoid negative impacts on native animals. Additionally, all authors agreed to the current sampling method to avoid as best as possible killing crabs in order to maintain and preserve this population of *C. rugosus*. Thus, 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.

An additional marking method was conducted during this study. After surveys in each sampling month, all sampled crabs were marked before being released into the natural habitat at the same point from where they were collected. The markings were made with a waterproof pen and then coated with nail varnish on crabs (on the outer surface of palm of the major cheliped) as well as their occupied shells (on the surface of the body whorl near the outer lip). From the results in preliminary trials, the markings persisted for at least one month in the natural habitat of crabs. Additionally, all recaptured crabs of each month were marked again, if encountered in the sampling quadrats.

Several characteristics of *C. rugosus* were investigated and measured, including cephalothoracic shield length (CSL; from the tip of the rostrum to the midpoint of the posterior edge of the cervical groove) and width (CSW; the greatest width of the cephalothoracic shield perpendicular to CSL), weight (CW), sex and reproductive stage (males, non-ovigerous females, and ovigerous females), major chela length (MCL; from the articulation between carpus and propodus to the tip of fixed finger of the left cheliped) and major chela width

(MCW; the greatest distance from the dorsal margin to the ventral margin of propodus of the left cheliped perpendicular to MCL).

Species of occupied and unoccupied shells were identified using several references (BRANDT, 1974; NIELSEN, 1976a, b; WIUM-ANDERSEN, 1977; TANTANASIRIWONG, 1978; MIDDELFART, 1997; POUTIERS, 1998; TAN & CLEMENTS, 2008). In addition, shells were compared with specimens deposited in the reference collection of PMBC to confirm their identities. The quantitative characteristics included shell length (SL), width (SW), weight (WW), internal volume (SIV), aperture length (SAL), and aperture width (SAW). We measured the internal volume of shells by gradually adding water from a graduated syringe (FLOETER *ET AL.*, 2000). If a shell was damaged, holes were closed with UHU® patafix glue pads (UHU GmbH & Co., Germany) before they were filled with water. We investigated all quantitative measurements to the nearest 0.01 mm for size using digital vernier calipers, 0.01 g for weight using digital weighing scales, and 0.1 ml for volume using graduated syringes.

Qualitative shell characteristics, including shell shape, aperture (shell opening) shape and shell quality, were categorized and recorded. The shell and aperture shapes were classified according to SPRINGSTEEN & LEOBRERA (1986) and POUTIER (1998). Tables 1 and 2 give descriptions and schematic drawings of representative categories of shell and aperture shapes. The categories of shell shapes included biconical, conical, elongately conical, fusiform, globose, oval, pyramidal, pyriform, turban and vermiform. The categories of shell aperture shapes were classified as elongately ovate, irregular, ovate, round and semicircular. The shell quality categories were undamaged and damaged shells. Damaged shells included those with a broken apex, a hole, damaged inner lip, broken outer lip of the last whorl, or greater damage in a large portion of the shell (BARNES, 1999). Finally, the ratio between the shell internal volume and weight (SIV/W ratio) was calculated for all shell species occupied by *C. rugosus* as a predictor of shell quality (OSORNO *ET AL.*, 1998).

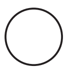
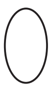
## Statistical Analysis

The data of all recaptured individuals of *C. rugosus* were excluded to avoid possible pseudosamples. Crabs were classified into groups according to reproductive stage as either male, female, non-ovigerous female, or ovigerous female. We used chi-square ($\chi^2$) tests to compare the frequencies of occupation of different shell species between sexes and among crab reproductive groups (ZAR, 2010). The frequencies of occupation of three most used shell species by all individuals of *C. rugosus* were utilized in chi-square analysis. The 0.5-mm size classes (CSL) intervals were applied to facilitate the comparison in shell use as a function of hermit crab size, following NAKASONE (2001), SALLAM *ET AL.* (2008) and BUNDHITWONGRUT *ET AL.* (2014). To determine relationships between characters of hermit crabs and occupied shells, regression analyses were performed using the power function equation ($Y = aX^b$) (SALLAM *ET AL.*, 2008). In all statistical tests, alpha was set to 0.05. All statistical analyses were performed using SPSS Statistics 17.0 (SPSS INC., 2008).

Table 1. Categories of shell shapes used in the present study.

| Shell shape | Description | Shell shape | Description |
|---|---|---|---|
| Biconical  | Resembling two equal or nearly equal cones placed base to base. | Oval  | Resembling conical, but with a relatively larger body whorl and an egg or elliptical shape outline. |
| Conical  | Resembling a cone with shell length equal or nearly equal to shell width, but not more than 1.5 times; a drop of water. | Pyramidal  | Resembling conical, but with flat-sided whorls and a nearly triangular outline; a pyramid shape. |
| Elongately conical  | Resembling an elongate cone with a long to very long spire; shell length more than 1.5 times of shell width. | Pyriform  | Resembling two unequal cones placed base to base with a large body whorl and a rather short spire; a pear shape. |
| Fusiform  | Resembling two nearly equal elongate cones placed base to base, tapering at both ends; a spindle shape. | Turban  | Resembling conical with a nearly globular body whorl, but with a broad conical spire and a convex base. |
| Globose  | Resembling a spherical shape with a nearly globular body whorl and a very short spire. | Vermiform  | Resembling a worm; an irregularly coiled tubular shell. |

Table 2. Categories of shell aperture (opening) shapes used in the present study.

| Shell aperture shape | Description |
|---|---|
| Round  | Resembling a circle with aperture length equal or nearly equal to aperture width, but not more than 1.2 times. |
| Ovate  | Resembling an egg or elliptical shape with aperture length 1.2–2.5 times aperture width. |
| Elongately ovate  | Resembling an egg or elliptical shape, but aperture length more than 2.5 times aperture width. |
| Semicircular  | Resembling a half circle; a D-shape. |
| Irregular  | Having an irregular shape, resulted from damage to original aperture. |

# RESULTS

## Shell Utilization Patterns of *Coenobita rugosus*

A total of 1,322 individuals of *C. rugosus* were collected, including 711 males and 611 females (507 non-ovigerous females and 104 ovigerous females) which were used for data analysis.

