การใช้เปลือกหอยและนิเวศวิทยาประชากรของปูเสฉวนบก *Coenobita rugosus* ที่แหลมพันวา จังหวัดภูเก็ต

นายธนาคม บัณฑิตวงศ์รัตน์

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรดุษฎีบัณฑิต
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SHELL UTILIZATION AND POPULATION ECOLOGY OF LAND
HERMIT CRAB *Coenobita rugosus* AT CAPE PANWA, PHUKET PROVINCE

Mr. Thanakhom Bundhitwongrut

A Dissertation Submitted in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy Program in Biological Sciences
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Thesis Title	SHELL UTILIZATION AND POPULATION ECOLOGY OF LAND HERMIT CRAB *Coenobita rugosus* AT CAPE PANWA, PHUKET PROVINCE
By	Mr. Thanakhom Bundhitwongrut
Field of Study	Biological Sciences
Thesis Advisor	Assistant Professor Art-ong Pradatsundarasar, Ph.D.
Thesis Co-Advisor	Associate Professor Kumthorn Thirakhupt, Ph.D.

Accepted by the Faculty of Science, Chulalongkorn University in Partial Fulfillment of the Requirements for the Doctoral Degree

....Dean of the Faculty of Science
(Professor Supot Hannongbua, Dr.rer.nat.)

THESIS COMMITTEE

....Chairman
(Noppadon Kitana, Ph.D.)
....Thesis Advisor
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....Thesis Co-Advisor
(Associate Professor Kumthorn Thirakhupt, Ph.D.)
....Examiner
(Assistant Professor Duangkhae Sitthicharoenchai, Ph.D.)
....Examiner
(Assistant Professor Tosak Seelanan, Ph.D.)
....Examiner
(Professor Somsak Panha, Ph.D.)
....External Examiner
(Anuwat Nateewathana, Ph.D.)

ธนาคม บัณฑิตวงศ์รัตน์ : การใช้เปลือกหอยและนิเวศวิทยาประชากรของปูเสฉวนบก *Coenobita rugosus* ที่แหลมพันวา จังหวัดภูเก็ต (SHELL UTILIZATION AND POPULATION ECOLOGY OF LAND HERMIT CRAB *Coenobita rugosus* AT CAPE PANWA, PHUKET PROVINCE) อ.ที่ปรึกษาวิทยานิพนธ์หลัก: ผศ. ดร.อาจอง ประทัดสุนทรสาร, อ.ที่ปรึกษาวิทยานิพนธ์ร่วม: รศ. ดร.กำธร ธีรคุปต์, 131 หน้า.

การศึกษาการใช้เปลือกหอยและนิเวศวิทยาประชากรของปูเสฉวนบก *Coenobita rugosus* ที่แหลมพันวา จังหวัดภูเก็ตได้ดำเนินการโดยวิธีการสุ่มตัวอย่างแบบวางแปลงหลายแปลงระหว่างเดือนเมษายน 2554 ถึงเดือนมีนาคม 2555 พบว่าปูเสฉวนบกชนิดนี้ใช้เปลือกหอย 63 ชนิดในสัดส่วนที่แตกต่างกันในแหล่งอาศัยตามธรรมชาติ โดยเป็นเปลือกหอยฝาเดียว 20 วงศ์ 62 ชนิด และเปลือกหอยสองฝา 1 ชนิดซึ่งเป็นรายงานการใช้เปลือกหอยสองฝาเป็นครั้งแรกสำหรับปูเสฉวนบก ความหลากชนิดของเปลือกหอยที่ใช้โดยปูเสฉวนบกชนิดนี้เพิ่มขึ้นตามขนาดของปูที่เพิ่มขึ้นในปูขนาดเล็กจนถึงปูขนาดกลาง แต่ลดลงในปูขนาดใหญ่ เปลือกหอยชนิด *Nerita albicilla* เป็นชนิดที่ปูเสฉวนบกชนิดนี้ใช้มากที่สุด (19.6%) แต่เปลือกหอยชนิดนี้ไม่ใช่เปลือกหอยที่เบาที่สุดในแง่ของอัตราส่วนระหว่างปริมาตรภายในและน้ำหนักซึ่งแตกต่างกับสมมติฐานการประหยัดพลังงาน เปลือกหอยรูปทรงกลมและช่องเปิดเปลือกรูปทรงไข่เป็นรูปทรงเปลือกหอยและช่องเปิดเปลือกที่ปูเสฉวนบกชนิดนี้ใช้มากที่สุด รูปแบบการใช้เปลือกหอยของปูเสฉวนบกชนิดนี้แตกต่างกันในปูขนาดต่างๆ และระหว่างปูเพศผู้ เพศเมียที่ไม่มีไข่ และเพศเมียที่มีไข่ นอกจากนี้ยังพบสหสัมพันธ์ในระดับสูงระหว่างปริมาตรภายในและขนาดของช่องเปิดเปลือกหอยที่ใช้โดยปูเสฉวนบกชนิดนี้กับลักษณะทางสัณฐานต่างๆ ของปูซึ่งแสดงให้เห็นว่าปริมาตรภายในและขนาดของช่องเปิดเปลือกหอยเป็นตัวกำหนดหลักสำหรับการใช้เปลือกหอยของปูเสฉวนบกชนิดนี้ ผลการทดลองการเลือกใช้เปลือกหอยโดยปูเสฉวนบกชนิดนี้ในห้องปฏิบัติการพบว่าทั้งปูเพศผู้และเมียเลือกใช้เปลือกหอยชนิด *Thais hippocastanum* มากกว่าชนิดอื่นอย่างชัดเจน (84% โดยปูเพศผู้และ 92% โดยปูเพศเมีย) ทั้งปูเพศผู้และเมียแสดงอัตราการไม่เลือกเปลือกหอยที่เคยใช้ก่อนหน้านี้ (*N. albicilla*) อย่างสมบูรณ์ (100%) เปลือกหอยที่ถูกเลือกใช้มีปริมาตรภายในและอัตราส่วนระหว่างปริมาตรภายในและน้ำหนักมากกว่าเปลือกหอยที่เคยใช้ก่อนหน้านี้อย่างมีนัยสำคัญทางสถิติ ($p < 0.001$) แต่เปลือกหอยที่ถูกเลือกใช้มีน้ำหนักมากกว่าเปลือกหอยที่เคยใช้ก่อนหน้านี้อย่างมีนัยสำคัญทางสถิติ ($p < 0.001$) ซึ่งอาจแสดงให้เห็นว่าปูเสฉวนบกชนิดนี้ในแหล่งอาศัยตามธรรมชาติอาจพยายามหาและใช้เปลือกหอยที่เบากว่าในการเปลี่ยนเปลือกหอยแต่ละครั้งเพื่อความเหมาะสมสำหรับการดำรงชีวิตของปู

ผลการศึกษาในแง่ของนิเวศวิทยาประชากรของปูเสฉวนบกชนิดนี้พบว่าการกระจายความถี่ของขนาดปูในประชากรในรอบปีของทั้งปูเพศผู้ เพศเมียที่ไม่มีไข่ และเพศเมียที่มีไข่มีแนวโน้มการกระจายของข้อมูลแบบฐานนิยมเดี่ยว ก้ามใหญ่ข้างซ้ายของปูเสฉวนบกชนิดนี้ (มีขนาดใหญ่กว่าในปูเพศผู้ตัวเต็มวัย) ถูกพบว่าเป็นลักษณะทางสัณฐานเชิงปริมาณที่ใช้ในการแยกเพศได้เป็นครั้งแรกสำหรับปูเสฉวนบก ความหนาแน่นเฉลี่ยของปูเสฉวนบกชนิดนี้ในช่วงที่ทำการศึกษามีค่าเท่ากับ 6.98 ± 0.36 ตัว/ตรม. รูปแบบการกระจายตัวในประชากรของปูเพศผู้และเพศเมียที่ไม่มีไข่ของปูเสฉวนบกชนิดนี้เป็นแบบรวมกลุ่ม ส่วนของปูเพศเมียที่มีไข่เป็นแบบสม่ำเสมอเป็นส่วนใหญ่ตลอดช่วงเวลาที่ทำการศึกษา อัตราส่วนเพศทั้งปีเป็นแบบมีเพศผู้มากกว่า (1:0.86 เพศผู้:เพศเมีย) อย่างไรก็ตามอัตราส่วนเพศในแต่ละเดือนและระหว่างปูขนาดต่างๆ มีค่าใกล้เคียงกับแบบมีเพศผู้เท่ากับเพศเมีย พบว่าอาหารของปูเสฉวนบกชนิดนี้ส่วนมากเป็นส่วนของใบและดอกไม้ที่เน่าเปื่อยของพืช 16 ชนิด และยังพบว่าปูชนิดนี้กินซากสัตว์ 3 ชนิด ในจำนวนนี้พบว่าเป็นการกินปูเสฉวนบกชนิดเดียวกันเองหนึ่งครั้ง การสืบพันธุ์ของปูเสฉวนบกชนิดนี้พบว่ามีการสืบพันธุ์ตลอดปี โดยพบว่ามีสัดส่วนของจำนวนปูเพศเมียที่มีไข่ต่อปูเพศเมียทั้งหมดสูงสุดในเดือนเมษายนและกันยายน 2554 (31.2% และ 31.6% ตามลำดับ)

ดังนั้น ข้อมูลจากการศึกษาครั้งนี้สามารถใช้เป็นองค์ความรู้เชิงเปรียบเทียบในเรื่องการใช้เปลือกหอยและนิเวศวิทยาประชากรของปูเสฉวนบกชนิด *Coenobita rugosus* กับปูเสฉวนบกชนิดอื่นๆ และยังสามารถใช้เป็นองค์ความรู้พื้นฐานสำหรับการอนุรักษ์สัตว์กลุ่มนี้ด้วย

สาขาวิชา วิทยาศาสตร์ชีวภาพ ลายมือชื่อนิสิต ____________________

ปีการศึกษา 2557 ลายมือชื่อ อ.ที่ปรึกษาหลัก ____________________

ลายมือชื่อ อ.ที่ปรึกษาร่วม ____________________

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THANAKHOM BUNDHITWONGRUT: SHELL UTILIZATION AND POPULATION ECOLOGY OF LAND HERMIT CRAB *Coenobita rugosus* AT CAPE PANWA, PHUKET PROVINCE. ADVISOR: ASST. PROF. ART-ONG PRADATSUNDARASAR, Ph.D., CO-ADVISOR: ASSOC. PROF. KUMTHORN THIRAKHUPT, Ph.D., 131 pp.

The study on shell utilization and population ecology of the land hermit crab *Coenobita rugosus* at Cape Panwa, Phuket Province, Andaman Coast of Thailand were investigated by multiple quadrat sampling from April 2011 to March 2012. In natural habitat, *C. rugosus* was found using 63 molluscan shell species in different percentages. Among these, 62 gastropod shell species from 20 families were used by *C. rugosus*. Interestingly, the first record of the bivalve shell use by land hermit crab was noted and discussed. The diversity of shells used increased with increases in body size from small to medium sized crabs, but decreased in larger crabs. The most commonly occupied shell species by *C. rugosus* was *Nerita albicilla* (19.6 %). However, *N. albicilla* used by *C. rugosus* was not the lightest shell species in relation to the ratio between internal volume and weight, which is in contrast to the energy saving hypothesis. Globose shell and ovate aperture shape were the most occupied shell and aperture shapes, respectively. The shell utilization patterns of *C. rugosus* at the study site were different between sexes and 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*. As for shell preference experiment in laboratory, both sexes of *C. rugosus* obviously preferred shells of *Thais hippocastanum* (84% of males and 92% of females). Both males and females of *C. rugosus* showed 100% of dissatisfaction rate with previously occupied shells of *N. albicilla*. The preferred shells had significantly larger internal volume and higher ratio between internal volume and weight than the original shells ($p < 0.001$), but the weight of preferred shells was significantly higher than that of original shells ($p < 0.001$). This may suggest that crabs in natural habitat probably try to search and occupy the lighter shells in each shell exchange for their appropriate adequacy.

Regarding to population ecology of *C. rugosus*, tendency of unimodality of annual size frequency distributions was 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/m^2. 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).

Therefore, the information from this study provides comparative knowledge on shell use and population ecology of *C. rugosus* and other coenobitid crabs and can be used as fundamental knowledge for the conservation of these animals.

Field of Study: Biological Sciences
Academic Year: 2014

Student's Signature ____________________
Advisor's Signature ____________________
Co-Advisor's Signature ____________________

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
C1–5	Coxae of pereopods 1–5 of the land hermit crab
CSL	Cephalothoracic shield length
CSW	Cephalothoracic shield width
CW	Crab weight
FG	Freshwater gastropod
GC	Green’s coefficient
MB	Marine bivalve
MCL	Major chela length
MCW	Major chela width
MG	Marine gastropod
M:F	Male:Female
PMBC	Phuket Marine Biological Center
r	Correlation coefficient
r^2	Determination coefficient
TG	Terrestrial gastropod
SAL	Shell aperture length
SAW	Shell aperture width
SIV	Shell internal volume
SIV/W	The ratio between shell internal volume and weight
SL	Shell length
SW	Shell width
WW	Shell weight
χ^2	Chi-square

CHAPTER 1

INTRODUCTION

Land or terrestrial hermit crabs play an important role as scavengers in coastal ecosystem, accelerating the rate of recycling of nutrients and energy in food chain (Laidre 2013). 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). Furthermore, land hermit crabs represent an important component in insular and coastal habitats (Morrison & Spiller 2006).

In Thailand, several impacts from human activities, especially habitat destruction and pollution, have caused the considerable decline of the number of land hermit crabs. In addition, land hermit crabs are caught to sell as pet animals, leading directly to the decrease of their number in natural habitats. As a result of the low price of land hermit crabs, the dealers harvest them in a large number. In addition, the excessive shell exploitation by humans for souvenirs and decorations has apparently caused numerous individuals of land hermit crabs to inhabit garbage, such as open food cans, broken glass, and other vacant artificial materials (Bundhitwongrut 2001).

Therefore, this research focused mainly on the pattern of shell utilization by the population of land hermit crab *C. rugosus* at Cape Panwa, Phuket Province, Thailand in order to obtain better understanding of the most valuable shell resource occupied by hermit crabs. In addition, the investigation on population ecology in several aspects of this land hermit crab species was also carried out at the study site during the study of shell use of the crabs. The results from this research will be fundamental information for the sustainable conservation of these animals in the future.

Objectives

1. To study the pattern of shell utilization of land hermit crab *C. rugosus* in natural habitats at Cape Panwa, Phuket Province, and in the laboratory condition
2. To determine the correlations between important characteristics of the shells used by *C. rugosus* and morphological characters of the crabs
3. To study the population ecology of *C. rugosus* during the study of shell use of the crabs, including population structure, density, dispersion, sex ratio, diet, and reproduction

CHAPTER 2

LITERATURE REVIEW

2.1 General information on hermit crabs

Hermit crabs are decapod crustaceans inhabiting discarded gastropod shells. Some hermit crabs live in tusk shells, tubes of marine worms, corals, sponges or a piece of bamboos (Brusca & Brusca 2003; McLaughlin *et al.* 2007). Shells are used as mobile homes and to protect their soft twisted abdomen (Hazlett 1981). These crabs grow and increase their size by molting (Greenaway 2003). At each molting, they seemingly change into larger shells to accommodate their larger size (Burggren & McMahon 1988; Fox 2010).

There are two groups of hermit crabs, distinguished by their habitats. The first group is composed of land hermit crabs and coconut crab, living in supralittoral zone and sometimes as far away as in beach forests, while the second group is marine hermit crabs found in several aquatic habitats in both marine and brackish environments from the river mouths, mangroves, coastal areas to subtidal zones. However, life cycles of both groups, especially planktonic larval stages, require submerging in sea water. Fertilized females of land hermit crabs, therefore, need to return to the shore to release their eggs into seawater (Pitagsalee 1980; Bundhitwongrut 2001; Greenaway 2003).

2.2 Systematic background

The classification of hermit crabs is shown below (De Grave *et al.* 2009; McLaughlin *et al.* 2010).

Phylum Arthropoda

 Subphylum Crustacea

  Class Malacostraca Latreille, 1806

   Subclass Eumalacostraca Grobben, 1892

    Superorder Eucarida Calman, 1904

     Order Decapoda Latreille, 1802

      Suborder Pleocyemata Burkenroad, 1963

       Infraorder Anomura MacLeay, 1838

        Superfamily Paguroidea Latreille, 1802

         Family Coenobitidae Dana, 1851

         Family Diogenidae Ortmann, 1892

         Family Paguridae Latreille, 1802

         Family Parapaguridae Smith, 1882

         Family Pylochelidae Bate, 1888

         Family Pylojacquesidae McLaughlin and Lemaitre, 2001

There are 1,106 valid species from six families of hermit crabs worldwide (McLaughlin *et al.* 2010). Only the members of family Coenobitidae inhabit terrestrial area. Other five families live in various habitats in marine and brackish environments (McLaughlin *et al.* 2007). The diagnostic characters used to distinguish land and marine hermit crabs are antennules. Land hermit crabs possess antennules with tip of flagella terminating bluntly and somewhat stick-like, whereas marine hermit crabs have antennules with tip of flagella terminating in tapered filament and not stick-like (McLaughlin 2003).

Family Coenobitidae contains two genera, *Birgus* Leach, 1816 and *Coenobita* Latreille, 1829. *Birgus* is a monotypic genus, containing only a single species, *Birgus latro* Linnaeus, 1767, namely the coconut or robber crab. The adults of coconut crabs live without using empty shells (Burggren & McMahon 1988). Sixteen species of land hermit crabs belong to the genus *Coenobita*, occurring throughout the world (Martin & Davis 2001; De Grave *et al.* 2009; McLaughlin *et al.* 2010). These crabs primarily distribute in tropical region and also in subtropical area (Greenaway 2003).

In Thailand, 57 species of both land and marine hermit crabs have been reported. However, only three land hermit crab species, *C. brevimanus* Dana, *C. rugosus* H. Milne Edwards and *C. violascens* Heller, have been recorded from both coasts of the Gulf of Thailand and Andaman Sea (Pitagsalee 1980; Bundhitwongrut 2001; McLaughlin 2002).

2.3 General biology of land hermit crabs

In some tropical islands, land 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). Land hermit crabs mainly inhabit supralittoral zones on sandy shore, beach forest and mangrove (Barnes 1997b). Some species live inland far away from seashores (e.g. *C. clypeatus*, *C. brevimanus* and *C. compressus*) (Wilde 1973; Burggren & McMahon 1988). These crabs are primarily nocturnal and they aggregate and seek shelters under debris or vegetation or burrow in shallow sand as refuges to avoid desiccation due to heat during the daytime and other environmental stresses (Page & Willason 1982). Nevertheless, they may show diurnal activity in high humidity or raining day (Greenaway 2003).

Land hermit crabs are generally scavengers or detritus feeders. The crabs forage mainly at night starting at crepuscular time (Burggren & McMahon 1988). Their foods are composed of decaying plant materials, mangrove propagules, fallen fruits and seeds, strand line detritus, faeces of animals and humans, and animal carcasses (Barnes 1997a; Greenaway 2003). Because of foraging mainly on decomposing vegetation and carrion, land hermit crabs play a critical role in the coastal ecosystem as scavengers helping in effectively recycling energy and nutrients in the ecosystem (Laidre 2013). Some people call them beach cleaners. As for foraging behavior, coenobitid crabs do not select food randomly. Land hermit crabs prefer foods by odours that have not experienced recently during previous 6–9 h rather than foods recently consumed. Broader diets due to short-term avoidance of food odours probably facilitate growth of hermit crabs and limit exposure to toxins (Thacker 1996, 1998).

The reproductive seasons of land hermit crabs are different among species and localities. Some species living far from the coastline migrate to the area near the shore where the reproduction occurs. This migration lasts several weeks. More than thousands of crabs move together in long distances of the same route every year. Copulation of hermit crabs occurs during this migration (Nakasone 2001; Nieves-Rivera & Williams 2003). During the copulation, both crabs extend cephalothorax from shells and turn the ventral sides together. Then, male crab transfers spermatophore to female. After copulation, the female releases the eggs to fertilize with sperm from male. The female, then, gathers eggs to attach to the left pleopods. This group of fertilized eggs is protected inside the occupied shell of female from predators and desiccation (Greenaway 2003). The number of eggs depends on the size of the female. Normally, a female crab lays approximately 1,000–50,000 eggs per clutch (Wilde 1973).

Although land hermit crabs live in terrestrial environments, the larvae of these crabs still depend on planktonic development in marine surroundings to complete their life cycle (Burggren & McMahon 1988). Fertilized eggs are released into sea about 30 days after laying by ovigerous or egg-carrying females at the strand lines. The eggs immediately hatch as planktonic larvae after being released into sea water (Wilde 1973).

The development of larvae of land hermit crabs begins with hatching larvae called zoea emerging from eggs. Due to marine planktonic life style, some zoea might disperse to other areas by tide and oceanic current, but some still live in the same area. This larva has the number of different stages depending on species, generally five stages with developing time around 3–7 weeks (Greenaway 2003; Wang *et al.* 2007). The zoeal larvae later develop to postlarvae, specifically named glaucothoe larvae or megalopae. This larval stage is initially similar to adult, living by swimming as well as crawling on substratum in the sea to seek empty gastropod shell to occupy. The time of development of glaucothoe larva is approximately one month (Brodie & Harvey 2001). The postlarval stage, which migrates to live on land, then metamorphoses to juvenile (Brodie 2002). After several moltings, juvenile becomes adult at about two years old that is mature and able to reproduce (Burggren & McMahon 1988; Greenaway 2003). As for longevity, one record of the land hermit crab *C. clypeatus,* which was maintained in captivity, lived for 11 years (Chace 1972).

The unique shell-carrying habit of land hermit crabs provides many types of benefits, including protection against predators and from water loss. The crabs fill and store water into their shells as a portable water source to maintain body moisture. This allows them to be able to forage farther inland (Wilde 1973; Greenaway 2003). Thus, gastropod shells obviously play important roles in all respects of life cycles of land hermit crabs. Generally, empty gastropod shells are limited resources for land hermit crabs (Willason & Page 1983). Therefore, population size and structure may be affected by the availability of suitable gastropod shells (Sallam *et al.* 2008).

Shell access sometimes is simply by encountering vacant gastropod shells although this case is somewhat rare. Nevertheless, the pattern of shell exchange frequently occurs in the situation of shell fighting (Osorno *et al.* 1998). Other individuals of land hermit crabs could also locate the empty shell of the dead conspecific for exchange by attraction of its odour (Small & Thacker 1994). Several shell characteristics have been reported to be correlated with crab morphological characters, including shell length, shell weight, aperture shape, shell shape, internal volume, shell condition and others (Hazlett 1981). Furthermore, shell resources for land hermit crabs in different areas have effects on population characteristics such as abundance, maximum size and reproduction (Sallam *et al.* 2008).

2.4 The land hermit crab, *Coenobita rugosus* H. Milne Edwards, 1837

2.4.1 Distribution

Coenobita rugosus H. Milne Edwards, 1837 is one of 16 validly described species of land hermit crabs in family Coenobitidae (Figure 2.1). *Coenobita rugosus* is widely distributed in the Indo-Pacific region, including East Africa, Madagascar, Seychelles, Red Sea, India, Andaman Sea, Gulf of Thailand, Indonesia, Vietnam, Taiwan, Japan, Tuamotu Archipelago and French Polynesia (Nakasone 1988; McLaughlin *et al.* 2007; Reshmi & Bijukumar 2010). In Thailand, *C. rugosus* has been recorded from coasts in Chon Buri, Chanthaburi and Trat Provinces in the Gulf of Thailand, and Phangnga, Phuket, Krabi, Trang and Satun Provinces on Andaman coasts of Thailand (Pitagsalee 1980; Bundhitwongrut 2001; McLaughlin 2002).

Coenobita rugosus was considered as a somewhat widely to widely distributed hermit crab species found in both coasts of Thailand (Bundhitwongrut 2001).

Figure 2.1 Land hermit crab *Coenobita rugosus* (Anomura, Coenobitidae) (photo by Thanakhom Bundhitwongrut).

Figure 2.2 Major or left cheliped of *Coenobita rugosus* showing stridulatory mechanism composed of series of oblique laminar tubercles on the upper outer surface of the palm (photo by Thanakhom Bundhitwongrut).

2.4.2 Morphological characteristics

The body of *C. rugosus* is divided into three main parts: head or cephalon, thorax, and abodomen or pleon. The head and thorax fuse together to form cephalothorax, which is covered by calcified trapezoid shield called carapace. *Coenobita rugosus* has two pairs of antennae. The first pair of antennae or antennules is located between eyes. The antennules of *C. rugosus* have tip of flagella terminating bluntly and somewhat stick-like (McLaughlin 2003). The second pair of antennae or antennas is positioned on lateral sides of eyes. The antennal acicle is fused to the second peduncular segment (McLaughlin *et al.* 2007). *Coenobita rugosus* has five pairs of pereopods extending from the thorax. The first pereopods develop into chelipeds. The inner surfaces of upper margins of both chelipeds are covered with dense tuff of stiff setae (McLaughlin 2002). Stridulatory mechanism composed of series of oblique laminar tubercles is on the upper outer surface of the palm of the left chela (Nakasone 1988; McLaughlin *et al.* 2007) (Figure 2.2). This character is the obvious diagnosis for separating both adult and juvenile *C. rugosus* from the other two sympatric coenobitid species, *C. brevimanus* and *C. violascens* in Thailand (Bundhitwongrut 2001). The second and third pereopods are modified into walking legs. The fourth and fifth pereopods are characterized by small subchelate. The abdomen of *C. rugosus* is asymmetrical, soft and twisted. The color pattern of *C. rugosus* is variable, ranging from white, cream, red, purplish, bluish-gray to dark blue, gray to dark gray, or mixture of these colors (Bundhitwongrut 2001; McLaughlin *et al.* 2007).

2.4.3 Sexual dimorphism

Sexes of *C. rugosus* are separated by gonopore position (Figure 2.3). Male gonopores and sexual tubes are situated at the bases or coxae of the fifth pereopods and males have short left pleopods or have none. In contrast, female gonopores are located at the base of the third pereopods and females have long left pleopods for attachment of fertilized eggs (Pitagsalee 1980; Bundhitwongrut 2001).

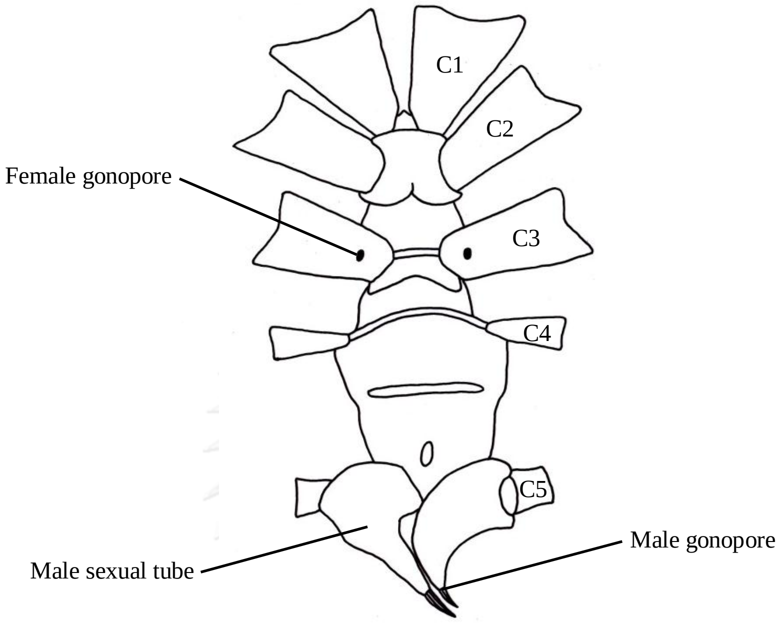


Figure 2.3 Ventral side of cephalothorax of *Coenobita rugosus* showing gonopores, sexual tubes, thoracic sternites and coxae of pereopods. Abbreviation: C1–5 = coxae of pereopods 1–5 (drawing by Thanakhom Bundhitwongrut).

2.4.4 Habitat

Coenobita rugosus is usually found living in supralittoral zones of sandy beaches and beach forests (Boneka *et al.* 1995; Barnes 2002; McLaughlin *et al.* 2007). *Coenobita rugosus* also dwells in fringe mangrove habitat (Barnes 1999, 2001a). In Thailand, *C. rugosus* is found living mainly in sandy beaches in supralittoral areas

(84.6%) and also in beach forests (15.4%) (Bundhitwongrut 2001). *Coenobita rugosus* is found near the shore and inland from the beach, but never more than about 100 m from high tide (Page & Willason 1982; Burggren & McMahon 1988).

Individuals of *C. rugosus* normally hide and aggregate under dry fallen leaves or among vegetation in its habitat during the day time (Bundhitwongrut 2001; McLaughlin *et al.* 2007). Most *C. rugosus* are frequently found aggregated around the base of plants, *Scaevola* and *Messerschmidia* at Enewetak Atoll, Marshall Islands (Page & Willason 1982). *Coenobita rugosus* can bury in sand up to 20 cm to avoid heat from sunlight during the diurnal period (Greenaway 2003). *Coenobita rugosus* is largely disappeared in the area with no vegetation in supralittoral areas, and the existence and abundance of this species, therefore, could be utilized as reliable indicator of the quality of supralittoral zones of the beaches (Brook *et al.* 2009).

2.4.5 Natural History

Coenobita rugosus is a medium sized land hermit crab species. The largest cephalothoracic shield length (CSL) size recorded in Taiwan was 15.9 mm (McLaughlin *et al.* 2007). The maximum size of carapace length was 8–9 mm at Enewetak Atoll, Marshall Islands (Page & Willason 1982). Size ranges of *C. rugosus* from both coasts of Thailand, based on CSL, were 3.8–16.3 mm for all individuals, 4.6–16.3 mm for males, 3.8–15.2 mm for non-ovigerous females, and 9.0 mm CSL for ovigerous female, sampled between June 1999 and January 2002 (Bundhitwongrut 2001).

Different distributions and activities among groups of *C. rugosus* have been reported. At Enewetak Atoll, Marshall Islands, individuals of *C. rugosus* found in the interior part were larger than those found in the beach and nearshore habitats. Individuals on the beach at night were generally ovigerous females that had recently released their eggs or had eggs ready for hatching on their pleopods (Page & Willason 1982). At Quirimba Island, Mozambique, crabs in the largest size class (18 g) of *C. rugosus* were found only in the open sand scrub beach, not in mangrove habitat (Barnes 1999). Nevertheless, smaller *C. rugosus* in mangrove vertically climbed on trees up to 1.5 m above high tide (Barnes 1997b). In Thailand, *C. rugosus* has been reported as the most common species among three land hermit crab species found in this area. However, *C. rugosus* was proposed its status as an uncommon species of hermit crabs based on the criteria of relative abundance and occurrence (Bundhitwongrut 2001).

A variety of decomposing organic materials has been recorded as diets of *C. rugosus*. At Quirimba Island, Mozambique, *C. rugosus* in the open sand scrub beach was observed eating mainly on rotting terrestrial vegetation only at night, whereas *C. rugosus* in the fringe mangrove habitat consumed the same food item as well as human faeces during both diurnal and nocturnal periods. Cannibalism was also recorded for *C. rugosus* at night in the open sand scrub habitat (Barnes 1997a). On Aldabra Atoll in Indian Ocean, organic materials and decaying algae on strand line, fresh tortoise faeces and dead tortoises were consumed by *C. rugosus* (Grubb 1971; Alexander 1979). At Enewetak Atoll, Marshall Islands in Pacific Ocean, *C. rugosus* consumed fruits of *Scaevola* and *Morinda*, coconut meat and husks, the insides of a fallen coconut tree, washed up algae *Laurencia* and *Halimida*, a dead subtidal brachyuran crab and a dead coconut crab. Nevertheless, *C. rugosus* was observed to not forage on living parts of plants (Page & Willason 1983).

Regarding to reproduction, the breeding season of *C. rugosus* in Okinawa, Japan was in late May to November. The size of ovigerous females from this population ranged 3.93–12.58 mm CSL. Some females at this location may lay eggs during the second year of their life. The smallest male in Okinawa reached sexual maturity and had spermatophores at 4.24 mm CSL. The mean length and width ± SD of non-eyed eggs of *C. rugosus* were 0.658 ± 0.045 and 0.616 ± 0.041 mm, respectively, while the mean length and width ± SD of eyed eggs were 0.736 ± 0.040 and 0.641 ± 0.040 mm, respectively (Nakasone 2001). The larvae of *C. rugosus* hatched in seawater as zoeae and spend 20–31 days to pass through five zoeal stages before metamorphosing to megalopae or glaucothoe. The sizes of zoeae ranged 2.6–5.5 mm in total length, whereas the total length of megalopae was 3.74 mm (Shokita & Yamashiro 1986).

Interactions and relationship between *C. rugosus* and other animals have been recorded from several areas. Along the south coast of Aldabra Atoll, *C. rugosus* and Aldabra tortoises inhabited the same shelters under *Guettarda* and other bushes. Under each bush, 200 or more individuals of *C. rugosus* could be found (Grubb 1971). In New Guinea, the springtail *Coenaletes vangoethemi* (Order Collembola) was found in the shells of *C. rugosus* as a free-living and obligate symbiont (Williams & McDermott 2004). In addition, three mite species (Order Acari) were found as ectoparasites on the branchial area of *C. rugosus*. The crabs are their definitive hosts. *Ereynetes (Anereynetes) papuanus* was found associated with *C. rugosus* in Papua

New Guinea. *Askinasia aethiopicus* and *Hoogstraalacarus tiwensis* were found with *C. rugosus* in Kenya (McDermott *et al.* 2010). Regarding to predator, small *C. rugosus* was heavily preyed by a shore-dwelling grapsid crab, *Geograpsus crinipes*, and a ghost crab, *Ocypode cordimana*, on Aldabra Atoll (Alexander 1979).

2.4.6 Shell utilization

Investigations on shells used by *C. rugosus* have been studied in Eastern Africa (Barnes 1999, 2001b, 2002), Enewetak Atoll, Marshall Islands (Willason & Page 1983), Fiji (Szabo 2012), Okinawa, Japan (Nakasone 2001) and Indonesia (Boneka *et al.* 1995). However, in Thailand, only the preliminary list of occupied shells was recorded (Bundhitwongrut 2001). In addition, shell-searching behavior of *C. rugosus* was investigated and comprehensively described by Kinosita and Okajima (1968).

At Quirimba Island, Mozambique, *C. rugosus* was found occupying 20 shell species in different proportion. The shells of *Turbo coronatus* were used as the most occupied shell species (43%) and were used by every size class of *C. rugosus*. Larger *C. rugosus* occupied shells of *Volema paradisica* and *Fasciola trapezium* (Barnes 1999).

In southwestern Madagascar, *C. rugosus* was found occasionally using fossil shells of the short-spired, shore-dwelling marine snails, *Nassarius, Nerita* and *Turbo,* as a substitute (Barnes 2001b). At this site, *C. rugosus* lived under bushes as refuge in the sand scrub habitat in supralittoral zone, and mostly used short- to mid-spired shells (Barnes 2002).

At Enewetak Atoll, Marshall Islands, *C. rugosus* more frequently utilized shorter shells (e.g. *Nerita*). Ovigerous females occupied 22 shell species in different percentage. Both the percentage of ovigerous females and fecundity of *C. rugosus* were not influenced by the shell species occupied. Empty shells were generally rare. In shell preference in the laboratory, the rounded *Nerita*-type shells were preferred by *C. rugosus* over the elongated *Rhinoclavis sinensis* (Willason & Page 1983).

In Fiji, *C. rugosus* mainly occupied strong, low-spired and round-apertured shells in family Neritidae, Turbinidae and Muricidae and rejected shell in family Strombidae. Shells used by crabs were characterized by some diagnosis caused by damage and/or crab modification, including eroded or damage on columella, lightened shell wall, aperture modification, and drag mark (Szabo 2012).

At Okinawa, Japan, female *C. rugosus* was found using shells of marine snail *Lunella granulata*, which was recorded from observations on reproductive behavior at the site for releasing eggs and larvae on the Hyakuna coast (Nakasone 2001).

On Bunaken Island, Sulawesi, Indonesia, *C. rugosus* used 19 genera of gastropod shells. The most occupied shells of *C. rugosus* were in the genus *Nassarius* (44.1%), followed by *Cerithium* (10.6%). Adult *C. rugosus* entirely inhabited *Turbo* shells, whereas juvenile utilized *Melanella* and *Nassarius* shells. Medium sized crabs were found in *Morula*, *Drupella*, *Liotina*, *Nerita* and *Cerithium* shells. Shells of *Cypraea*, *Conus*, *Phytia* and *Trochus* were not used by *C. rugosus*. The carapace width of *C. rugosus* was highly correlated with the width of shell aperture. Crab weight was also correlated with shell weight (Boneka *et al.* 1995).

In Thailand, Bundhitwongrut (2001) preliminary reported that 17 molluscan shell species were used by *C. rugosus* from both the Gulf of Thailand and Andaman coasts of Thailand. *Coenobita rugosus* utilized 14 species of marine gastropod shells (*Hemifusus ternatanus*, *Lunella cinirea*, *Monodonta* sp., *Murex trapa*, *Nassarius* sp., *Natica vitellus*, *Nerita* sp., *Polinices tumidus*, *Pugilina cochlidium*, *Rhinoclavis vertagus*, *Thais hippocastanum*, *Thais tuberosa*, *Turbo bruneus* and *Turbo petholatus*). Three shell species of land snails (*Amphidromus schomburgki*, *Cyclophorus volvulus* and *Cyclophorus* sp.) were occupied by *C. rugosus* from this location.

2.5 Previous researches on hermit crabs in Thailand

Previous studies on hermit crabs in Thailand have concerned mainly the identification and inventory of species (Table 2.1). Pitagsalee (1980) reported 28 species and one subspecies on both coasts of the country. Rahayu and Komai (2000) reported 17 species of shallow-water hermit crabs from Phuket Island. Bundhitwongrut (2001) found 35 species and one subspecies from Gulf of Thailand and Andaman Sea with details on the relative abundance, habitats and status. McLaughlin (2002) reviewed the systematic of hermit crabs in the same area with particular emphasis on the Andaman Sea, and reported 55 species, including three new species.

Table 2.1 The number of species of hermit crabs reported in previous studies in Thailand.