### *Diversity and groups of shells used*

*Coenobita rugosus* was found occupying at least 63 species of molluscan shells (Table 3), including 62 gastropod shell species of 20 families. Interestingly, a valve of one marine bivalve species, *Chama* sp., was occupied by one individual of *C. rugosus* (Figure 1).

*Coenobita rugosus* occupied the shells of 59 species of marine gastropods and only two species of freshwater gastropods and one species of terrestrial gastropod. The gastropod family with the highest number of species utilized by *C. rugosus* was Muricidae (27.0%; 17 species), followed by Neritidae (12.7%; 8 species) and Turbinidae (9.5%; 6 species) (Table 3).

### *Unused shells found in sampling quadrats*

In the sampling quadrats we found 132 shells of 18 gastropod species that were not used by hermit crabs during the study period. Most of unoccupied shells were damaged or plugged with gravel at the aperture. These shells were apparently unable to be used by crabs. One species of gastropod shell, *Trochus maculatus* ($n = 2$), was unoccupied by land hermit crabs at the study site.


Figure 1. *Coenobita rugosus* (8.25 mm CSL, male) inhabited the bivalve shell, *Chama* sp., at 20 m from the mean sea level at Cape Panwa, Phuket Island, Thailand on 27 November 2011 (Photos by Thanakhom Bundhitwongrut). A, dorsolateral view; B, ventral view.

Table 3. Shells utilized by *Coenobita rugosus* at Cape Panwa, Phuket Island, from April 2011 to March 2012. Shell group: MG = marine gastropod, FG = freshwater gastropod, TG = terrestrial gastropod, MB = marine bivalve. SIV/W = shell internal volume/weight ratio as mean ± SD for species that $n > 1$ and as value for species that $n = 1$.

| Shell group | Family | Scientific name | SIV/W |
|---|---|---|---|
| MG | Buccinidae | *Cantharus tranquebaricus* (Gmelin, 1791) | 0.422 ± 0.144 |
| | | *Cantharus undosus* (Linnaeus, 1758) | 0.401 ± 0.083 |
| | Bursidae | *Tutufa bubo* (Linnaeus, 1758) | 0.637 ± 0.240 |
| | Cerithiidae | *Clypeomorus batillariaeformis* Habe & Kosuge, 1966 | 0.309 ± 0.096 |
| | | *Rhinoclavis sinensis* (Gmelin, 1791) | 0.365 ± 0.161 |
| | Fasciolariidae | *Fusinus nicobaricus* (Roding, 1798) | 0.729 |
| | | *Pleuroploca filamentosa* (Roding, 1798) | 0.528 ± 0.218 |
| | Littorinidae | *Littorina scabra* (Linnaeus, 1758) | 0.325 |
| | Melongenidae | *Pugilina cochlidium* (Linnaeus, 1758) | 0.836 ± 0.106 |
| | | *Pugilina colosseus* Lamarck, 1816 | 0.833 |
| | Muricidae | *Chicoreus brunneus* (Link, 1807) | 0.300 ± 0.069 |
| | | *Chicoreus capucinus* (Lamarck, 1816) | 0.422 ± 0.159 |
| | | *Chicoreus ramosus* (Linnaeus, 1758) | 0.847 ± 0.486 |
| | | *Chicoreus torrefactus* (Sowerby, 1841) | 0.440 ± 0.067 |
| | | *Cronia margariticola* (Broderip, 1833) | 0.298 ± 0.098 |
| | | *Drupa rubusidaeus* Roding, 1798 | 0.297 |
| | | *Drupella rugosa* (Born, 1778) | 0.363 ± 0.125 |
| | | *Murex occa* Sowerby, 1834 | 0.614 ± 0.127 |
| | | *Murex pecten* Lightfoot, 1786 | 1.072 |
| | | *Purpura panama* (Roding, 1798) | 1.008 |
| | | *Rapana rapiformis* (Born, 1778) | 0.504 |
| | | *Semiricinula marginatra* (Blainville, 1832) | 0.259 ± 0.075 |
| | | *Thais echinata* (Blainville, 1832) | 0.400 ± 0.186 |
| | | *Thais hippocastanum* (Linnaeus, 1758) | 0.415 ± 0.194 |
| | | *Thais malayensis* Tan & Sigurdsson, 1996 | 0.584 ± 0.220 |
| | | *Thais mancinella* (Linnaeus, 1758) | 0.398 ± 0.111 |
| | | *Thais tuberosa* Roding, 1798 | 0.547 ± 0.155 |
| | Nassariidae | *Nassarius dorsatus* (Roding, 1798) | 1.191 ± 0.201 |
| | Naticidae | *Natica gualteriana* Recluz, 1844 | 0.717 ± 0.165 |
| | | *Natica tigrina* (Roding, 1798) | 0.870 ± 0.144 |
| | | *Polinices didyma* (Roding, 1798) | 0.948 |
| | | *Polinices mammilla* (Linnaeus, 1758) | 0.620 ± 0.151 |
| | Neritidae | *Nerita albicilla* Linnaeus, 1758 | 0.364 ± 0.114 |
| | | *Nerita articulata* Gould, 1847 | 1.122 ± 0.111 |
| | | *Nerita chamaeleon* Linnaeus, 1758 | 0.672 ± 0.210 |
| | | *Nerita costata* Gmelin, 1791 | 0.632 ± 0.263 |
| | | *Nerita insculpta* Recluz, 1841 | 0.853 ± 0.337 |
| | | *Nerita planospira* Anton, 1839 | 0.825 ± 0.293 |

Table 3 (continued).

| Shell group | Family | Scientific name | SIV/W |
|---|---|---|---|
| MG | Neritidae | *Nerita polita* Linnaeus, 1758 | 0.747 ± 0.207 |
| | | *Nerita squamulata* Le Guillou, 1841 | 0.677 ± 0.264 |
| | Potamididae | *Cerithidea cingulata* (Gmelin, 1791) | 0.216 |
| | | *Cerithidea obtusa* (Lamarck, 1822) | 0.696 ± 0.182 |
| | Ranellidae | *Cymatium muricinum* (Roding, 1798) | 0.585 |
| | | *Cymatium pileare* (Linnaeus, 1758) | 1.519 |
| | | *Cymatium succinctum* (Linnaeus, 1771) | 0.793 |
| | | *Cymatium* sp. | 0.383 ± 0.035 |
| | | *Gyrineum bituberculare* (Lamarck, 1816) | 0.436 ± 0.161 |
| | Siliquariidae | *Tenagodus cumingii* Morch, 1861 | 0.290 |
| | Strombidae | *Strombus canarium* Linnaeus, 1758 | 1.137 ± 0.125 |
| | | *Strombus urceus* Linnaeus, 1758 | 0.863 ± 0.196 |
| | Trochidae | *Monodonta labio* (Linnaeus, 1758) | 0.716 ± 0.260 |
| | Turbinidae | *Angaria delphinus* (Linnaeus, 1758) | 0.372 ± 0.107 |
| | | *Astraea semicostata* (Fischer, 1875) | 0.209 ± 0.046 |
| | | *Turbo argyrostomus* Linnaeus, 1758 | 0.463 ± 0.128 |
| | | *Turbo bruneus* (Roding, 1798) | 0.373 ± 0.168 |
| | | *Turbo cinereus* Born, 1778 | 0.401 ± 0.175 |
| | | *Turbo petholatus* Linnaeus, 1758 | 0.379 ± 0.203 |
| | Turritellidae | *Turritella terebra* (Linnaeus, 1758) | 0.533 ± 0.315 |
| | | *Turritella* sp. | 0.398 ± 0.207 |
| FG | Ampullariidae | *Pomacea canaliculata* (Lamarck, 1819) | 3.589 ± 0.985 |
| | Viviparidae | *Filopaludina martensi* (Frauenfeld, 1865) | 1.494 ± 0.402 |
| TG | Cyclophoridae | *Cyclophorus pfeifferi* (Reeve, 1861) | 1.061 |
| MB | Chamidae | *Chama* sp. | 0.485 |

***Shell species used in relation to crab reproductive groups***

The shell utilization pattern of *C. rugosus* varied in relation to shell species (Table 4). The most-used shell species was *Nerita albicilla* (19.6%, $n$ = 259), followed by *N. chamaeleon* (11.6%, $n$ = 153) and *N. polita* (11.3%, $n$ = 149).

Male and female *C. rugosus* utilized the same number of shell species (53 species) with 43 species (81%) used by both sexes. Ten shell species were occupied only by males and ten other shell species were occupied only by females. Males used shells of *N. albicilla* in highest proportion (20.8%, $n$ = 148), followed by *N. polita* (13.2%, $n$ = 94) and *N. chamaeleon* (12.5%, $n$ = 89). Females also occupied *N. albicilla* shells the most (18.2%, $n$ = 111), followed by *N. chamaeleon* (10.5%, $n$ = 64) and *Drupella rugosa* (9.3%, $n$ = 57). There was no significant difference in shell species occupation between males and females ($\chi^2 = 1.4$, *d.f.* = 2, $p = 0.486$).

Non-ovigerous females utilized more diverse shell species (51 species) than ovigerous females (22 species). There were significant differences in shell species occupation between non-ovigerous females and ovigerous females ($\chi^2 = 30.5$, *d.f.* = 2, $p < 0.001$). Non-ovigerous females mostly used *N. albicilla* (20.3%, $n$ = 103), followed by *D. rugosa* (11.2%, $n$ = 57) and *N. chamaeleon* (9.5%, $n$ = 48). The most occupied shell species by ovigerous females of *C.*

*rugosus* were *N. polita* (23.1%, $n$ = 24) and *N. chamaeleon* (15.4%, $n$ = 16) and followed by *N. costata* (10.6%, $n$ = 11). There were also significant differences in shell species occupation between males and non-ovigerous females ($\chi^2 = 9.6$, *d.f.* = 2, $p = 0.008$) and between males and ovigerous females ($\chi^2 = 14.9$, *d.f.* = 2, $p = 0.001$).