Study area	Number of species (subspecies)		Studied by
	Land hermit crabs	**Marine hermit crabs**	
Gulf of Thailand & Andaman Sea	2	26 (1)	Pitagsalee (1980)
Phuket, Andaman Sea	-	17	Rahayu and Komai (2000)
Gulf of Thailand & Andaman Sea	3	32 (1)	Bundhitwongrut (2001)
Gulf of Thailand & Andaman Sea	3	52	McLaughlin (2002)

2.6 Previous researches and information on shell utilization by land hermit crabs

Shells are very important resources for land hermit crab life. The unique shell carrying habit of coenobitid crabs provides benefits in many aspects, including protection against predators and from desiccation (Burggren & McMahon 1988; Greenaway 2003). The space inside the occupied shells is available for storing water to maintain crab body moisture, allowing them to forage further inland (Wilde 1973). Several characteristics of occupied shells have been reported to be correlated with hermit crab morphological characters (e.g. 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). In addition, inhabited shells possibly affect growth, reproduction, and risk of predation (Blackstone 1985; Mantelatto *et al.* 2002; Osorno *et al.* 2005; Sallam *et al.* 2008; Sallam 2012). Furthermore, shell resources for hermit crabs in different areas influence particular characteristics of their populations, such as abundance, size and reproduction (Fotheringham 1976; Sallam *et al.* 2008). In addition, the difference of shell utilization pattern is able to exist as a function of different areas of occurrence of the hermit crabs (Garcia & Mantelatto 2000; Mantelatto & Garcia 2000).

Coenobitid crabs retreating into a well proportional sized shells form a pseudo-operculum, which is composed of the palm of the major or left cheliped and the dactyl of the third left pereopod, completely blocking at aperture plain (Abrams 1978). Crabs withdrawing into these shells and blocking the aperture with the cheliped are hard to be extracted from the occupied shells by predators (Ball 1972). *C. clypeatus* living in suitably sized shells in good condition has better opportunity to invade further inland for more resources (i.e. freshwater, food and shade), while crab in ill-sized shells are confined near the coast and depended on sea water (Wilde 1973).

Land hermit crabs usually inhabit worn and old shells, which have been used previously by other crabs for a long time (Abrams 1978; Boneka *et al.* 1995). Utilized shells of land hermit crabs are characterized by some diagnosis caused by damage and/or crab modification, including eroded or missing columella, lightened shell wall, aperture modification, and drag mark. The columella of occupied shells of *Coenobita* is possibly abraded by the repeated movement of crabs in and out the shells, resulting in partially removed or eroded to missing columella in extreme case. Abrasive and/or chemical effect from crabs inclines to thin the whole shell as lightened shell wall in most cases. The enlargement of shell aperture modified by crabs is also noted for shells inhabited by coenobitid crabs. The drag mark on external surface of terrestrial hermit crab shells is a polished nacreous area, existed due to crab movement against the substrate (Ball 1972; Abrams 1978; Walker 1994; Szabo 2012).

The old and worn shells with modification by crabs, which were reutilized by several successive individuals, usually occupied by land hermit crabs are nominated as remodeled shells by Laidre (2012b). The experiments on used shells of *C. compressus* were carried out to compare the characters between remodeled shells (or hermit-derived shells; shells previously occupied by hermit crabs) and unremodeled shells (or gastropod-derived shells; empty shells never previously occupied by hermit crabs) in the same size range of *Nerita scabricosta* shells (Laidre 2012b). The results showed that remodeled shells possessed significantly larger width of shell aperture than unremodeled shells. In addition, the internal volume of remodeled shells was significantly higher than and in approximately two times that of unremodeled shells. Another experiment was conducted by introducing the new available shells of *Nerita scabricosta* into the population of *C. compressus* at Osa Peninsula, Costa Rica (Laidre 2012a). The results revealed that after almost one year of new shell introduction, the recovered shells occupied by *C. compressus* were remodeled by crabs. The columella of all recovered shells was missing. Additionally, the recovered shells were significantly lighter in weight, possessed nearly double the internal volume, and had almost two time larger aperture. Therefore, the recovered shells were characterized by the similar structure modifications observed in used shells by *C. compressus* in the natural population.

Most studies on shell use and selection of land hermit crabs have been carried out in Western Atlantic (Morrison & Spiller 2006), Eastern Pacific (Abrams 1978;

Guillen & Osorno 1993; Osorno *et al.* 1998; Laidre & Vermeij 2012), North Pacific (Willason & Page 1983), Western Pacific (Boneka *et al.* 1995; Nakasone 2001), Red Sea (Sallam *et al.* 2008; Sallam 2012) and Western Indian Ocean (Barnes 1999, 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. There are few studies on shells used by hermit crabs in Thailand. Arunlertaree and Rodboon (2006) investigated shell selection and growth rate of the marine hermit crab, *Clibanarius longitarsus*, in three natural shell patterns. Their experiment was carried out only in laboratory condition. Only Bundhitwongrut (2001) mentioned species of gastropod shells occupied by land hermit crabs *Coenobita* in Thailand. Fourteen marine gastropod and three land snail shell species were utilized by *C. rugosus*. Thus, at present, knowledge on shell use and selection of land hermit crabs of Thailand and Eastern Indian Ocean is poorly known.

2.6.1 Shell use patterns in natural habitats

The pattern of shells used of land hermit crabs in natural habitats have been usually reported in terms of the diversity shell species and the using percentage by all individuals as well as different sexes, reproductive stages and sizes. In addition, several characteristics of hermit crabs and shell characters and condition have been investigated and compared among crab categories and shell species used (Abrams 1978; Willason & Page 1983; Barnes 1999; Nakasone 2001; Sallam *et al.* 2008). In addition, the investigations on shell exchange behavior by land hermit crabs have been studied (Osorno *et al.* 1998; Lewis & Rotjan 2009; Rotjan *et al.* 2010).

Table 2.2 The number of shell species used by land hermit crabs *Coenobita* from previous studies.

Crab species	Number of shell species used	Study area	Studied by
C. cavipes	21	Mozambique	Barnes (1999)
C. clypeatus	4	Bermuda	Walker (1994)
C. clypeatus	14	Bahamas	Morrison and Spiller (2006)
C. compressus	28	Panama & Costa Rica	Abrams (1978)
C. compressus	11	Mexico	Guillen and Osorno (1993)
C. compressus	41	Costa Rica	Laidre and Vermeij (2012)
C. rugosus	20	Mozambique	Barnes (1999)
C. scaevola	29	Egypt	Volker (1967)
C. scaevola	10	Egypt	Sallam *et al.* (2008)

The numbers of shell species used by land hermit crabs are varied across several locations investigated around the world, ranging from 4 to 41 species (Volker 1967; Abrams 1978; Guillen & Osorno 1993; Walker 1994; Barnes 1999; Morrison & Spiller 2006; Sallam *et al.* 2008; Laidre & Vermeij 2012) (Table 2.2). In natural habitats, land hermit crabs usually occupy one shell species in higher percentage over other species (Abrams 1978; Achituv & Ziskind 1985; Guillen & Osorno 1993; Walker 1994; Barnes 1999; Morrison & Spiller 2006; Sallam *et al.* 2008; Laidre & Vermeij 2012) (Table 2.3). The members in Neritidae and Turbinidae are generally shell species used by many species of coenobitid crabs (Abrams 1978; Osorno *et al.* 1998; Barnes 1999; Sallam *et al.* 2008; Sallam 2012; Szabo 2012).

Table 2.3 The dominant shell species used by land hermit crabs *Coenobita* from previous studies.

Crab species	**Dominant shell species used**	**Study area**	**Studied by**
C. cavipes	*Terebralia palustris*	Mozambique	Barnes (1999)
C. clypeatus	*Cittarium pica*	Bermuda	Walker (1994)
C. clypeatus	*C. pica*	Bahamas	Morrison and Spiller (2006)
C. compressus	*Nerita scabricosta*	Panama & Costa Rica	Abrams (1978)
C. compressus	*N. scabricosta*	Mexico	Guillen and Osorno (1993)
C. compressus	*N. scabricosta*	Costa Rica	Laidre and Vermeij (2012)
C. rugosus	*Turbo coronatus*	Mozambique	Barnes (1999)
C. scaevola	*Polinices mammilla*	Israel	Achituv and Ziskind (1985)
C. scaevola	*N. undata*	Egypt	Sallam *et al.* (2008)

In Panama and Costa Rica, *C. compressus* was found occupying at least 30 gastropod shell species with different proportion. The most used shell species by *C. compressus* was *Nerita scabricosta*. The smallest crabs (< 5 mm dactyl length) usually utilized shells of *Planaxis planicostatus*, *Nerita funiculata* and small *Nerita scabricosta*. Small individuals (5–10 mm dactyl length) were frequently found using shells of *Nerita scabricosta*, *Nerita funiculata* and *Strombus gracilior*. Medium to large sized crabs generally occupied shells of *Nerita scabricosta*, *Turbo saxosus* and *Natica* sp. (Abrams 1978).

On Isabel Island, Mexico, *C. compressus* occupied 11 gastropod shell species. *Nerita scabricosta* was the most occupied shell species by *C. compressus*, followed by shells of *Thais speciosa* (Guillen & Osorno 1993). In addition, *Nerita scabricosta* possessed the highest internal volume / weight ratio (SIV/W ratio). This shell species is the lightest species of all available shells on this island. Therefore, Osorno *et al.* (1998) proposed “the energy saving hypothesis” that crabs should select the lightest available shell species, according to SIV/W ratio, to occupy in order to save energy that is then presumably used in growth or reproduction.

At Osa Peninsula, Costa Rica, *C. compressus* was reported using 40 marine and freshwater gastropod shell species and utilizing palm nuts as occupied shells (Laidre & Vermeij 2012). These authors also proposed the number of shells used by hermit crabs (or the diversity of used shells of hermit crabs) to be able to use as a possible and convenient biodiversity index of ecosystem for comparing different sites around the world.

At Quirimba Island, Mozambique, *C. cavipes* was found using 20 shell species in different percentage. The most utilized shell species by *C. cavipes* was *Terebralia palustris* (46%). Small individuals (1–5 g) mainly occupied shells of *Terebralia palustris*. Medium sized crabs (5–10 g) mostly used shells of *Volema paradisica* and large individuals (28 g) utilized shells of *Fasciola trapezium* (Barnes 1999).

In southwestern Madagascar, *C. rugosus* and *C. pseudorugosus* inhabiting the sand scrub beach mainly occupied short-spired shells, whereas *C. cavipes* living in mangrove mainly used shells with tall spire (Barnes 2002).

In Egypt, Red Sea, *C. scaevola* occupied ten gastropod shell species. The most used shell species by *C. scaevola* was *Nerita undata* (86%), followed by *Turbo radiatus* (7.2%). *Nerita undata* was utilized by a wide size range of crabs (2.5–8.5 mm CSL). Small individuals (2.5–3.5 mm CSL) used shells of *Planaxis sulcatus* and

Nassarius arcularius plicatus. Larger crabs (8.5–9.5 mm CSL) inhabited shells of *Turbo radiatus, Polinices milanostomus* and *Monodonta canilifera*. The shell utilization pattern of *C. scaevola* was different between sexes. *Littorina scabra*, *Monodonta canilifera* and *Nassarius arcularius plicatus* were used only by male crabs (Sallam *et al.* 2008).

In addition, ovigerous females of *C. scaevola* in Egypt, Red Sea used eight species of gastropod shells. The most utilized shell species by these females was *Nerita undata* (65.7%). The size range of most ovigerous females using *Nerita undata* shells was 5.0–7.0 mm CSL. Small ovigerous females (4.0–5.0 mm CSL) used shells of *Nassarius coronatus* and *Cerithium caeruleum*. Shells of *Nerita polita*, *Modulus tectum* and *Turbo radiatus* were utilized by larger ovigerous females (6.0–7.0 mm CSL). The variation of fecundity of *C. scaevola* in function of the shell species utilized by the females was recorded (Sallam 2012).

At Enewetak Atoll, Marshall Islands, *C. perlatus* was found using long and narrow shells (e.g. *Rhinoclavis*) more often. Large individuals of *C. perlatus*, including all ovigerous females with the carapace length larger than 20 mm, mainly used shells of *Turbo argyrostomus* (Willason & Page 1983).

At Okinawa, Japan, smaller females of *C. purpureus* and females of *C. rugosus* occupied shells of *Lunella granulata*, while large females of *C. purpureus* and *C. cavipes* used shells of the land snail *Achatina fulica*. Land hermit crabs living in areas with poor shell quality or with a low supply of shells seemingly reproduce at smaller sizes (Nakasone 2001).

Large individuals of *C. scaevola*, *C. compressus* and *C. perlatus* were found using fewer shell species than smaller ones (Niggemann 1968; Abrams 1978; Willason & Page 1983). Nevertheless, the increase of the diversity of shells used by *C. scaevola* with the increasing of crab size was reported in Egypt, Red Sea (Sallam *et al.* 2008).

The unusual shell use by land hermit crabs has been recorded. Fossil shells have been reported utilizing by *C. scaevola* at Red Sea (Volker 1967), *C. clypeatus* in Bermuda (Walker 1994), and *C. rugosus* in southwestern Madagascar (Barnes 2001b). The palm nuts were used by *C. compressus* at Osa Peninsula, Costa Rica as its shelters (Laidre & Vermeij 2012).The plastic debris was recorded using by the unidentified land hermit crab at Kuramahti Island, Maldives Archipelago (Barreiros & Luiz Jr 2008).

2.6.2 Relationship between characteristics of land hermit crabs and occupied shells

Several characters of land hermit crabs and used shells have been usually quantified and recorded to investigate inferred relationship. Nevertheless, particular characters of land hermit crabs have been reported having significant correlation with occupied shell characteristics (Boneka *et al.* 1995; Sallam *et al.* 2008; Sallam 2012).

Shell internal volume was significantly correlated with characters of *C. scaevola*. Therefore, this shell character constitutes mainly the determinant for shell use of *C. scaevola* in Egypt, Red Sea (Sallam *et al.* 2008). On Bunaken Island, Sulawesi, Indonesia, the shell aperture width was highly correlated with the carapace width of *C. rugosus*. Shell weight was also correlated with crab weight (Boneka *et al.* 1995). In addition, the fecundity of *C. scaevola* was found to be highly correlated with the internal volume of the used shells (Sallam 2012).

2.6.3 Shell selection in laboratory condition

The laboratory experiments on shell preference have been mostly investigated in marine hermit crabs, whereas a few studies were reported in land hermit crabs (Abrams 1978; Osorno *et al.* 2005; Contreras-Garduno *et al.* 2009).

Shell size selections by *C. compressus* were significantly different between similarly sized individuals collected from different locations. *C. compressus* also preferred shells that had previously been occupied by other individuals of coenobitid crabs. In addition, *C. compressus* inhabiting *Nerita scabricosta* shells preferred larger shells than previously occupied shell of the same species by approximately 3 mm in shell length for all crab sizes in laboratory condition (Abrams 1978). Regarding to the long-term cost of utilizing heavy shells, the growth of *C. compressus* was negatively correlated with occupied shell weight and rejected thin and light shells (Osorno *et al.* 2005). In addition, the growth of *C. compressus* inhabiting shells < 50% heavier than the preferred shell was higher than that of individuals inhabiting shells that were > 50% heavier. When the difference between two shells was > 50%, and when the shell weight was more than 60% of the crab weight, a heavy shell was significantly to be more likely rejected by *C. compressus* over a lighter shell (Contreras-Garduno *et al.* 2009).

2.7 Previous researches and information on population ecology of land hermit crabs

Knowledge on population characters, including size structure, sex ratio, 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 on population ecology have been made in certain species (e.g. *C. brevimanus*, *C. perlatus* and *C. rugosus* in Fiji (Page & Willason 1982, 1983); *C. cavipes* and *C. rugosus* in Mozambique (Barnes 1997b, a); *C. cavipes*, *C. purpureus* and *C. rugosus* in Okinawa, Japan (Nakasone 2001); *C. clypeatus* in Bahamas (Morrison & Spiller 2006); *C. scaevola* in Egypt, Red Sea (Sallam & Mantelatto 2010; Sallam 2012)). Nevertheless, data on populations in the east coast of Indian Ocean, especially the Andaman Sea, are scant.

2.7.1 Population structure

Population structure can be characterized by displaying through size frequency distribution as the most used parameter because the changes occur throughout the time period as a result of reproduction, recruitment from larvae, and death (Sallam & Mantelatto 2010). Size structure of populations is able to be displayed in histograms for both annual and monthly size frequency distribution (Nakasone 2001; Sallam & Mantelatto 2010).

In land hermit crabs, a few populations were investigated in respect of size frequency distribution (Nakasone 2001; Sallam *et al.* 2008; Sallam & Mantelatto 2010). The monthly size frequency distributions of female *C. rugosus* and *C. purpureus* at Okinawa, Japan, were analyzed in respect of reproduction (Nakasone 2001). The population of *C. scaevola* in Egypt, Red Sea showed a unimodal pattern of annual size frequency distribution (Sallam *et al.* 2008; Sallam & Mantelatto 2010). This unimodal annual size frequency distribution revealed the occurrence of slight monthly variations and probably resulted from the balance between the continuous recruitment without class disruption and mortality rates. The monthly size frequency distributions of *C. scaevola* were also investigated (Sallam & Mantelatto 2010).

2.7.2 Sexual dimorphism

Although sexes of land hermit crabs are distinguished based on the position of gonopores, sexual dimorphism has also been observed in other characters. Males possess sexual tubes situated at the base of the fifth pereopods (McLaughlin *et al.* 2007). In addition, sexual dimorphism in relation to size has been recorded in land hermit crabs. Males of *C. clypeatus* and *C. scaevola* attain larger sizes than females (Wilde 1973; Sallam & Mantelatto 2010). This sexual size dimorphism is presumably attributed to male crabs growing more rapidly than females because of differences in their energy consumption and utilization / allocation (Abrams 1988).

2.7.3 Population density

Density is frequently used to quantify the quality or attractiveness of a habitat (Calow 1999). There are two ways to measure density (i.e. absolute and relative density). Absolute density is the number of organisms per unit area or volume, whereas relative density is the density of one population relative to that of another population (Krebs 1999).

There are few quantitative investigations on density of land hermit crabs (Barnes 2001a; Morrison & Spiller 2006). In Mozambique, the width of mangrove significantly influenced the density of *C. cavipes* and *C. rugosus*. The density of *C. rugosus* was highest at just 1 m width and decreased until absent by 20 m and wider, while the density of *C. cavipes* increased from mangrove absence to 100 m width but decreased from 100 m to 1 km width (Barnes 2001a). Relative densities of *C. clypeatus* were significantly different among three island groups of Bahamas. The mean densities of *C. clypeatus* ranged between 0.013 ± 0.021 and 13.20 ± 14.31 crabs/m^2 and the range of densities was 0.00–46.17 crabs/m^2, which were sampled by baited pitfall traps in the vegetated areas on three islands of Bahamas (Morrison & Spiller 2006).

2.7.4 Population dispersion

Dispersion of individuals in population can portray valuable insight into interactions between individuals of a species and their biotic and abiotic environment. Three main patterns of dispersion are recognized (i.e. clumping, uniform and random). Clumping infers that individuals are aggregated in more favorable parts of habitat that is probably due to gregarious behavior, environmental heterogeneity, reproductive mode, and others. Uniform dispersion results from negative interactions between individuals in population, such as competition for food or space. Random dispersion implies environmental homogeneity and/or nonselective behavioral pattern (Ludwig & Reynolds 1988).

The aggregation of land hermit crabs during the day time are frequently recorded (Page & Willason 1982; Burggren & McMahon 1988; Greenaway 2003). Nevertheless, little attention has been paid for quantitative investigation on crab dispersion.