Table 4. Percentage of shell species inhabited by *Coenobita rugosus* at Cape Panwa, Phuket Island from April 2011 to March 2012. Numbers in parentheses after percentage indicate the number of crab individuals.

| Shell species used | Males | Non-ovigerous females | Ovigerous females | Total |
|---|---|---|---|---|
| *Astraea semicostata* | 2.8 (20) | 6.5 (33) | - | 4.0 (53) |
| *Drupella rugosa* | 11.4 (81) | 11.2 (57) | - | 10.4 (138) |
| *Monodonta labio* | 3.0 (21) | 2.6 (13) | 6.7 (7) | 3.1 (41) |
| *Nerita albicilla* | 20.8 (148) | 20.3 (103) | 7.7 (8) | 19.6 (259) |
| *Nerita chamaeleon* | 12.5 (89) | 9.5 (48) | 15.4 (16) | 11.6 (153) |
| *Nerita costata* | 2.8 (20) | 3.6 (18) | 10.6 (11) | 3.7 (49) |
| *Nerita polita* | 13.2 (94) | 6.1 (31) | 23.1 (24) | 11.3 (149) |
| *Thais hippocastanum* | 3.1 (22) | 3.9 (20) | 5.8 (6) | 3.6 (48) |
| *Turbo cinereus* | 3.9 (28) | 5.5 (28) | 4.8 (5) | 4.6 (61) |
| *Turbo petholatus* | 2.4 (17) | 2.2 (11) | 1.9 (2) | 2.3 (30) |
| Others-53 species | 24.1 (171) | 28.6 (145) | 24.0 (25) | 25.8 (341) |
| Total | (711) | (507) | (104) | (1322) |

### *Shell species used in relation to crab size*

Shell utilization pattern of *C. rugosus* varied in relation to crab size (Figures 2 and 3). The diversity of shells used by *C. rugosus* increased with body size from small to medium-sized crabs, but decreased in larger size classes (Figure 2). Medium-sized crabs (3.5–9.5 mm CSL, $n$ = 43–129 in each size class) utilized more diverse shell species (17–27 species) than smaller (<3.5 mm, $n$ = 18–64 in each size class, 7–11 species) and larger (>9.5 mm, $n$ = 1–21 in each size class, 1–11 species) crabs.

The three most-occupied shell species in the genus *Nerita* were inhabited by small to medium crabs (2.5–11.5 mm CSL) (Figure 3). *Nerita albicilla* was used by crabs 2.5 to 10.5 mm in size ($n$ = 259), while *N. chamaeleon* was occupied by crabs of sizes 3.0–11.0 mm ($n$ = 153) and *N. polita* was utilized by crabs of size 3.0–11.5 mm ($n$ = 149). Most small crabs (2.5–6.5 mm) occupied shells of *D. rugosa* (10.4%, $n$ = 138). Shells used in the genus *Turbo*, which were mainly *T. cinereus* (4.6%, $n$ = 61) and *T. petholatus* (2.3%, $n$ = 30), were inhabited by a wide range of size classes of crabs (3.5–16.0 mm).

### *Shell use in relation to shell shape*

Shell utilization patterns of *C. rugosus* varied in relation to shell shape (Figure 4). Globose shells (53.9%, $n$ = 712) were the most-used shell shape by all *C. rugosus*, followed by biconical shells (18.4%, $n$ = 243) and shells with a turban shape (11.5%, $n$ = 152). Males were found occupying more categories of shell shape (10 shapes) than non-ovigerous females (9 shapes) and ovigerous females (5 shapes).

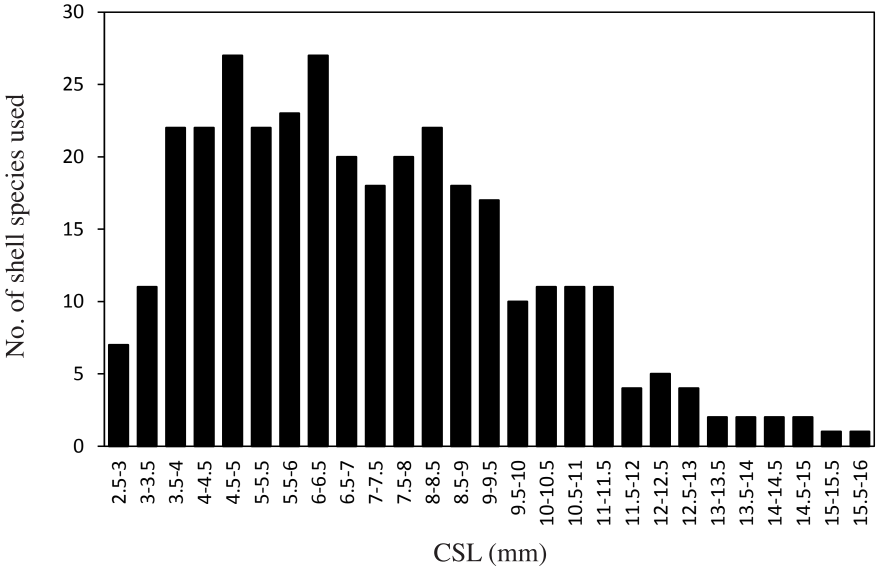



Figure 2. The number of shell species used by each size class of *Coenobita rugosus* at Cape Panwa, Phuket Island from April 2011 to March 2012.

***Shell use in relation to shell aperture shape***

Shell utilization patterns of *C. rugosus* varied in relation to shape of shell aperture (Figure 5). Shells with ovate apertures (75.0%, *n* = 992) were most used by all *C. rugosus*, followed by the shells with round (13.5%, *n* = 179) and semicircular apertures (4.8%, *n* = 64). Males and non-ovigerous females of *C. rugosus* were found occupying shells in all five categories of aperture shape, while ovigerous females were found using four categories. Shells with elongately ovate apertures were not occupied by ovigerous females.

***Shell use in relation to shell damage***

All crab groups used both damaged and undamaged shells. Crabs used undamaged shells (50.5%, *n* = 668) slightly more than damaged shells (49.5%, *n* = 654). Nevertheless, ovigerous females occupied undamaged shells (75.0%, *n* = 78) obviously more than damaged shells (25.0%, *n* = 26).