2.7.5 Sex ratio

Sex ratio is used to refer to the relative numbers of males and females of organisms, usually animals with separate sexes (Calow 1999). Males and females are produced in approximately equal numbers in most species with separate sexes as natural selection favors the expected 1:1 ratio according to Fisher’s theory of sex ratio (Fisher 1930; Wenner 1972). The analysis on sex ratio of populations is able to be displayed as overall, monthly and size-class sex ratio (Sallam & Mantelatto 2010).

The investigations on sex ratio of populations have been carried out mostly in marine hermit crabs, while few studies were reported in land hermit crabs (Sallam *et al.* 2008; Sallam & Mantelatto 2010). Most species of hermit crabs show a female-biased overall sex ratio, including another coenobitid crab species, *C. scaevola* in

Egypt, Red Sea (M:F = 1:1.2 (Sallam *et al.* 2008); M:F = 1:1.9 (Sallam & Mantelatto 2010)).

In respect of sex ratio as a function of size class, Wenner (1972) proposed four patterns found in marine crustaceans (i.e. standard, reversal, intermediate and anomalous patterns). Standard pattern is characterized by an approximately equal proportion of males and females in the smaller size classes and subsequent deviation towards a certain sex (male or female) at the larger size classes. The diagnosis of reversal pattern is the occurrence of only one sex in the smallest size classes and the occurrence of only opposite sex in the largest size classes with transitional proportion between sexes in the intermediate size classes. Intermediate pattern is characterized by the pattern intermediate between the standard and reversal patterns. The diagnosis of anomalous pattern is a decrease in the males/females ratio in the intermediate size classes and subsequent increase in the largest size classes (Wenner 1972).

Little information is available concerning sex ratio as a function of size class of land hermit crabs (Sallam & Mantelatto 2010). *C. scaevola* lived in variable environment in the hyper arid region (Achituv & Ziskind 1985), showing an anomalous pattern of the sex ratios of size classes (Sallam & Mantelatto 2010). Nevertheless, this pattern has been recorded in populations of hermit crabs living in intertidal and infralittoral areas (Mantelatto *et al.* 2007).

2.7.6 Diet

Most information on diets of land hermit crabs has been recorded as common names of food items (Page & Willason 1983; Burggren & McMahon 1988). Nevertheless, the identification to the level of scientific name of these diets is scant (Laidre 2013). Land hermit crabs are commonly considered as scavengers or detritus feeders. Diets consumed by land hermit crabs are fallen or decaying parts of plants and animal carrion. The food items recorded include a variety of decaying plant materials, fallen fruits and seeds, mangrove propagules, strand line detritus, faeces and carrion of animals (Ball 1972; Wilde 1973; Page & Willason 1983; Burggren & McMahon 1988; Barnes 1997a; Greenaway 2003; Linton & Greenaway 2007; Laidre 2013). Fallen flowers of *Bombacopsis sessilis* were consumed by *C. compressus* in Panama as its common food item (Small & Thacker 1994; Thacker 1994). Human faeces were the main food source eaten by *C. cavipes* living near human population at Quirimba Island, Mozambique (Barnes 1997a). The most diverse variety of diets of *C. compressus* was recorded from the population at Osa Peninsula, Costa Rica, including fruits, nuts, seeds and other parts of plants, as well as faeces and carcasses of both invertebrates and vertebrates, and also algae and fungi (Laidre 2013).

Cannibalism is described as intraspecific predation (Fox 1975). This phenomenon has been also observed in land hermit crabs. Cannibalism was recorded for *C. clypeatus* in the laboratory experiment (Wilde 1973) and *C. rugosus* in the natural habitat (Barnes 1997a). Nevertheless, dead conspecifics of *C. perlatus* in Micronesia and *C. compressus* in Panama were not consumed in the field experiments

(Small & Thacker 1994). In addition, the colonization by flies may be reduced or prevented by the removal of carrion by land hermit crabs (Page & Willason 1983).

2.7.7 Reproduction

The reproductive activity of populations of land hermit crabs are frequently determined by the occurrence and proportion of ovigerous or egg-carrying females as a function of time as well as fecundity (Nakasone 2001; Sallam & Mantelatto 2010; Sallam 2012). In addition, the smallest ovigerous female is usually used to be the potential minimum sexual maturity size, as a morphological criterion to determine juvenile and adult stages of land hermit crabs (Nakasone 2001; Sallam & Mantelatto 2010).

The reproduction of land hermit crabs have been investigated (Nakasone 2001; Sallam & Mantelatto 2010; Sallam 2012). At Okinawa, Japan, the breeding season ranged from late May to mid-September for *C. purpureus*, from late May to November for *C. rugosus*, and from mid-May to late August for *C. cavipes*. The smallest ovigerous female was 3.83 mm CSL for *C. purpureus*, 3.93 mm CSL for *C. rugosus*, and 9.49 mm CSL for *C. cavipes*. The smallest males having spermatophores in vas deferens were 4.94 mm CSL for *C. purpureus* and 4.24 mm CSL for *C. rugosus*. The same larval release sites were used by the smaller and larger females of *C. purpureus* for over 13 years, from 1986 to 1999 (Nakasone 2001). In Egypt, Red Sea, ovigerous females of *C. scaevola* occurred only in three discontinuous months (May, July and September) and the percentages of these females to total females collected were between 12.2% in September and 45.4% in

July. The size range of ovigerous female *C. scaevola* was 4.1–7.3 mm. The mean fecundity ± SD of *C. scaevola* was 679.8 ± 140 eggs. The range of the number of fertilized eggs per female was from 422 (4.1 mm CSL) to 945 eggs (7.3 mm CSL) (Sallam & Mantelatto 2010; Sallam 2012).

CHAPTER 3

METHODOLOGY

3.1 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. This site is located in Tambon Wichit, Mueang District, Phuket Province. 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 Province, Andaman coast of Thailand (Figure 3.1). The beach of Cape Panwa is an open sand scrub beach, comprising rather coarse sand patches of shale (phylitte) (Nielsen 1976a) (Figure 3.2). 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 of 2.15–2.27 m at spring tide to 0.85–1.15 m at neap tide (Limpsaichol 1981). The PMBC is under the Department of Marine and Coastal Resources, 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.

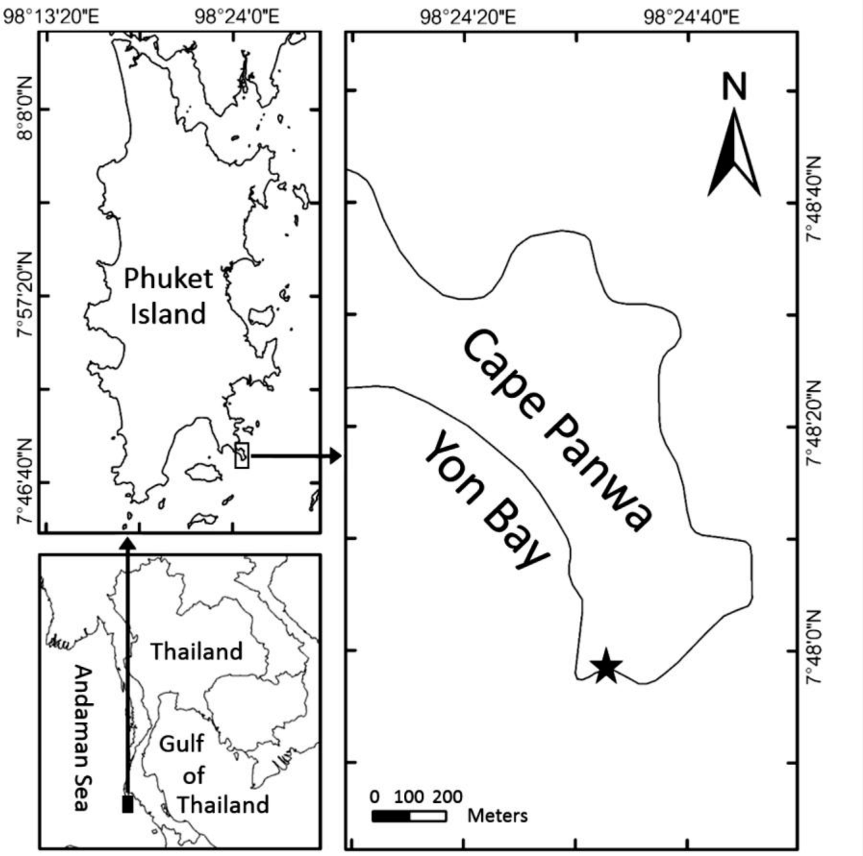


Figure 3.1 Map of the study site (marked as the star) at Cape Panwa, Phuket Province, Andaman Coast of Thailand.

Figure 3.2 The study beach in the supralittoral zone at Cape Panwa, Phuket Province, Andaman Coast of Thailand (photo by Thanakhom Bundhitwongrut).

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

3.2 Specimen sampling

At Cape Panwa, Phuket Province, *Coenobita rugosus*, *C. violascens* and *C. brevimanus* 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 author: Thanakhom Bundhitwongrut) (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 m^2 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 (Figure 3.3).

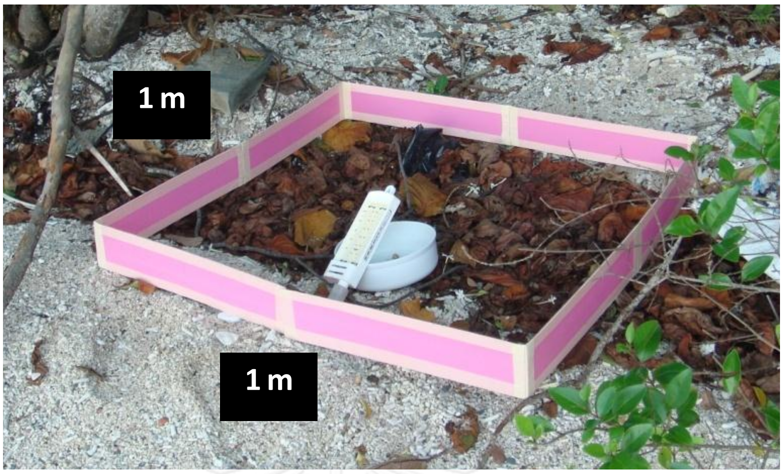


Figure 3.3 Sampling quadrat of 1 m^2 with walls of 10 cm high to prevent crabs from escaping (photo by Thanakhom Bundhitwongrut).

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. However, 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 the native animals. In addition, the author 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 Province, 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. The additional marking method was conducted for the study on shell use in natural habitat. After investigation 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 by a waterproof pen and then coated by nail vanish on both crabs (on the outer surface of palm of the major cheliped) and their occupied shells (on the surface of the body whorl near the outer lip). From the results in preliminary trials, the markings were durable at least one month in the natural habitat of crabs. Additionally, all recaptured crabs in every month were marked again, if encountered in the sampling quadrats.

3.3 Measurement of 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 over the study year (April 2011 to March 2012) at this site.

3.4 Specimen and data analysis

3.4.1 Shell utilization of *Coenobita rugosus*

3.4.1.1 Shell utilization of *Coenobita rugosus* in natural habitat

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) (Figure 3.4), major chela length (MCL; from the articulation between carpus and propodus to the tip of fixed finger of the left cheliped) and width (MCW; the greatest distance from the dorsal margin to the ventral margin of propodus of the left cheliped perpendicular to MCL) (Figure 3.5), weight (CW), sex and reproductive stages (males, non-ovigerous females, and ovigerous females (Figure 3.6)).

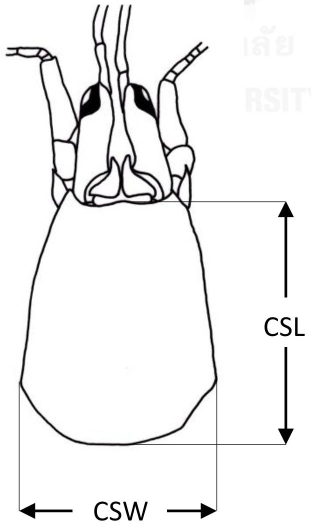


Figure 3.4 The measurement of cephalothoracic shield length (CSL) and width (CSW) of *Coenobita rugosus* (drawing by Thanakhom Bundhitwongrut).

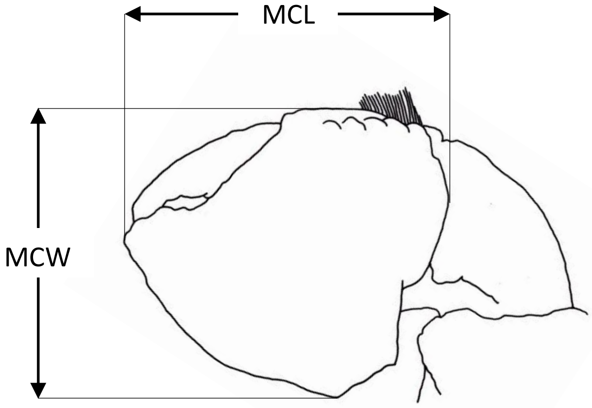


Figure 3.5 The measurement of major chela length (MCL) and width (MCW) of *Coenobita rugosus* (drawing by Thanakhom Bundhitwongrut).

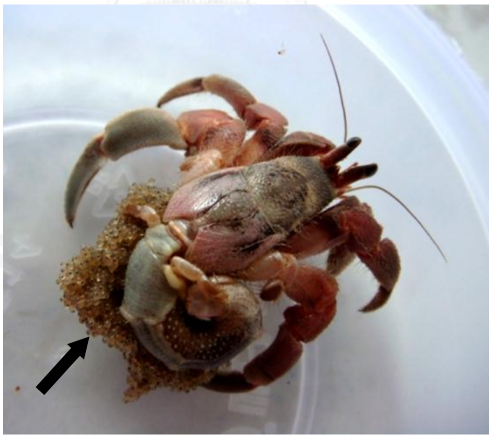


Figure 3.6 Ovigerous female *Coenobita rugosus* out of its occupied shell. Fertilized eggs are attached to pleopods on the left side of the abdomen (indicated by the arrow) (photo by Thanakhom Bundhitwongrut).

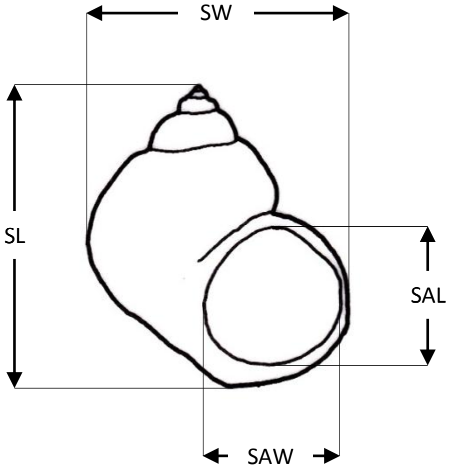
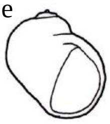
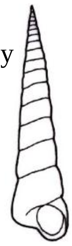
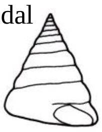


Figure 3.7 The measurement of shell length (SL), shell width (SW), aperture length (SAL) and aperture width (SAW) of the occupied shell of *Coenobita rugosus* (drawing by Thanakhom Bundhitwongrut).

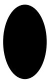
Species of occupied and unoccupied shells were identified using several references (Brandt 1974; Nielsen 1976a, b; Wium-Andersen 1977; Tantanasiriwong 1978; Abbott 1989; Middelfart 1997; Poutiers 1998; Abbott & Dance 2000; Tan & Clements 2008). In addition, shells were compared with the specimens deposited in the reference collection of PMBC to confirm their identities. The quantitative characteristics were composed of shell length (SL; from the apex to the lower tip of aperture), width (SW; the greatest width of the body whorl perpendicular to shell length), weight (WW), internal volume (SIV), aperture length (SAL; the longest distance of aperture parallel to shell length), and aperture width (SAW; the greatest distance from the inner margin of the outer lip to the inner wall of the inner lip perpendicular to aperture length) (Figure 3.7). The measurement of internal volume of shells was investigated by using a graduated syringe to fill water into shells (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. All quantitative measurements were determined 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.

Table 3.1 Categorizations of shell shapes used in the present study (drawings by Thanakhom Bundhitwongrut).

Shell shape	**Description**
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
Biconical 	resembling two equal or nearly equal cones placed base to base
Globose 	resembling a spherical shape with a nearly globular body whorl and a very short spire
Elongately Conical 	resembling an elongate cone with a long to very long spire; shell length more than 1.5 times of shell width
Pyramidal 	resembling conical, but with flat-sided whorls and a nearly triangular outline; a pyramid shape

Shell shape	**Description**
Oval 	resembling conical, but with a relatively larger body whorl and an egg or elliptical shape outline
Turban 	resembling conical with a nearly globular body whorl, but with a broad conical spire and a convex base
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
Vermiform 	resembling a worm; an irregularly coiled tubular shell

Table 3.2 Categorizations of shell aperture (opening) shapes used in the present study (drawings by Thanakhom Bundhitwongrut).

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 of aperture width
Elongately ovate 	resembling an egg or elliptical shape, but aperture length more than 2.5 times of aperture width
Semicircular 	resembling a half of a circle; a D-shape
Irregular 	having an irregular shape, resulted from damage of original aperture shapes

The 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 and Leobrera (1986) and Poutiers (1998). Table 3.1 and 3.2 give descriptions and schematic drawings of representative categories of shell and aperture shapes. The categories of shell shapes were composed of biconical, conical, elongately conical, fusiform, globose, oval, pyramidal, pyriform, turban and vermiform (Table 3.1). The categories of shell aperture shapes were classified as elongately ovate, irregular, ovate, round and semicircular (Table 3.2). The shell quality categories were undamaged and damaged shells. The damaged shells were shells with broken apex, a hole, damaged inner lip, broken outer lip of last whorl or greatly damage in large portion of shell (Barnes 1999). Furthermore, the proportion 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).

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. The chi-square tests (χ^2) were used to compare the frequencies of occupation of different shell species, shell and aperture shapes, and the rate of occupancy of the undamaged and damaged shells between sexes and among crab reproductive groups (Zar 2010). Small samples ($n \leq 5$) were pooled before using chi-square tests. 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) and Sallam *et al.* (2008). To determine relationships between characters of hermit crabs and occupied shells, correlation and regression analyses were performed. Transformed values (using $ln(x)$) of both crab and shell characters were used to investigate correlation by Pearson product moment correlation (Zar 2010), and correlation matrix was constructed. The power function equation ($Y = aX^b$) was used in the regression analysis (Sallam *et al.* 2008). In all statistical tests, the critical significance level adopted was $p < 0.05$. All statistical analyses were performed using SPSS Statistics 17.0 (SPSS 2008).

3.4.1.2 Shell preference of *Coenobita rugosus* in laboratory condition

The experiment on shell selection was carried out to determine shell preference of *C. rugosus*. Twenty five individuals of male and non-ovigerous female *C. rugosus* in shells of *Nerita albicilla* as the most occupied shell species in natural habitat were used for the experiment. Crab size was selected to range from 6 to 7 mm CSL in order to avoid the effect of crab size and shell size between shell species. The five most used shell species by crabs in that size class (6–7 mm CSL) recorded in natural habitat were used in this experiment (*Astraea semicostata*, *N. albicilla*, *N. chamaeleon*, *N. polita* and *Thais hippocastanum*). All of the offered shells were free of damage and with size similar to individual crab original shell. The size of offered shells was determined by linear regression equations using data from the study in natural habitat (Ismail 2010). All offered shells were washed with freshwater and then were left to be dry at the ambient temperature before using in the experiment.