***Shell use in relation to SIV/W ratio***

The values of SIV/W ratio of shells used by *C. rugosus* at the study area ranged from 0.115 to 4.650. The most used shell species by *C. rugosus* at this site was not the lightest shell species as reflected by the ratio of SIV/W. *Nerita albicilla*, the most-occupied shell species, had a SIV/W ratio (mean ± SD) equal to 0.364 ± 0.114 (*n* = 259) (Table 3), but had a very low ranking SIV/W ratio (52$^{nd}$ out of 63 shell species). However, the lightest shell species was *P. canaliculata* with a SIV/W equal to 3.589 ± 0.985 (*n* = 4), but ranked 40$^{th}$ in terms of use by *C. rugosus*.

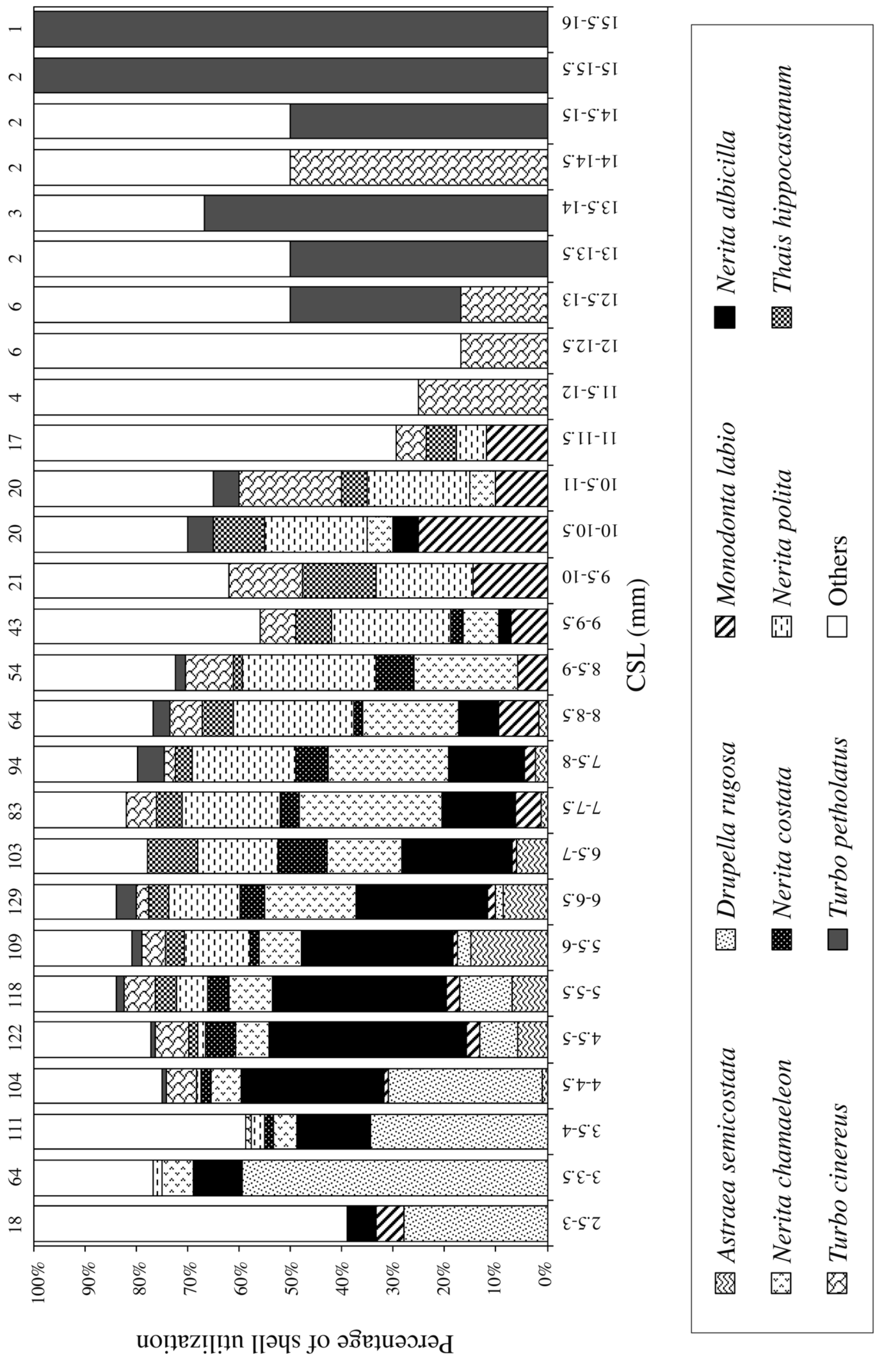



Figure 3. Shell utilization by *Coenobita rugosus* as a function of hermit crab size.

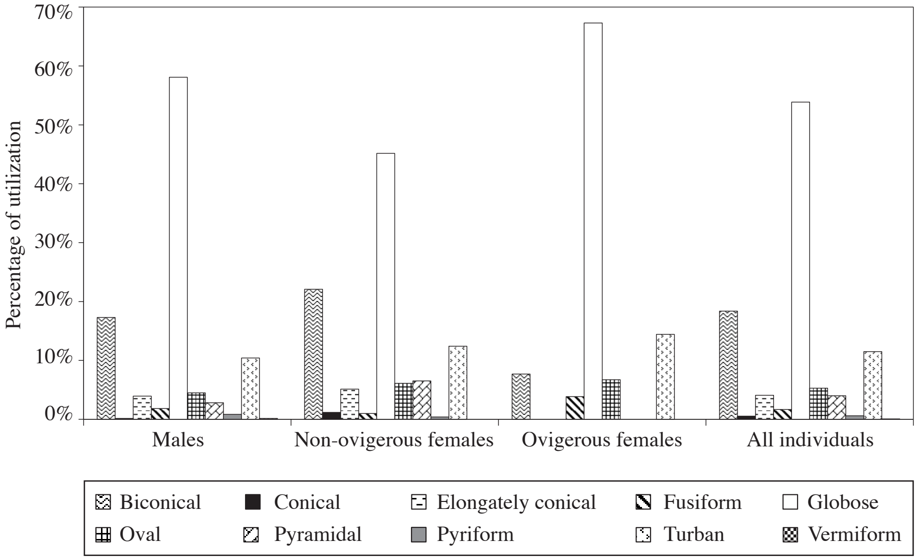



Figure 4. Percentage of shell shape categories utilized by *Coenobita rugosus* at Cape Panwa, Phuket Island from April 2011 to March 2012.

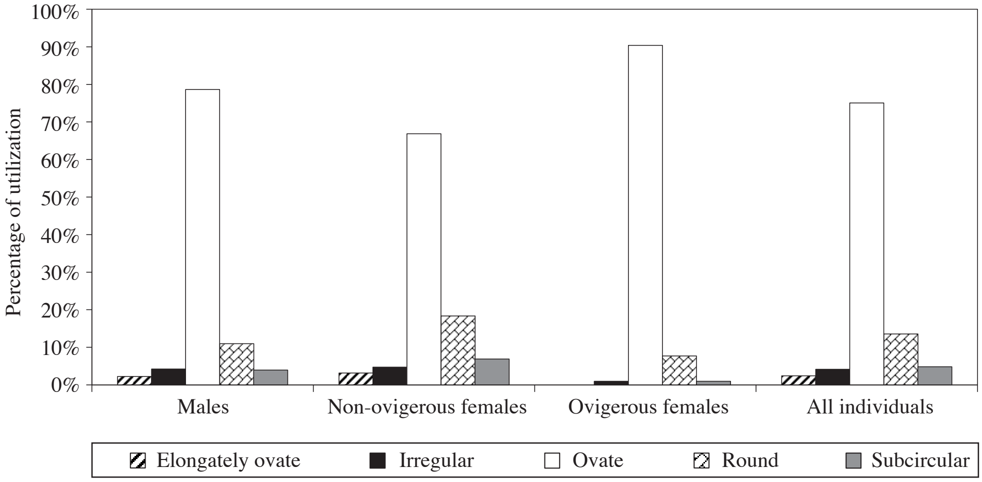



Figure 5. Percentage of aperture shape categories of shells used by *Coenobita rugosus* at Cape Panwa, Phuket Island from April 2011 to March 2012.

## Relationship between Crab and Shell Characteristics

The relationship between crab characters and occupied shells are shown in Table 5. The values of the determination coefficient ($r^2$) from the regression analysis ranged between 0.32 and 0.94. Strong correlations were observed between characters of crabs and internal volume, aperture width and length of utilized shells ($r^2 \geq 0.81$). Shell aperture width was the most correlated with crab characters ($r^2 \geq 0.92$) whereas shell length was least correlated with characters of crabs ($r^2 \leq 0.42$).

Table 5. The relationship between characters of hermit crab *Coenobita rugosus* and the inhabited shells sampled represented by regression equations. $r^2$ = determination coefficient; CSL = cephalothoracic shield length; CSW = cephalothoracic shield width; CW = crab wet weight; MCL = major chela length; MCW = major chela width; SL = shell length; SW = shell width; WW = shell wet weight; SIV = shell internal volume; SAL = shell aperture length; SAW = shell aperture width; $N$ = 1,322.

| Relations | $Y = aX^b$ | $r^2$ |
|---|---|---|
| SL x CSL | $SL = 7.068CSL^{0.596}$ | 0.39 |
| SL x CSW | $SL = 8.944CSW^{0.543}$ | 0.34 |
| SL x CW | $SL = 20.803CW^{0.212}$ | 0.42 |
| SL x MCL | $SL = 6.816MCL^{0.559}$ | 0.36 |
| SL x MCW | $SL = 8.069MCW^{0.493}$ | 0.32 |
| SW x CSL | $SW = 4.497CSL^{0.822}$ | 0.75 |
| SW x CSW | $SW = 5.005CSW^{0.893}$ | 0.78 |
| SW x CW | $SW = 19.939CW^{0.281}$ | 0.75 |
| SW x MCL | $SW = 3.999MCL^{0.806}$ | 0.76 |
| SW x MCW | $SW = 4.683MCW^{0.755}$ | 0.76 |
| WW x CSL | $WW = 0.09CSL^{1.792}$ | 0.59 |
| WW x CSW | $WW = 0.127CSW^{1.872}$ | 0.59 |
| WW x CW | $WW = 2.323CW^{0.625}$ | 0.62 |
| WW x MCL | $WW = 0.077MCL^{1.710}$ | 0.57 |
| WW x MCW | $WW = 0.116MCW^{1.562}$ | 0.54 |
| SIV x CSL | $SIV = 0.01CSL^{2.558}$ | 0.92 |
| SIV x CSW | $SIV = 0.02CSW^{2.581}$ | 0.92 |
| SIV x CW | $SIV = 1.055CW^{0.881}$ | 0.94 |
| SIV x MCL | $SIV = 0.007MCL^{2.491}$ | 0.91 |
| SIV x MCW | $SIV = 0.013MCW^{2.306}$ | 0.89 |
| SAL x CSL | $SAL = 2.188CSL^{0.886}$ | 0.81 |
| SAL x CSW | $SAL = 2.68CSW^{0.897}$ | 0.81 |
| SAL x CW | $SAL = 10.887CW^{0.303}$ | 0.82 |
| SAL x MCL | $SAL = 1.904MCL^{0.875}$ | 0.83 |
| SAL x MCW | $SAL = 2.273MCW^{0.816}$ | 0.82 |
| SAW x CSL | $SAW = 1.063CSL^{1.105}$ | 0.93 |
| SAW x CSW | $SAW = 1.301CSW^{1.165}$ | 0.93 |
| SAW x CW | $SAW = 7.868CW^{0.375}$ | 0.92 |
| SAW x MCL | $SAW = 0.907MCL^{1.084}$ | 0.94 |
| SAW x MCW | $SAW = 1.119MCW^{1.017}$ | 0.94 |