A single individual of *C. rugosus* in the original occupied shell of *N. albicilla* was placed in an aquarium (30 x 30 x 30 cm) with sand as substrate and with food and water for each trial. Ten shells (two for each shell species) were randomly distributed. In addition, the original shell was marked with a waterproof pen to avoid confusion with the offered shells (Shih & Mok 2000). The measurements of crabs and their original shells were recorded before beginning the experiment. Shell choices by *C. rugosus* were recorded after 12 h in all experiments. After the experiment, the characters of the preferred shell were measured. The shell weight, internal volume and SIV/W ratio of the original and preferred shells were determined and compared (Ismail 2010). To evaluate how many hermit crabs are satisfied with their shells, the methods proposed by Imafuku (1984) were applied. At the end of the experiments, the crabs selected their original shells were considered as “satisfied”, whereas those changed to new shells were regarded as “dissatisfied”.

To examine difference of weight, internal volume and SIV/W ratio between the original and preferred shells, paired t-test was used (Ismail 2010). Correlation of weight, internal volume and SIV/W ratio between the original and preferred shells was determined using Pearson product moment correlation (Zar 2010). Statistical significance was accepted at $p < 0.05$. All statistical analyses were determined by using SPSS Statistics 17.0 (SPSS 2008).

3.4.2 Population ecology of *Coenobita rugosus*

Population characteristics of *C. rugosus* in this study were evaluated in terms of population structure and sexual dimorphism, density, dispersion, sex ratio, diet, and reproduction. 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 (Zar 2010). Statistical significance was accepted at $p < 0.05$. SPSS Statistics 17.0 (SPSS 2008) was used for all statistical analyses.

3.4.2.1 Population structure and sexual dimorphism

Crab sizes were 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. 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 (McLaughlin 1980; Forest *et al.* 2000).

The total distribution of individuals in each size class, based on the CSL, was constructed as annual and monthly size frequency distribution to reveal the population structure. 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 recruitment in the population was characterized by the occurrence of juveniles, defined as individuals of either sex that were smaller than the smallest ovigerous female (Sallam & Mantelatto 2010).

3.4.2.2 Population density

The numbers of crabs in each quadrat were counted and used to calculate the population density. The difference in densities between sampling months was checked by analysis of variance (ANOVA). The relationship between crab density and environmental factors was tested by Spearman’s rank-order correlation (Zar 2010).

3.4.2.3 Dispersion

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).

3.4.2.4 Sex ratio

The sex ratio (male:female (M:F)) was calculated for the yearly and monthly samples as well as for each size class (Sallam & Mantelatto 2010). The sex ratio (M:F) of the population was tested by the Chi-square test. The pattern of sex ratio as a function of size class of *C. rugosus* was interpreted and compared to the patterns proposed by Wenner (1972).

3.4.2.5 Diet

All food items observed to be consumed by *C. rugosus* in the study area (at least five times of observations for plants during the study period) were identified to the level of scientific names and recorded.

3.4.2.6 Reproduction

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. The relationship between reproductive activity and physical parameters was analyzed by Spearman's rank-order correlation (Zar 2010).

CHAPTER 4

RESULTS

4.1 Hermit crab assemblages

Three species of land hermit crabs, *Coenobita rugosus*, *C. violascens* and *C. brevimanus*, were found sympatrically throughout the study period at Cape Panwa, Phuket Province, Andaman coast of Thailand. In addition, two marine hermit crabs, *Clibanarius virescens* and *Cl. merguiensis*, were found in the rocky pools in the intertidal area adjacent to the sampling site.

4.2 Shell utilization 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) and were used for data analysis.

4.2.1 Shell utilization of *Coenobita rugosus* in natural habitat

4.2.1.1 Diversity and groups of shells used

Coenobita rugosus was found occupying 63 species of molluscan shells (Table 4.1), 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* (n = 1) (Figure 4.1).

Table 4.1 Shells utilized by *Coenobita rugosus* at Cape Panwa, Phuket Province 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 mean 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

Table 4.1 (continued)

Shell group	Family	Scientific name	SIV/W
MG	Muricidae	*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
		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

Table 4.1 (continued)

Shell group	Family	Scientific name	SIV/W
MG	Turbinidae	*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

(A) **(B)**

Figure 4.1 *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 Province on 27 November 2011. Dorsolateral view (A); ventral view (B) (photos by Thanakhom Bundhitwongrut).

Coenobita rugosus occupied the shells of 59 species of marine gastropods and only two species of freshwater gastropod 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 4.1).

In sampling quadrats, there were 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.

Table 4.2 Percentage of shell species inhabited by *Coenobita rugosus* at Cape Panwa, Phuket Province from April 2011 to March 2012. The number in parenthesis after the percentage of shells used was 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)

4.2.1.2 Shell species used in relation to crab reproductive group

The shell utilization pattern of *C. rugosus* varied in relation to shell species (Table 4.2). The most common 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 (81.1%) used by both sexes. Ten shell species were occupied only by males (*Cerithidea cingulata* (*n* = 1), *Chama* sp. (*n* = 1), *Murex pecten* (*n* = 1), *Nerita articulata* (*n* = 3), *Polinices didyma* (*n* = 1), *Pomacea canaliculata* (*n* = 4), *Pugilina cochlidium* (*n* = 3), *Pugilina colosseus* (*n* = 1), *Purpura panama* (*n* = 1) and *Tenagodus cumingii* (*n* = 1)). In addition, ten other shell species were occupied only by females (*Cyclophorus pfeifferi* (*n* = 1), *Cymatium muricinum* (*n* = 1), *Cymatium pileare* (*n* = 1), *Cymatium succinctum* (*n* = 1), *Cymatium* sp. (*n* = 2), *Drupa rubusidaeus* (*n* = 1), *Fusinus nicobaricus* (*n* = 1), *Littorina scabra* (*n* = 1), *Rapana rapiformis* (*n* = 1) and *Turritella* sp. (*n* = 3)). 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* as the most used shell species (18.2%, *n* = 111), followed by *N. chamaeleon* (10.5%, *n* = 64) and *Drupella rugosa* (9.3%, *n* = 57). There were significant differences in shell species occupation between males and females (χ^2 = 34.125, *d.f.* = 18, *p* = 0.012).

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 ($\chi^2 = 39.494$, *d.f.* = 3, $p < 0.001$). Non-ovigerous females mostly used *N. albicilla* (20.3%, $n = 103$), followed by *D. rugosa* (11.2%, $n = 57$) and *N. chamaeleon* (9.5%, $n = 48$). Nevertheless, the most occupied shell species by ovigerous females of *C. rugosus* were *N. polita* (23.1%, $n = 24$), followed by *N. chamaeleon* (15.4%, $n = 16$) and *N. costata* (10.6%, $n = 11$). There were also significant differences in shell species occupation between males and non-ovigerous females ($\chi^2 = 44.168$, *d.f.* = 16, $p < 0.001$) and between males and ovigerous females ($\chi^2 = 14.832$, *d.f.* = 3, $p = 0.002$).

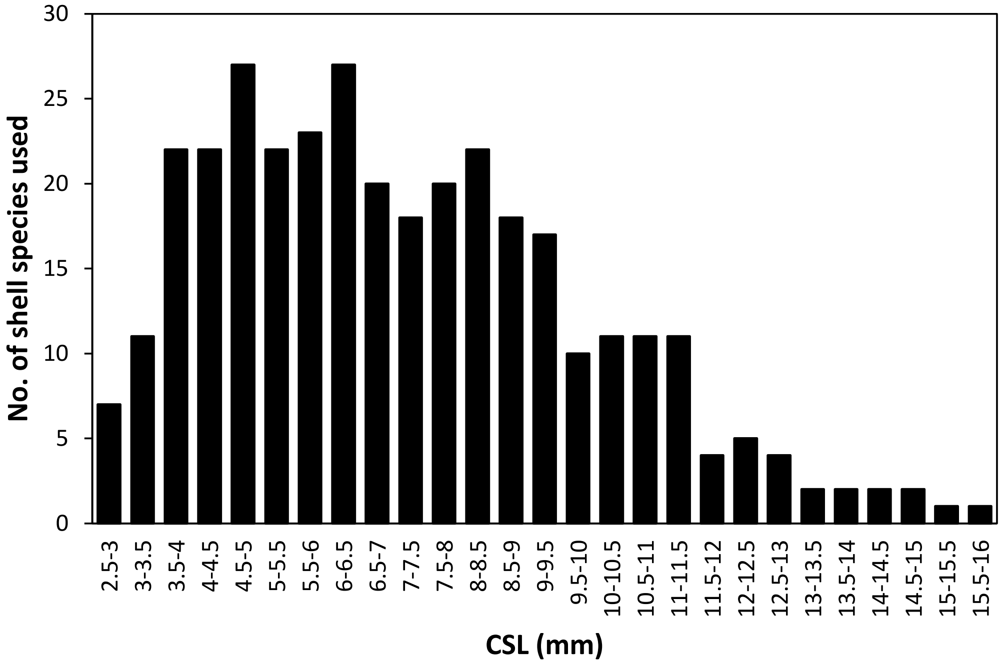


Figure 4.2 The number of shell species used by each size class of *Coenobita rugosus* at Cape Panwa, Phuket Province from April 2011 to March 2012.

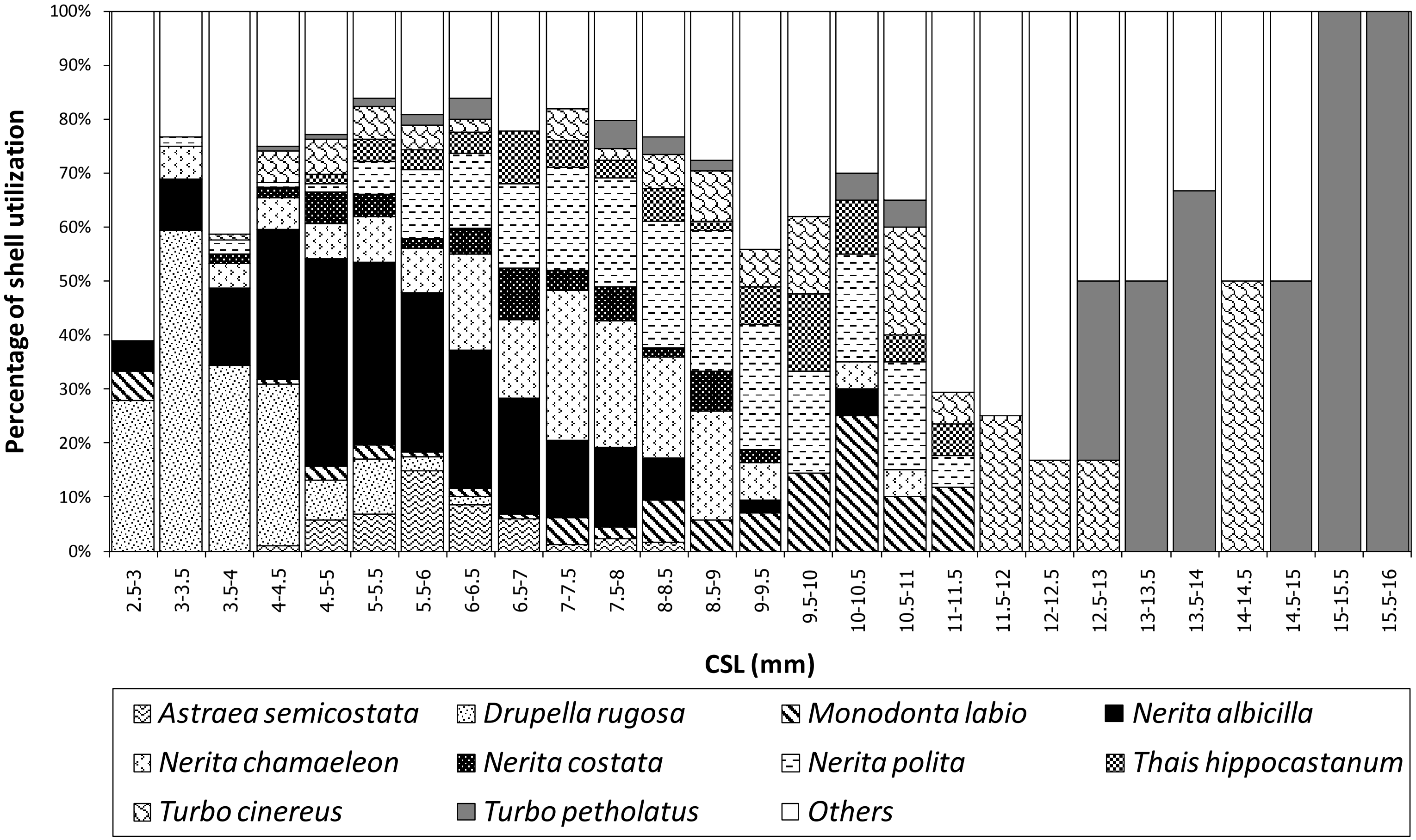


Figure 4.3 Shell utilization by *Coenobita rugosus* as a function of hermit crab size.

4.2.1.3 Shell species used in relation to crab size

Shell utilization pattern of *C. rugosus* varied in relation to crab size (Figures 4.2 and 4.3). The diversity of shells used by *C. rugosus* increased with increases in body size from small to medium-sized crabs, but decreased in larger size classes (Figure 4.2). Medium-sized crabs (3.5–9.5 mm) utilized more diverse shell species (17–27 species) than smaller (<3.5 mm CSL, 7–11 species) and larger (>9.5 mm CSL, 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 4.3). *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).

4.2.1.4 Shells used in relation to shell shape

Shell utilization patterns of *C. rugosus* varied in relation to shell shape (Figure 4.4). 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 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).

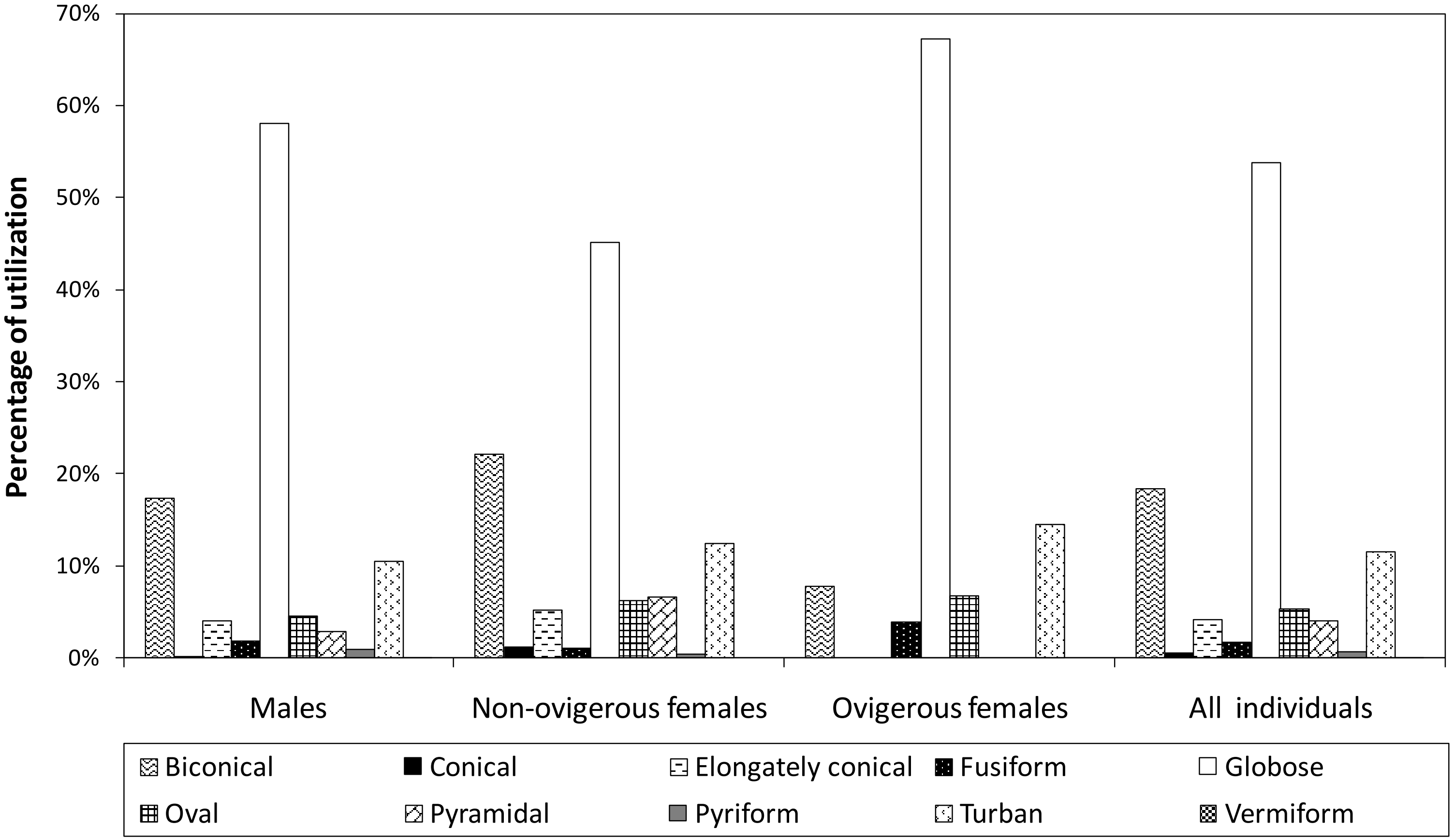


Figure 4.4 Percentage of shell shape categories utilized by *Coenobita rugosus* at Cape Panwa, Phuket Province from April 2011 to March 2012.

There were significant differences in shell shape occupation between males and non-ovigerous females (χ^2 = 34.335, *d.f.* = 9, p < 0.001), between males and ovigerous females (χ^2 = 18.756, *d.f.* = 9, p = 0.027) and between non-ovigerous females and ovigerous females (χ^2 = 36.612, *d.f.* = 8, p < 0.001).

4.2.1.5 Shells used in relation to shell aperture shape

Shell utilization patterns of *C. rugosus* varied in relation to shape of shell aperture (Figure 4.5). 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).

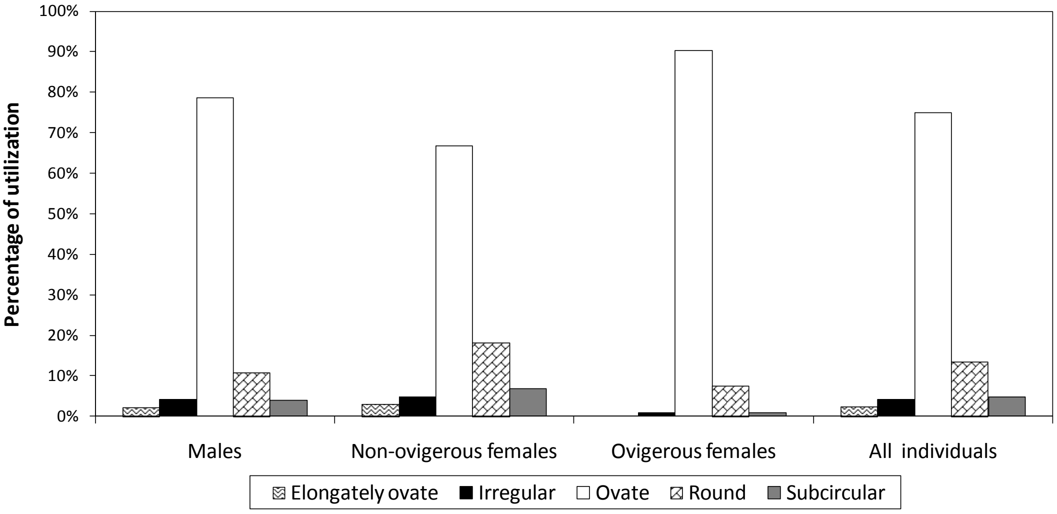


Figure 4.5 Percentage of aperture shape categories of shells used by *Coenobita rugosus* at Cape Panwa, Phuket Province from April 2011 to March 2012.