## DISCUSSION

At Cape Panwa, Phuket Island, the shell utilization pattern of *C. rugosus* appears to be similar to those of other congeneric species. The particular shell species occupied varied with the size of the crab. Shell utilization patterns of *C. rugosus* also varied in relation to shell and aperture shape. The body size of *C. rugosus* was most correlated with shell internal volume and aperture size. The plasticity of use of shell resources by *C. rugosus* is inferred by the high species richness of shells used by this population at the study site compared with other land hermit crab species and populations, including the first record of bivalve shell use by a land hermit crab.

*Coenobita rugosus* at the study site was found using the highest number of shell species (63 species) compared with other reported coenobitid species (*C. scaevola* [29 shell species] by VOLKER [1967]; *C. compressus* [28 species] by ABRAMS [1978]; *C. compressus* [11 species] by GUILLEN & OSORNO [1993]; *C. clypeatus* [4 species] by WALKER [1994]; *C. cavipes* [21 species] and *C. rugosus* [20 species] by BARNES [1999]; *C. clypeatus* [14 species] by MORRISON & SPILLER [2006]; *C. scaevola* [10 species] by SALLAM *ET AL.* [2008]; *C. compressus* [41 species] by LAIDRE & VERMEIJ [2012]). The disparity in shell utilization patterns (i.e., shell species used) is probably a function of the different areas of occurrence of the hermit crabs (GARCIA & MANTELATTO, 2000; MANTELATTO & GARCIA, 2000). This is also probably influenced by gastropod life cycles, abiotic environmental factors, and pressure from predation (SALLAM *ET AL.*, 2008). Moreover, the Andaman Coast of Thailand including Cape Panwa, has many species of gastropod molluscs (382 species) (TANTANASIRIWONG, 1978) that probably supplies shell resources for hermit crab fauna living in this area.

The first record of the unusual occupation of a valve of a marine bivalve by a land hermit crab was observed at this study site. The shell of bivalves used as shelter was previously recorded only in marine hermit crabs in the genera *Alainopagurus*, *Bivalvopagurus*, *Patagurus*, *Porcellanopagurus*, *Solitariopagurus* (LEMAITRE, 1993; ANKER & PAULAY, 2013) and *Dardanus venosus* (GARCIA *ET AL.*, 2003). The individual *C. rugosus* inhabiting the bivalve shell in this study was in poor physical condition with a short abdomen compared to other similar-sized crabs (personal observation). This individual may have been a defender (defined by OSORNO *ET AL.* (1998)) whose shell was lost to an attacking crab during a shell exchange. The large opening and small internal space of the bivalve shell of this crab were inappropriate for living because it was unable to withdraw completely into the shell. Most parts of the crab, including chelipeds, ambulatory legs and anterior part of cephalothorax, were beyond the shell opening when the crab was fully retracted and the crab could have been easily be pulled out by predators. The shells of this bivalve, *Chama* sp., were sporadically found during the study period (personal observation) although its abundance was not evaluated.

*Coenobita rugosus* at the study site showed occupation of one species of gastropod shell over others as previously recorded (ABRAMS, 1978; ACHITUV & ZISKIND, 1985; GUILLEN & OSORNO, 1993; WALKER 1994; BARNES, 1999; MORRISON & SPILLER, 2006; SALLAM *ET AL.*, 2008; LAIDRE & VERMEIJ, 2012). The different proportions of shell species occupied by *C. rugosus* may indicate active behavior in shell selection (SALLAM *ET AL.*, 2008), although shell availability will need to be quantified to evaluate this appropriated.

The shell utilization patterns of *C. rugosus* at the study site tended to be different among reproductive stages. This finding is similar to those of a previous study of *C. scaevola* (SALLAM *ET AL.*, 2008). This result may be attributed to the fact that crab individuals of each reproductive stage compete for shells and allot shell resources according to their appropriateness, such as size and reproductive condition (SALLAM *ET AL.*, 2008). Furthermore, the discrepancy in shell use among reproductive stages may result from intraspecific competition, behavior, reproductive strategies and differences in size (IMAZU & ASAKURA, 1994; ASAKURA, 1995; GARCIA & MANTELATTO, 2000).

Differences in shell use among different sized crabs were noted in this population of *C. rugosus*. It is possible that *C. rugosus* at the study site utilize the shells of at least two different gastropod species as they grow. For instance, the most utilized shell species in the genus *Nerita* were inhabited by a wide size range of small to medium crabs (2.5–11.5 mm). However, larger crabs (>11.5 mm) used other larger shell species rather than nerite shells. In another case, *Turbo* shell species were also commonly used by a wide range of crab sizes (3.5–16.0 mm). However, smaller individuals (<3.5 mm) needed to use other smaller-shell species before reaching the size allowing crabs to occupy *Turbo* shells. This inference is similar to the study by MORRISON & SPILLER (2006) who pointed out that *C. clypeatus* probably uses the shells of two or three different gastropod species during their lifetime. Therefore, the conservation of shell diversity is required to preserve hermit crabs because these crabs need different types and sizes of shells to complete their life cycle.

*Coenobita rugosus* occupied certain types of shells and aperture shapes. Most shell shapes used by *C. rugosus* at the study site were low-spired shells frequently occupied by this coenobitid species in other areas as previously recorded by WILLASON & PAGE (1983), BARNES (1999) and SZABO (2012). *Coenobita rugosus* is considered as a burrowing species according to its behavioral ecology, in which selection of low-spired shells probably facilitates burrowing to avoid desiccation during the day (BARNES, 1999). Additionally, shells with ovate, round and semicircular or D-shape apertures were the most occupied aperture shapes by *C. rugosus* at the study area, although availability was not assessed. *Coenobita rugosus* mostly occupied shells with round to circular and D-shape apertures probably because such apertures enable the crabs to avoid desiccation by allowing the crabs to fully seal the aperture with the major chela (BARNES, 1999; SZABO, 2012). Nevertheless, further studies on shell availability are needed to understand shell choice in this hermit crab species.

Although there was no significant discrepancy between utilization of damaged and undamaged shells by *C. rugosus*, most shells occupied by crabs were in worn condition (unpublished data), and probably used previously by other crabs over a period of many years (BALL, 1972; ABRAMS, 1978; BONEKA *ET AL.*, 1995). Moreover, the columella of most shells used was missing (unpublished data) as previously recorded by KINOSITA & OKAJIMA (1968), BALL (1972), LAIDRE (2012) and SZABO (2012). Additionally, unoccupied shells in good condition were scarce at the study site, as also noted earlier (BALL, 1972; MORRISON & SPILLER, 2006; LAIDRE & VERMEIJ, 2012). Therefore, shell supply in this population of *C. rugosus* probably circulates through these old and worn shells that are still suitable, especially for adult crabs, as a result of shell facilitation rather than competition according to ABRAMS (1978). Nevertheless, further investigations of other shell conditions as well as shell exchange of *C. rugosus* in natural habitats are required to test this hypothesis.

The carrying of the lightest shell available, that of *P. canaliculata,* ought to be advantageous for *C. rugosus* because it would save energy, but its thin shell wall may render it more vulnerable to predators such as the rough red-eyed crab, *Eriphia smithii,* that was frequently encountered during the study (BUNDHITWONGRUT *ET AL.*, 2014). Although the most occupied shell species by *C. rugosus* in this study was not the lightest species according to the energy saving hypothesis proposed by OSORNO *ET AL*. (1998), it is possible that crabs may try to search and occupy the lightest shells in each shell exchange. Although the availability of the lightest shells at the study site was not evaluated, it may be a limiting factor. Consequently, it is possible that crabs use the remaining shells, which are subsequently inferior to the lightest ones, with higher SIV/W ratios compared to their previously occupied shells. Further investigation of shell exchanges in natural habitats and shell selection under laboratory conditions would help answer this question.

There is a possibility that ovigerous female *C. rugosus* in the present study show greater shell selectivity. From our investigation, these females used fewer shell species and shell and aperture shapes than other crab groups, although the shell availability at the study site was not evaluated. This result presumably suggests that ovigerous females more specifically selected shells, probably due to their reproductive condition that requires more space inside the occupied shells (i.e., shell internal volume) for fertilized eggs, which are attached to their abdomen. For example, the shell species most occupied by ovigerous females had a higher SIV/W ratio than those mainly used by other crab groups. The lighter shells (higher SIV/W) probably help egg-carrying females save energy for reproductive activity (OSORNO *ET AL*., 1998). Ovigerous female *C. rugosus* in this study used more shell species (22 species) than egg-carrying female *C. scaevola* in the Red Sea (8 species) studied by SALLAM (2012). This is probably associated with shell availability that is different between the areas (GARCIA & MANTELATTO, 2000; MANTELATTO & GARCIA, 2000).

The significant relationships were detected between characters of utilized shells and *C. rugosus* at our study area similar to studies by BONEKA *ET AL*. (1995) and SALLAM *ET AL*. (2008). The results appear to indicate that these shell characteristics are the main determinants of shell "selection" of *C. rugosus* at the study site. Specifically, the strong relationship between shell internal volume and crab characters possibly indicates that internal volume is important in providing ample space for *C. rugosus* to store water inside to maintain body moisture, which is crucial for terrestrial life (WILDE, 1973; GREENAWAY, 2003). In addition, more space in occupied shells may allow crabs to grow rapidly or retain more fertilized eggs during reproduction (OSORNO *ET AL*., 1998). Furthermore, the strong correlations between shell aperture size and crab morphology allow *C. rugosus* to effectively seal the aperture firmly when retreating into the shell, thereby resulting in more protection against predators and from desiccation (BALL, 1972; ABRAMS, 1978; SANVICENTE-ANORVE & HERMOSO-SALAZAR, 2011).

In conclusion, the present study has portrayed the patterns of shell utilization by *C. rugosus* at Cape Panwa, Phuket Island, as well as the relationship between crab and shell characters. The shell utilization patterns of *C. rugosus* at the study site are seemingly similar to those of other coenobitid species. The great shell diversity used by this population suggests more plasticity in the use of shell resources by *C. rugosus* and may indicate the importance of shell diversity in maintaining this population of *C. rugosus* and perhaps other coenobitid crabs.

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