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 only four categories. Shells with elongately ovate apertures were unoccupied by ovigerous females. There were significant differences in shell aperture shape occupation between males and non-ovigerous females (χ^2 = 23.139, *d.f.* = 4, $p < 0.001$), between males and ovigerous females (χ^2 = 9.622, *d.f.* = 4, $p = 0.047$) and between non-ovigerous females and ovigerous females (χ^2 = 24.113, *d.f.* = 4, $p < 0.001$).

4.2.1.6 Shells used 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). There was no significant difference in the rate of occupancy of undamaged and damaged shells between males and non-ovigerous females (χ^2 = 3.376, *d.f.* = 1, $p = 0.066$). Nevertheless, there were significant differences in the rate of occupancy of the undamaged and damaged shells between males and ovigerous females (χ^2 = 21.543, *d.f.* = 1, $p < 0.001$) and between non-ovigerous females and ovigerous females (χ^2 = 30.318, *d.f.* = 1, $p < 0.001$). Ovigerous females occupied undamaged shells (75.0%, n = 78) obviously more than damaged shells (25.0%, n = 26).

4.2.1.7 Shells used 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. *N. albicilla*, the most-occupied shell species, had a SIV/W ratio (mean ± SD) equal to 0.364 ± 0.114 (n = 259) (Table 4.1), but had a very low ranking SIV/W ratio (52nd 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 40th in terms of use by *C. rugosus*.

4.2.1.8 Relationship between crab and shell characteristics

The relationship between crab characters and occupied shells are shown in Tables 4.3 and 4.4. Tendency of linear relationship was observed in scatter plot matrix between transformed values of crab characters and utilized shells (Appendix A). The values of correlation coefficient (r) from correlation matrix ranged between 0.56 and 0.97 (Table 4.3). In the correlation matrix, strong correlations were noted between characters of crabs and internal volume, aperture width and length of occupied shells ($r \geq 0.90$). Additionally, the values of determination coefficient (r^2) from regression equations ranged between 0.32 and 0.94 (Table 4.4). Strong correlations were also observed in the equations between characters of crabs and internal volume, aperture width and length of utilized shells ($r \geq 0.90$). Shell aperture width was the most correlated shell character with crab characters ($r > 0.95$) whereas shell length was the shell character with least correlation with characters of crabs ($r \leq 0.65$).

Table 4.3 The correlation matrix between transformed values of characters of hermit crab *Coenobita rugosus* and the inhabited shells sampled. *r* = correlation 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. ** Correlation is significant at the 0.01 level.

		*ln*CW	*ln*CSL	*ln*CSW	*ln*MCL	*ln*MCW	*ln*WW	*ln*SIV	*ln*SL	*ln*SW	*ln*SAL	*ln*SAW
*ln*CW	*r*	1	.991**	.993**	.988**	.982**	.788**	.968**	.650**	.867**	.904**	.960**
	p value		.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
	N	1322	1322	613	1321	1321	1322	1290	1322	1322	1322	1322
*ln*CSL	*r*	.991**	1	.994**	.988**	.984**	.769**	.957**	.621**	.865**	.900**	.964**
	p value	.000		.000	.000	.000	.000	.000	.000	.000	.000	.000
	N	1322	1322	613	1321	1321	1322	1290	1322	1322	1322	1322
*ln*CSW	*r*	.993**	.994**	1	.990**	.986**	.765**	.960**	.582**	.881**	.900**	.963**
	p value	.000	.000		.000	.000	.000	.000	.000	.000	.000	.000
	N	613	613	613	613	613	613	598	613	613	613	613
*ln*MCL	*r*	.988**	.988**	.990**	1	.992**	.752**	.954**	.598**	.869**	.911**	.969**
	p value	.000	.000	.000		.000	.000	.000	.000	.000	.000	.000
	N	1321	1321	613	1321	1321	1321	1289	1321	1321	1321	1321
*ln*MCW	*r*	.982**	.984**	.986**	.992**	1	.734**	.945**	.562**	.869**	.907**	.970**
	p value	.000	.000	.000	.000		.000	.000	.000	.000	.000	.000
	N	1321	1321	613	1321	1321	1321	1289	1321	1321	1321	1321
*ln*WW	*r*	.788**	.769**	.765**	.752**	.734**	1	.824**	.752**	.860**	.701**	.750**
	p value	.000	.000	.000	.000	.000		.000	.000	.000	.000	.000
	N	1322	1322	613	1321	1321	1322	1290	1322	1322	1322	1322
*ln*SIV	*r*	.968**	.957**	.960**	.954**	.945**	.824**	1	.695**	.879**	.905**	.946**
	p value	.000	.000	.000	.000	.000	.000		.000	.000	.000	.000
	N	1290	1290	598	1289	1289	1290	1290	1290	1290	1290	1290
*ln*SL	*r*	.650**	.621**	.582**	.598**	.562**	.752**	.695**	1	.498**	.635**	.566**
	p value	.000	.000	.000	.000	.000	.000	.000		.000	.000	.000
	N	1322	1322	613	1321	1321	1322	1290	1322	1322	1322	1322
*ln*SW	*r*	.867**	.865**	.881**	.869**	.869**	.860**	.879**	.498**	1	.791**	.885**
	p value	.000	.000	.000	.000	.000	.000	.000	.000		.000	.000
	N	1322	1322	613	1321	1321	1322	1290	1322	1322	1322	1322
*ln*SAL	*r*	.904**	.900**	.900**	.911**	.907**	.701**	.905**	.635**	.791**	1	.875**
	p value	.000	.000	.000	.000	.000	.000	.000	.000	.000		.000
	N	1322	1322	613	1321	1321	1322	1290	1322	1322	1322	1322
*ln*SAW	*r*	.960**	.964**	.963**	.969**	.970**	.750**	.946**	.566**	.885**	.875**	1
	p value	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	
	N	1322	1322	613	1321	1321	1322	1290	1322	1322	1322	1322

Table 4.4 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

4.2.2 Shell preference of *Coenobita rugosus* in laboratory condition

Both sexes of *C. rugosus* obviously preferred shells of *Thais hippocastanum* (84% of males and 92% of females), followed by *Nerita chamaeleon* (8% of males and 4% of females) and *N. polita* (4% of males and 4% of females) (Table 4.5). Shells of *Astraea semicostata* were not selected by *C. rugosus*.

Table 4.5 Shell selection by *Coenobita rugosus* in laboratory condition (*n* = 25 individuals for each sex)

Shell species	**Number of chosen shells**			
	Males	**Females**	**Total**	**Total %**
Astraea semicostata	0	0	0	0
Nerita albicilla	1	0	1	2
N. chamaeleon	2	1	3	6
N. polita	1	1	2	4
Thais hippocastanum	21	23	44	88

Both sexes of *C. rugosus* showed 100% of dissatisfaction rate with previously occupied shells of *N. albicilla*. No individual of *C. rugosus* selected their original shells at the end of the experiment. All crabs chose new shells with most preference of *T. hippocastanum* by both sexes. Additionally, there was no significant correlation of weight between the original and preferred shells (Pearson product moment correlation, $r = 0.132$, $p = 0.361$), while significant correlation of internal volume between the original and preferred shells was detected (Pearson product moment correlation, $r = 0.526$, $p < 0.001$). There was also no significant correlation of SIV/W ratio between the original and preferred shells (Pearson product moment correlation, *r* = -0.066, *p* = 0.647). Furthermore, the weight of preferred shells (4.09 ± 0.86 g; *n* = 50) was significantly higher than that of original shells (3.34 ± 0.63 g; *n* = 50) (Paired t-test, *t* = 5.326, *p* < 0.001), whereas the internal volume of preferred shells (1.7 ± 0.3 ml; *n* = 50) was significantly larger than that of original shells (1.2 ± 0.2 ml; *n* = 50) (Paired t-test, *t* = 14.702, *p* < 0.001). The SIV/W ratio of preferred shells (0.44 ± 0.09; *n* = 50) was also significantly higher than that of original shells (0.38 ± 0.06; *n* = 50) (Paired t-test, *t* = 3.960, *p* < 0.001).

4.3 Population ecology of *Coenobita rugosus*

4.3.1 Population structure and sexual dimorphism

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%) (Table 4.6 and 4.7). The mean size ± 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 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 4.7).

Table 4.6 Size frequency distribution of individuals of *Coenobita rugosus* at Cape Panwa, Phuket Province, Thailand from April 2011 to March 2012.

Size class (mm)	Frequency (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 4.7 Number, percentage and sex ratio of individuals of *Coenobita rugosus* sampled monthly at Cape Panwa, Phuket Province from April 2011 to March 2012.

Month	**Number of individuals**				**Sex ratio**	**χ^2 test**
	Males*	**Non-ovigerous females***	**Ovigerous females***	**Total**		**(*p*-value)**
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

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, $p < 0.001$).

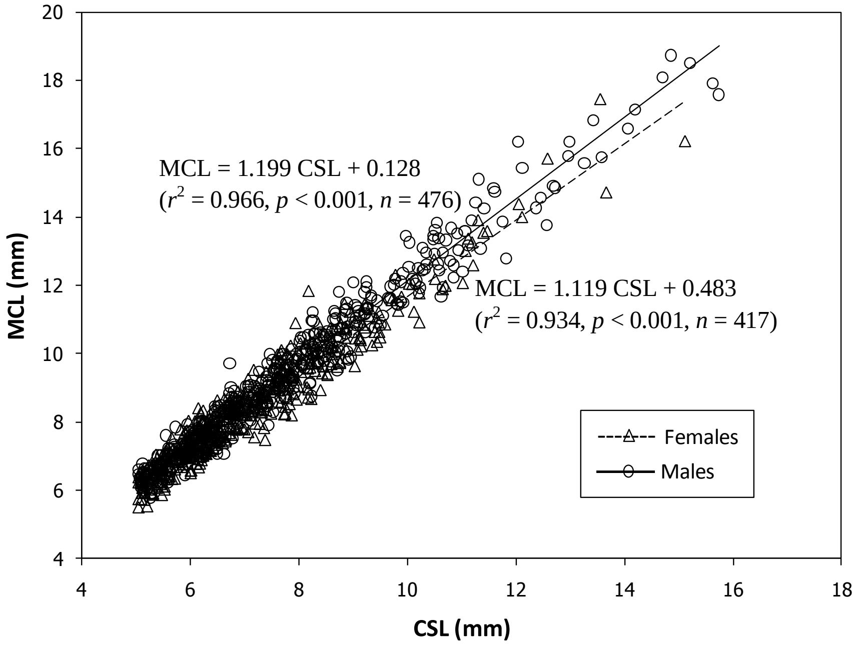


Figure 4.6 Relationship between the cephalothoracic shield length (CSL) and major chela length (MCL) in *Coenobita rugosus*. Data are shown for the 893 adult male and female *Coenobita rugosus* (CSL larger than or equal to 5.06 mm), sampled over the study period.

Significant variation in the MCL, a secondary sexual character, was detected between males and females by ANCOVA (Figure 4.6), 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 CSL + 0.128 (r^2 = 0.966, $p < 0.001$, n = 476) and MCL = 1.119 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, $p < 0.001$).

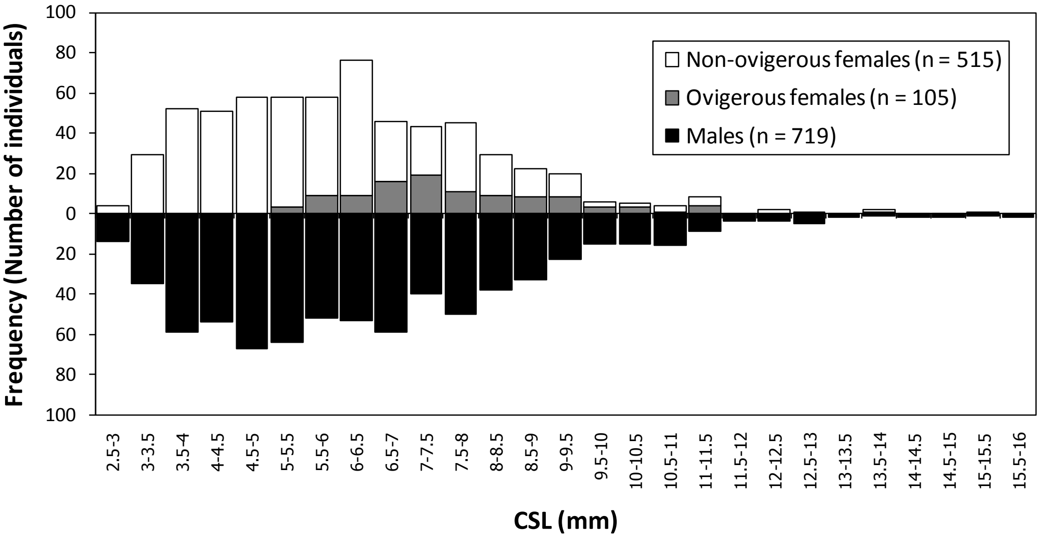


Figure 4.7 Overall size frequency distribution based on the cephalothoracic shield length (CSL) of *Coenobita rugosus.* Data are from the 1,339 individuals of *Coenobita rugosus* sampled over the study period.

When the yearly size (CSL) frequency distribution of all *C. rugosus* sampled during the study period (Table 4.6) was plotted (Figure 4.7), 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

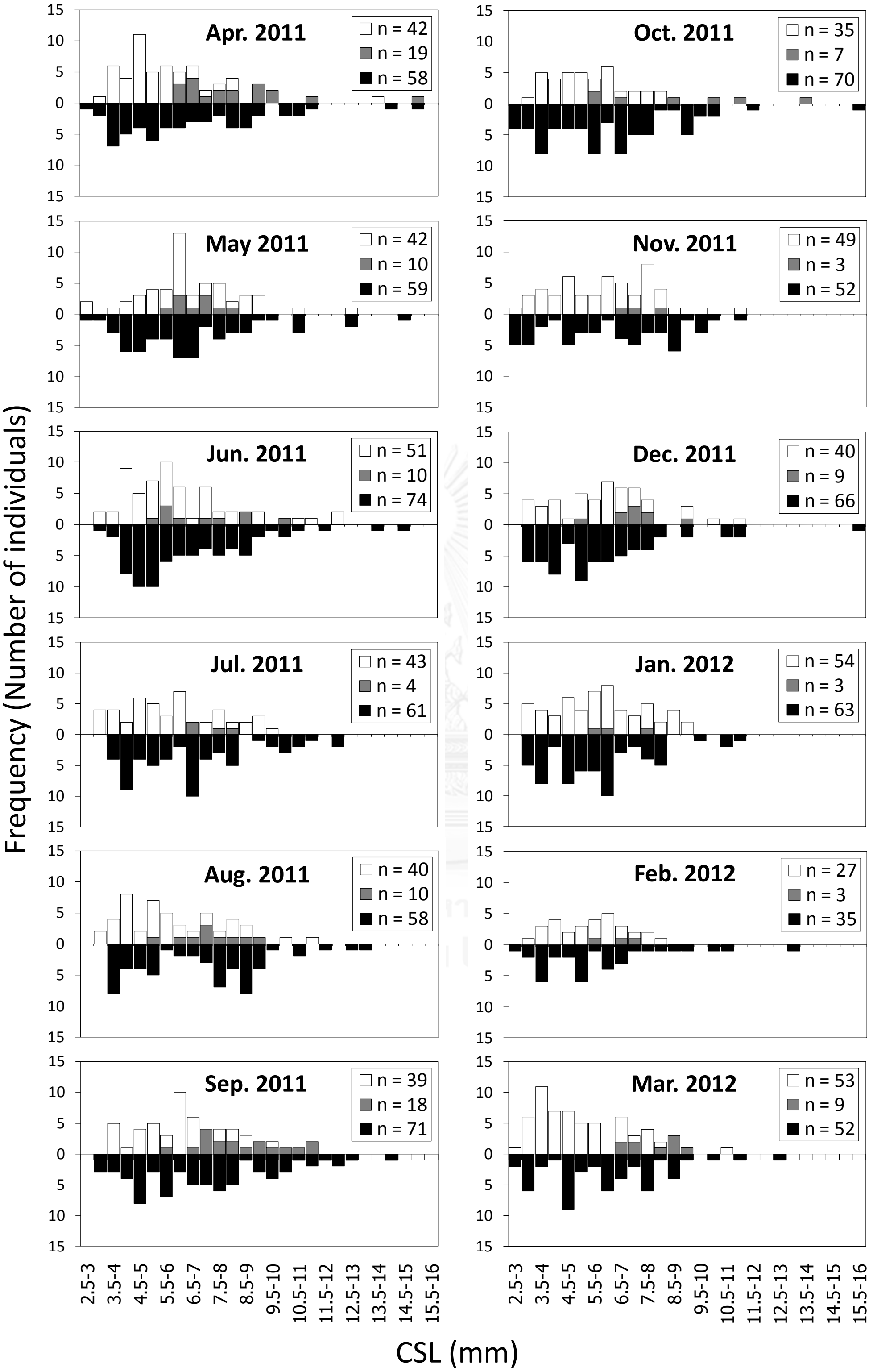


Figure 4.8 Monthly size frequency distribution of *Coenobita rugosus*.

☐ = Non-ovigerous females; ▨ = Ovigerous females; ■ = Males.

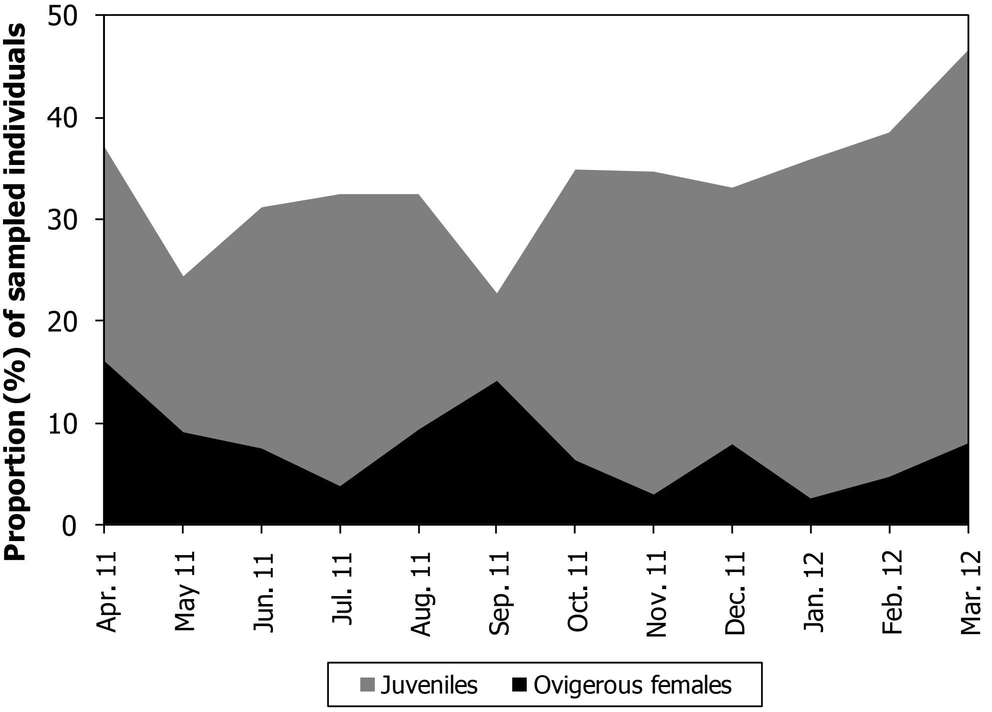


Figure 4.9 The relative proportion (%) of juvenile and ovigerous female *Coenobita rugosus*. Data are from the 446 juvenile (both male and female with CSL smaller than 5.06 mm) and 105 ovigerous female (CSL larger than or equal to 5.06 mm) *Coenobita rugosus*, sampled over the study period.

ovigerous females (Kolmogorov-Smirnov test, $K = 1.163$, $p = 0.133$). 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 4.8.

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 4.9) 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 4.8).

4.3.2 Population density

The average density of *C. rugosus* between April 2011 to March 2012 was 6.98 ± 0.36 crabs/m^2, whilst the monthly density ranged from 4.06 ± 3.94 (February 2012) to 8.44 ± 4.34 crabs/m^2 (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 (air temperature, seawater salinity, relative humidity and rainfall amount) were not significant (Spearman's rank-order correlation, $p > 0.05$) (Figure 4.10).

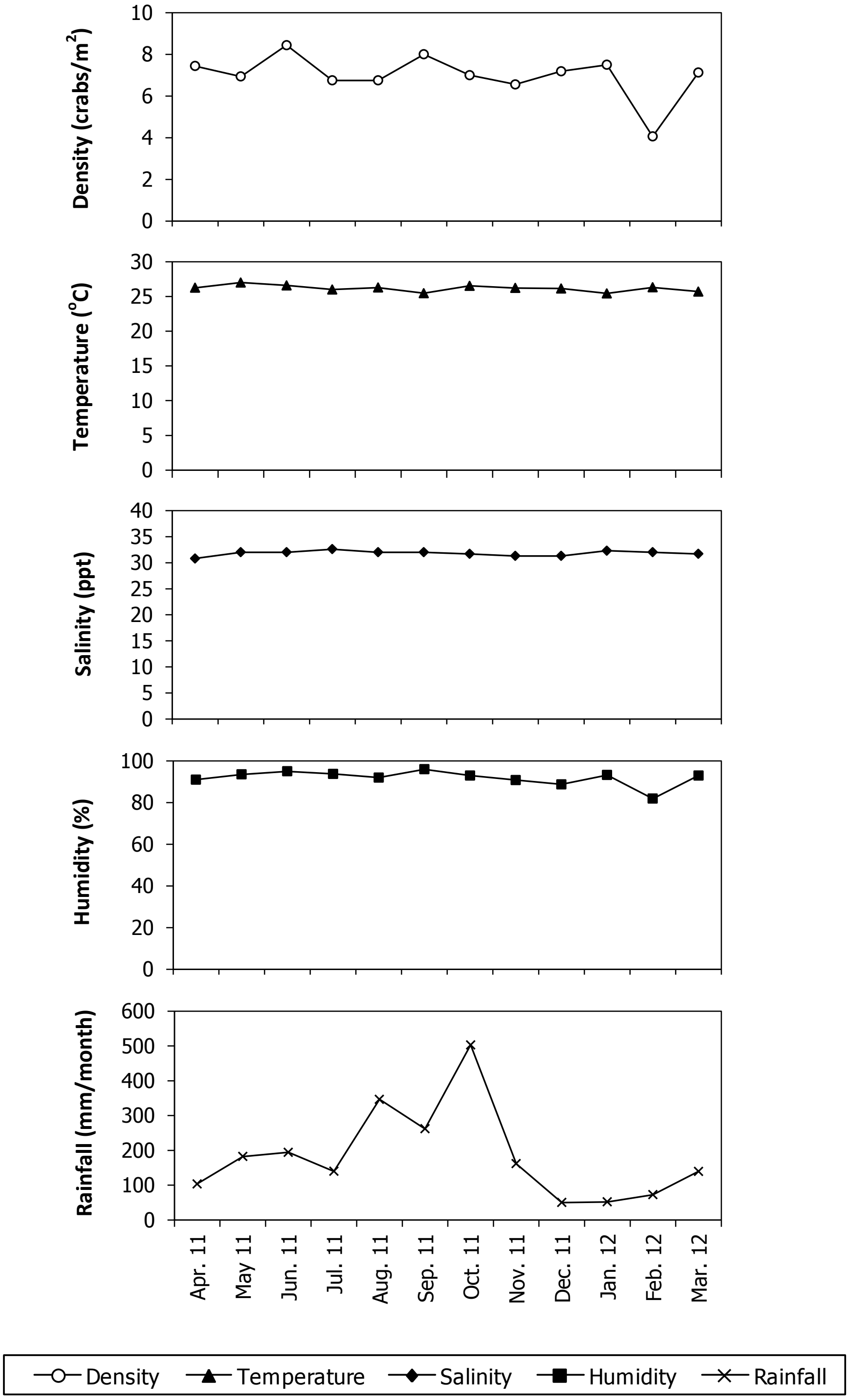


Figure 4.10 Average population density of *Coenobita rugosus* and various environmental factors.

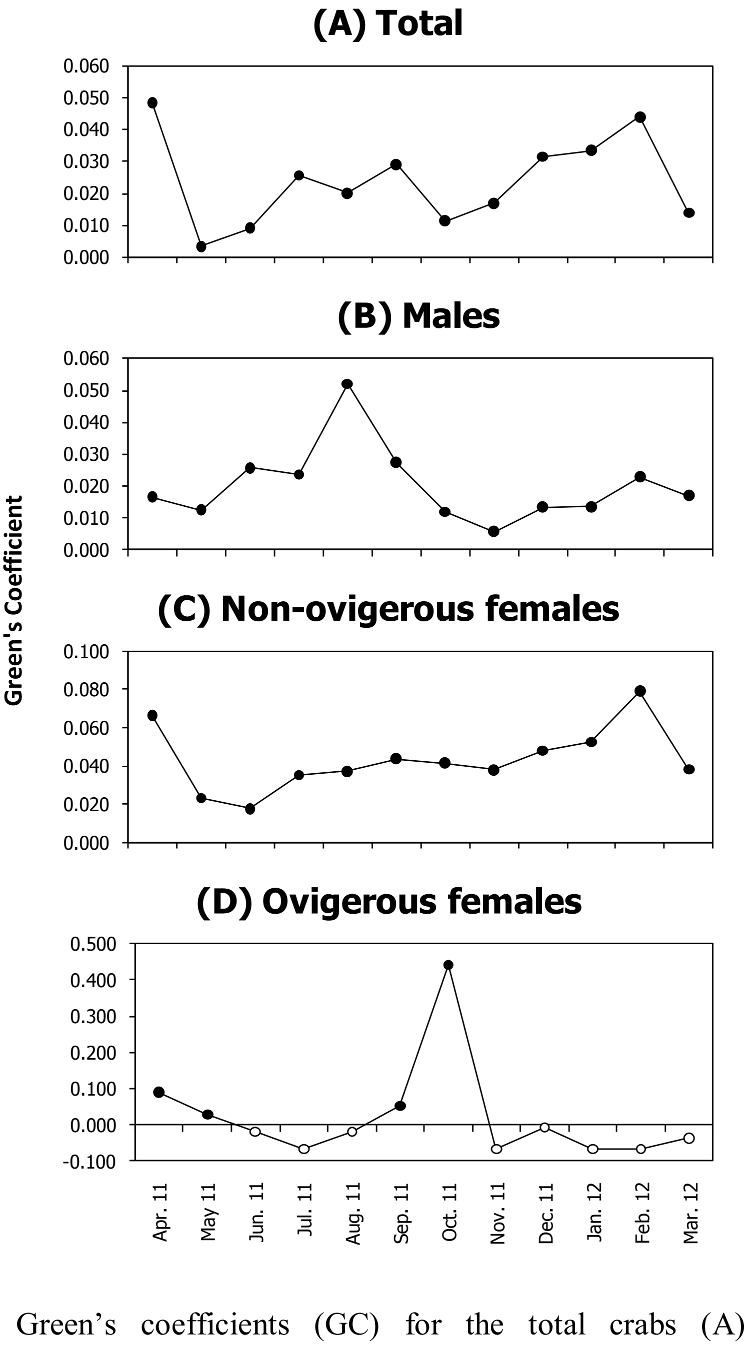


Figure 4.11 Green's coefficients (GC) for the total crabs (A), males (B), non-ovigerous females (C), and ovigerous females (D) of *Coenobita rugosus* sampled over the study period.

4.3.3 Dispersion

The GC values were calculated to reveal any potential dispersion patterns in *C. rugosus* at the study site, and are shown in Figure 4.11. 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).

4.3.4 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 4.7). 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 4.12). Nevertheless, the 2.5–3.0 mm and the three size classes between 9.5–11.0 mm had male-biased sex ratios (χ^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 (χ^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).

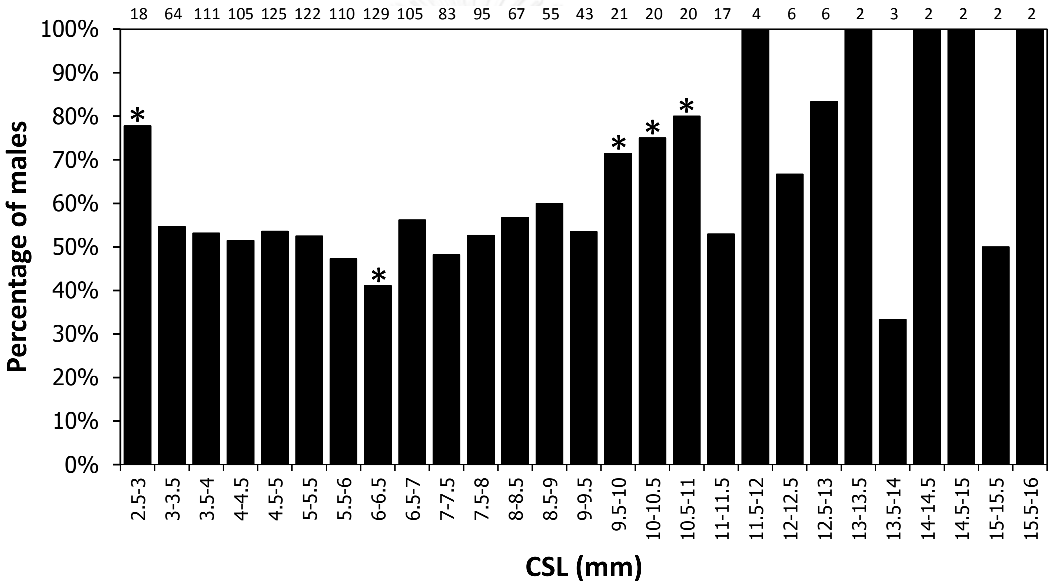


Figure 4.12 Sex ratio of *Coenobita rugosus*. The sex ratio is shown as the percentage of males based on the CSL size. * = Significant ($p < 0.05$) deviation from the expected 1:1 sex ratio. Value above each column is the total number of individuals in each size class.

4.3.5 Diet

During the observation of this study, 16 species of plants and three species of animal carcass were observed being consumed by *C. rugosus* (Table 4.8).

Table 4.8 List of foods eaten by *Coenobita rugosus* at Cape Panwa, Phuket Province, Thailand from April 2011 to March 2012.

Species	**Family**	**Thai name**	**Parts of food eaten***
Acacia auriculaeformis A. Cunn. ex Benth.	Leguminosae	กระถินณรงค์	Leaves (D)
Clerodendrum inerme (L.) Gaertn.	Lamiaceae	สำมะงา	Flowers (F, D), leaves (D)
Cordia subcordata Lam.	Boraginaceae	หมันทะเล	Flowers (F, D), leaves (D)
Derris scandens (Roxb.) Benth.	Leguminosae	เถาวัลย์เปรียง	Flowers (F, D)
Diospyros sp.	Ebenaceae	-	Fruits (D)
Enhalus acoroides (L.f.) Royle	Hydrocharitaceae	หญ้าทะเล อำพันแดง	Leaves (D)
Guettarda speciosa L.	Rubiaceae	โกงกางหูช้าง	Flowers (F, D), leaves (D)
Ipomoea violacea L.	Convolvulaceae	ผักบุ้งขัน ผักบุ้งทราย	Flowers (F, D), leaves (D)
Lagerstroemia sp.	Lythraceae	-	Flowers (F, D), leaves (D)
Lantana camara L.	Verbenaceae	ผกากรอง	Leaves (D)

Table 4.8 (continued)

Species	**Family**	**Thai name**	**Parts of food eaten***
Ruellia tuberosa L.	Acanthaceae	ต้อยติ่ง	Flowers (F, D), leaves (D)
Secamone elliptica R.Br.	Asclepiadaceae	เถาผักเลี้ยง	Leaves (D)
Stachytarpheta jamaicensis (L.) Vahl	Verbenaceae	พันงูเขียว	Leaves (D)
Thespesia populnea (L.) Soland. ex Corr.	Malvaceae	โพทะเล	Leaves (D)
Uraria crinita (L.) Desv. ex DC.	Leguminosae	หางหมาจอก	Leaves (D)
Wedelia prostata Hemsl.	Asteraceae	เบญจมาศน้ำเค็ม	Leaves (D)
Coenobita rugosus H. Milne Edwards	Coenobitidae	ปูเสฉวนบก	Carcass (cannibalism)
Grapsus albolineatus Latreille	Grapsidae	ปูแสมแกละ	Decaying articulations between segments of pereopods
Thalamita sp.	Portunidae	ปูกะตอย	Decaying articulations between segments of pereopods

* F = fresh and D = decaying

Decomposed leaves and fresh and decomposed flowers were the most common food 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* was also recorded, in terms of the consumption of a shell-less *C. rugosus* carcass (11.06 mm CSL adult male with a damage and slightly decomposed abdomen).

4.3.6 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 4.13).

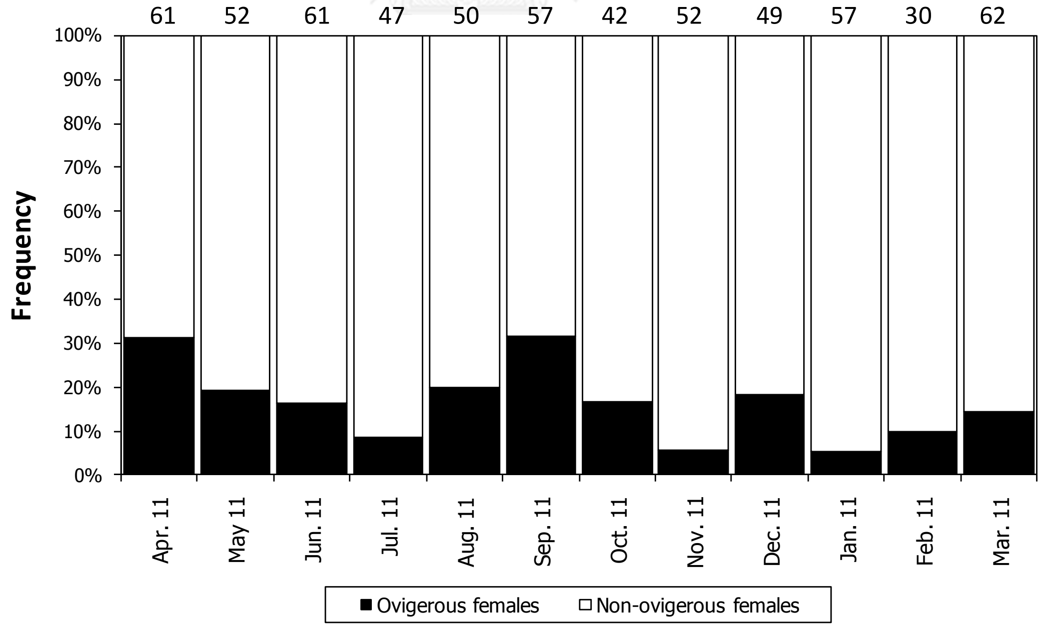


Figure 4.13 Proportion (%) of non-ovigerous and ovigerous female *Coenobita rugosus*. Data cover the sampling period. Value above each column is the total number of individuals sampled in that month.

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 4.14), 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.

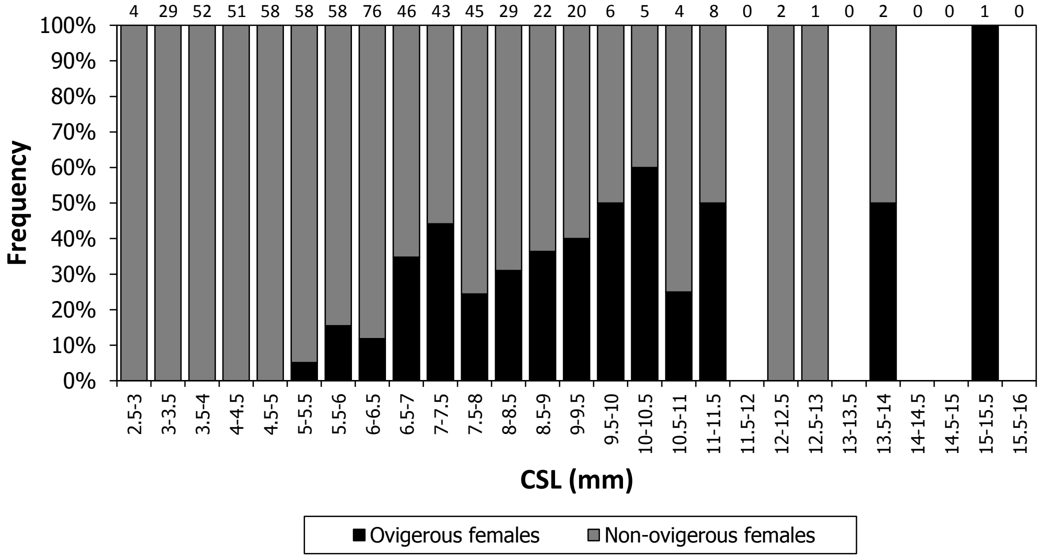


Figure 4.14 Size-dependent proportion of non-ovigerous female and ovigerous female *Coenobita rugosus*. Crab size classes are shown in terms of the CSL. Value above each column is the total number of individuals in that size class.

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

CHAPTER 5

DISCUSSION

5.1 Shell utilization of *Coenobita rugosus*

5.1.1 Shell utilization of *Coenobita rugosus* in natural habitat

At Cape Panwa, Phuket Province, 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 greatest shell diversity used by this population at the study site compared with other land hermit crab species and populations. Last but not least, the first record on bivalve shell used by land hermit crab was noted.

The shell use pattern of *C. rugosus* at Cape Panwa is possibly influenced by interactions with other hermit crabs in the natural habitats at the study site. Interspecific competition on shell resource normally occurs both with species in the same or different genus of hermit crabs (Hazlett 1981; Abrams 1987; Imazu & Asakura 1994). This situation may occur in the natural habitat of *C. rugosus* and congeneric species at the study site. *Coenobita rugosus* was found sympatrically with *C. violascens* and *C. brevimanus*. Fifteen shell species were utilized by both *C. rugosus* and *C. violascens*, whereas two shell species were used by both *C. rugosus* and *C. brevimanus* (unpublished data). Furthermore, shell resource partitioning between marine hermit crabs and *C. rugosus* might occur at the study site. Two marine hermit crabs, *Clibanarius virescens* and *Cl. merguiensis,* were encountered in the rocky pools in the intertidal area near the sampling site. These marine hermit crabs occupied some shell species as *C. rugosus* also used (unpublished data). Consequently, these phenomena may affect the shell utilization of *C. rugosus*. However, the degree of shell resource competition and allocation between *C. rugosus* and other hermit crabs at the study site is currently unknown. Further investigations on shell and other resources used by other hermit crab species at this site are required to understand these interactions.

5.1.1.1 Diversity and groups of shells used

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 shell species) by Abrams (1978); *C. compressus* (11 shell species) by Guillen and Osorno (1993); *C. clypeatus* (4 shell species) by Walker (1994); *C. cavipes* (21 shell species) and *C. rugosus* (20 shell species) by Barnes (1999); *C. clypeatus* (14 shell species) by Morrison and Spiller (2006); *C. scaevola* (10 shell species) by Sallam *et al.* (2008); *C. compressus* (41 shell species) by Laidre and Vermeij (2012)). Disparity of shell utilization pattern (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 probably influenced by gastropod life cycle, abiotic environmental factors, and pressure from predation (Sallam *et al.* 2008). Moreover, Andaman Coast of Thailand including Cape Panwa, Phuket Province has a high species number of gastropod molluscs (382 species) (Tantanasiriwong 1978) that probably supplies shell resources for hermit crab fauna living in this area.

The shells used by *C. rugosus* comprised both aquatically and terrestrially derived molluscan shells. The main composition of shells used by *C. rugosus* at the study site was marine gastropods as previously reported in other congeneric species (Abrams 1978; Willason & Page 1983; Boneka *et al.* 1995; Barnes 1999; Morrison & Spiller 2006; Sallam *et al.* 2008; Laidre & Vermeij 2012). Muricidae was the shell family with the highest number of species utilized by *C. rugosus*. It is probably because this family contains diverse and numerous marine molluscan species occurring in the Indo-Pacific region (Middelfart 1997). Neritidae and Turbinidae, which were mostly used by *C. rugosus* at the study site, are commonly used shell species by coenobitid crabs (Abrams 1978; Osorno *et al.* 1998; Barnes 1999; Sallam *et al.* 2008; Szabo 2012). However, one gastropod shell species, *Trochus maculatus*, was not used by *C. rugosus*. This result is similar to the previous investigation reported by Boneka *et al.* (1995) who pointed out that *Trochus* shells were probably rejected by this crab species because of its weight. Nevertheless, *Trochus* shells were occupied by marine hermit crabs (*Clibanarius virescens* and *Cl. merguiensis*) in rocky pools at Cape Panwa, Phuket Island (unpublished data).

The first record of the unusual occupation of a valve of marine bivalve by 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). *Coenobita rugosus* inhabiting a bivalve shell in this study possessed poor physical appearance with a short abdomen compared to the same sized crab (personal observation). This individual may be the defender (defined by Osorno *et al.* (1998)) whose shell is lost to the attacker crab during 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 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). Although shell availability was not evaluated, this different proportions of shell species occupied by *C. rugosus* may indicate active behavior in shell selection (Sallam *et al.* 2008). Three most used shell species by *C. rugosus* in this study were nerite shells. Other coenobitid species in many locations are also reported occupying nerite shell species as the most used shells over other kinds of shells (Abrams 1978; Guillen & Osorno 1993; Sallam *et al.* 2008; Laidre & Vermeij 2012). However, Boneka *et al.* (1995) reported that *C. rugosus* in Sulawesi, Indonesia occupied *Nassarius* shells as the most common used shell genus, and shells of *Nerita* was used only in small proportion without identification to specific levels of shells used. The disparity of shell use between these two populations of *C. rugosus* presumably reflects different types and size of shells used based on shell availability in each location (Ball 1972; Morrison & Spiller 2006).

5.1.1.2 Shell species used in relation to crab reproductive group

The shell utilization patterns of *C. rugosus* at the study site were different between sexes and among reproductive stages. This finding is similar to those of a previous study of *C. scaevola* (Sallam *et al.* 2008). In this study, the high number of shell species was used by both sexes, while some shell species were occupied only by males and other different shell species were used only by females. This result may be attributed to the fact that crab individuals of each sex and/or reproductive stage compete for shells and allot shell resources according to their appropriateness (Sallam *et al.* 2008). Furthermore, the discrepancy of shell use between sexes may result from intraspecific competition, behavior, reproductive strategies and different sizes (Imazu & Asakura 1994; Asakura 1995; Garcia & Mantelatto 2000).

There is a possibility that ovigerous female *C. rugosus* in the present study show selective greater tendency to select shells for use. These females used fewer shell species, and shell and aperture shapes than other crab groups. This result suggests that ovigerous females more specifically selected shells, probably due to their reproductive condition that requires more protection during the vulnerable egg-carrying period. 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).

Additionally, ovigerous females of *C. rugosus* in this study occupied only five categories of shell shapes. Some of the unused shell shapes, which were elongately conical and pyramidal shells, were high-spired shells that less occupied by *C. rugosus* as previously reported by Barnes (1999). This probably indicates that egg carrying females specifically select certain shell shapes for their most benefit. Interestingly, shells with elongately ovate aperture were unoccupied by ovigerous females. This is possible that egg carrying females living in elongately ovate-apertured shells are unable to seal the aperture completely when they retreat into the occupied shells. It may result in losing moisture inside shells that is important for vulnerable eggs (Wilde 1973). Moreover, 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).

5.1.1.3 Shell species used in relation to crab size

Differences in shell use among different sized crabs were noted in this population of *C. rugosus*. Small to medium crabs apparently used more diverse shell species than larger individuals. Large *C. rugosus* used fewer shell species than smaller individuals as previously recorded in other coenobitid crabs in different areas, including *C. scaevola* (Niggemann 1968), *C. compressus* (Abrams 1978) and *C. perlatus* (Willason & Page 1983). Interestingly, it is possible that *C. rugosus* at the study site utilized 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). Nevertheless, 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 and Spiller (2006) who pointed out that *C. clypeatus* probably uses the shells of two or three different gastropod species during their growth. 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.

5.1.1.4 Shells used in relation to shell and aperture shape

Coenobita rugosus showed occupation of certain types of shell 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 and 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 facilitate 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. *Coenobita rugosus* mostly occupied shells with round to circular and D-shape apertures probably because they enable the crabs to avoid desiccation by fully sealing the shell aperture with the major chela (Barnes 1999; Szabo 2012). Nevertheless, further studies on shell availability are needed to better understand shell choice in this hermit crab species.

5.1.1.5 Shells used in relation to shell damage

Although there was no significant discrepancy between utilization of damaged and undamaged shells by all individuals of *C. rugosus*, most shells occupied by crabs were in worn and old condition (unpublished data), which probably had been 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 and Okajima (1968), Ball (1972), Laidre (2012a) and Szabo (2012). Additionally, unoccupied shells in a good condition were scarce at the study site, as formerly reported (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 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 habitat may be required to test this hypothesis. Furthermore, damage of shells occupied by land hermit crabs may lead to vulnerability of desiccation and predation. The rate of water loss by evaporation probably increases in land hermit crabs inhabiting in damaged shells. The physical strength of damaged shells is possibly lower than that of undamaged shells. Thus, land hermit crabs occupying damaged shells might be vulnerable to predators that could crush the occupied shells easier to obtain crab bodies.

5.1.1.6 Shells used in relation to SIV/W ratio

The most occupied shell species by *C. rugosus* in this study, *Nerita albicilla*, was not the lightest species, which is in contrast to the energy saving hypothesis proposed by Osorno *et al.* (1998). It is possible that in fact crabs may try to search and occupy the lighter shells in each shell exchange for their appropriate adequacy. Consequently, crabs probably use the remaining shells, which are subsequently inferior to the lightest ones, with higher SIV/W ratio compared to their previously occupied shells. Further investigation of shell exchange in the natural habitat and shell selection in laboratory condition would help answer this question. In addition, the carrying of the lightest shell available, that of *Pomacea 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.

5.1.1.7 Relationship between crab and shell characteristics

The significant relationships were detected between characters of utilized shells and *C. rugosus* at the study area from both correlation and regression analyses, as previously reported by Boneka *et al.* (1995) and Sallam *et al.* (2008). The results appear to indicate that shell internal volume and aperture size are the main determinants of shell “selection” of *C. rugosus* at the study site. The intense degree of relationships 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, as appropriate microhabitat conditions, thereby resulting in more protection against predators and from desiccation (Ball 1972; Abrams 1978; Sanvicente-Anorve & Hermoso-Salazar 2011).

5.1.2 Shell preference in laboratory condition

C. rugosus showed species preference in shell selection in laboratory condition. Most of them preferred shell of *T. hippocastanum* over other shell species used in the experiment. This result confirms that *C. rugosus* performed an active selection behavior of shell preference and chose shells with larger shell dimensions (i.e. shell internal volume). This probably indicates that *C. rugosus* was optimizing the shell internal volume and resource partition occurred in the field mainly to ensure a good adequacy of individual’s size to shell availability (Floeter *et al.* 2000; Ismail 2010). The preference on larger shell dimensions was also reported in *C. compressus* (Abrams 1978; Osorno *et al.* 1998). Nevertheless, the significantly higher shell weight of preferred shells probably results from trade-off with the increasing of larger internal volume of newly occupied shells. However, the significantly higher SIV/W ratio of preferred shells by *C. rugosus* may suggest that crabs in natural habitat probably try to search and occupy the lighter shells in each shell exchange for their appropriate adequacy. Shell species preference between sexes of *C. rugosus* in laboratory condition was not different. This is probably explained by the insignificant difference in crab sizes used in the experiment although the disparity of shell utilization was evident in the quantitative study of this population in natural habitat.

With complete dissatisfaction rate shown by *C. rugosus* in the shell preference experiment, there is a possibility to infer that individuals of *C. rugosus* in natural habitat tend to and are promptly looking for shell exchange when there is an opportunity (Imafuku 1984). This probably implies that individuals of *C. rugosus* in natural population try to optimize their choices on shell resource availability for their own adequacy (Ismail 2010).

5.2 Population ecology of *Coenobita rugosus*

The characteristics of *C. rugosus* living at Cape Panwa, Phuket Province, 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.

5.2.1 Population structure and sexual dimorphism

Coenobita 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).

Furthermore, larger individuals tended to occur in smaller numbers compared with the intermediate and small size classes, which could reflect the rarity of suitable sized shells for larger crabs (Litulo 2005) and potentially also the vulnerability of larger sized individuals that are more easily detected by predators (Koga *et al.* 2010). The evidence for this hypothesis is possible that large unoccupied shells in sampling quadrats during the study period were found in low numbers and most were in poor or damaged condition, and the rough red-eyed crab, *Eriphia smithii*, a known predator of *C. rugosus*, was frequently found hiding in the supralittoral zone close to the sea level during crab sampling (personal observations).

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 erythrops* (Biagi & Mantelatto 2006) and *Loxopagurus loxochelis* (Mantelatto & Martinelli 2001). This sexual feature presumably infers that larger male crabs probably 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.

5.2.2 Population density

The density of *C. rugosus* did not significantly differ between 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 (6.98 ± 0.36 crabs/m^2), 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/m^2), which were evaluated by baited pitfall traps (Morrison & Spiller 2006). The inequality between these studies may reflect the different sampling methods, times and life histories as well as discrepancies between habitats of the two crab species.

5.2.3 Dispersion

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). *Coenobita 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 (Sallam *et al.* 2008), and therefore more difficult for researchers to detect.

5.2.4 Sex ratio

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).

5.2.5 Diet

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 this hypothesis.

Most individuals in this population seemingly relied on fallen and decomposed leaves and flowers as their foraging was mostly observed to be on plant items (personal observations). Fallen *Cordia subcordata* flowers as the most often consumed food item by *C. rugosus* in this study was similar to the results of Small and Thacker (1994) and Thacker (1994) where *C. compressus* in Panama commonly consumed fallen flowers of *Bombacopsis sessilis*. Most of the observed crabs' diet, and particularly the plants, were in a state of decay. Plant food items that are normally comprised of cellulose and hemicellulose are difficult for the crabs to digest. Furthermore, tannin in the vegetation may interrupt their digestion. The microbial flora and activity established in the decomposition process may diminish the amount of tannin in the plant structure prior to consumption by the crabs (Linton & Greenaway 2007). In addition, it is possible that some plants produce and accumulate certain toxic substances that might be harmful for crabs if consumed in a fresh form, whereas their decomposition may assist in breaking down these toxins, and so help the crabs avoid these hazards. 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 number of animal food items consumed by *C. rugosus* in this study was lower than that of plant food items. It is possible that animal carrion is more attractive to crabs and so crab individuals may prefer to consume this food items prior to plant food items. In the case of the consumed animal carcass, two marine brachyuran crabs were found on the strand line, whereas a naked *C. rugosus* carcass was found on coral rubbles on the seaward facing side in the supralittoral zone. Therefore, the removal of carrion by *C. rugosus* as diet at this site may help reduce or prevent colonization by flies (Page & Willason 1983). The carrion of the grapsid and portunid crab species had probably died in other places in the sea and then carried to the shore by wave action. 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. This corpse of *C. rugosus* may be the defender crab that was killed by the attacker crab during the shell exchange (Osorno *et al.* 1998). 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 and 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, and Laidre (2013) reported the conspecific consumption by *C. compressus* in natural condition at Osa Peninsula, Costa Rica. The cannibalistic behavior recorded in this study probably results from the high number of crab individuals in the population and resource competition among individuals. Besides, cannibalism may cause reductions in population size (Fox 1975), but this phenomenon was observed only one time for this population during the study period.

5.2.6 Reproduction

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 1983a). 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 1983b). 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 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*.

CHAPTER 6

CONCLUSION AND RECOMMENDATION

CONCLUSION

6.1 Shell utilization of *Coenobita rugosus*

The present study has portrayed the patterns of shell utilization by *Coenobita rugosus* at Cape Panwa, Phuket Province. In natural habitat, *C. rugosus* was found using 63 molluscan shell species in different percentages. The great shell diversity used by this population may infer plasticity on use of shell resources by *C. rugosus*. Interestingly, the first record of the bivalve shell use by land hermit crab was recorded in this study. *Coenobita rugosus* occupied the shells of 59 species of marine gastropods and only two species of freshwater gastropod and one species of terrestrial gastropod. The gastropod family with the highest number of species utilized by *C. rugosus* was Muricidae (17 species), followed by Neritidae (8 species) and Turbinidae (6 species). The most commonly occupied shell species by *C. rugosus* was *Nerita albicilla* (19.6 %).

Shell utilization patterns of *C. rugosus* varied in relation to crab sexes and reproductive stages. Male and female *C. rugosus* utilized the same number of shell species (53 species) with 43 species (81.1%) used by both sexes. Ten shell species were occupied only by males and ten other shell species were occupied only by females. Non-ovigerous females utilized more diverse shell species (51 species) than ovigerous females (22 species). There were significant differences in shell species occupation between crab sexes and among reproductive stages.

In addition, ovigerous females of *C. rugosus* in this study show selective greater tendency to select shells for use by occupying fewer shell species, and shell and aperture shapes than other crab groups. This probably suggests that ovigerous females more specifically selected shells, probably due to their reproductive condition that requires more protection during the vulnerable egg-carrying period.

Furthermore, shell utilization patterns of *C. rugosus* varied in relation to crab sizes. The diversity of shells used increased with increases in body size from small to medium sized crabs, but decreased in larger crabs. The three most-occupied shell species in the genus *Nerita* were inhabited by small to medium crabs (2.5–11.5 mm CSL). Most small crabs (2.5–6.5 mm) occupied shells of *Drupella. rugosa*. Shells used in the genus *Turbo* were inhabited by a wide range of size classes of crabs (3.5–16.0 mm). From the results of the present study, it is possible that *C. rugosus* at the study site used the shells of at least two different gastropod species as they grow.

Moreover, shell utilization patterns of *C. rugosus* varied in relation to shell and aperture shapes. Globose shells (53.9%) were the most used shell shape by *C. rugosus*. Males were found occupying more categories of shell shape (10 shapes) than non-ovigerous females (9 shapes) and ovigerous females (5 shapes). Shells with ovate apertures (75.0%) were most used by *C. rugosus*. 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 only four categories. There were significant differences in both shell and aperture shape occupation between crab sexes and among reproductive stages.

N. albicilla used by *C. rugosus* as the most used shell species was not the lightest shell species in relation to the ratio between internal volume and weight, which is in contrast to the energy saving hypothesis. The internal volume and aperture size of occupied shells were most positively correlated with characters of *C. rugosus* (i.e. cephalothoracic shield length and width, major chela length and width, crab weight). The results appear to indicate that these shell characteristics (i.e. internal volume and aperture length and width) are the main determinants of shell “selection” of *C. rugosus* at the study site.

In case of shell preference experiment in laboratory, both sexes of *C. rugosus* obviously preferred shells of *Thais hippocastanum* (84% of males and 92% of females). Both males and females of *C. rugosus* showed 100% of dissatisfaction rate with previously occupied shells of *N. albicilla*. Although the weight of preferred shells was significantly higher than that of original shells, the preferred shells had significantly larger internal volume and higher SIV/W ratio than the original shells. This result suggests that crabs in natural habitat may try to search and occupy the lighter shells in each shell exchange for their appropriate adequacy.

6.2 Population ecology of *Coenobita rugosus*

The current study has revealed the important aspects of the population ecology of *C. rugosus* at Cape Panwa, Phuket Province. Tendency of unimodality of size distributions was recorded for males, non-ovigerous females, and ovigerous females. The median CSL size of adult male *C. rugosus* was significantly larger than that of the adult females collected. In addition, the median size of adult males was significantly larger than that of adult non-ovigerous females, but not significantly different from that of ovigerous females. Ovigerous females were significantly larger than adult non-ovigerous females. Sexual size dimorphism was evident in relation to the larger size reached by males. Major chela length was determined quantitatively as a secondary sexual character (larger in males) for the first time in land hermit crabs. Continuous recruitment seems to occur throughout the year. The juveniles were found throughout the year and constituted 33.3% of the total crabs collected over the year.

The average density of *C. rugosus* during the study period was 6.98 ± 0.36 crabs/m^2, while the monthly density ranged from 4.06 ± 3.94 to 8.44 ± 4.34 crabs/m^2. There was no significant difference in density between sampling months that presumably reflects the almost constant environment in the study area. The relationships between crab density and the environmental factors (temperature, relative humidity, seawater salinity and rainfall amount) were not significant. 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 of *C. rugosus* was slightly male-biased (1:0.86 M:F). Nevertheless, the monthly sex ratios of *C. rugosus* sampled were close to the expected 1:1 ratio in all the months, except for in October 2011. The sex ratio in most size classes tended to be about 1:1 and was similar to a standard pattern described by Wenner (1972).

Individuals of *C. rugosus* were observed to consume 16 plant species, mostly decomposing leaves and flowers, but three species of animal carrion including one case of cannibalism were recorded. Fallen flowers of *Cordia subcordata* were found throughout the year and were the most frequently consumed food item by *C. rugosus*.

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 smallest ovigerous female sampled was 5.06 mm CSL and this was the potential minimum sexual maturity size as a morphological criterion to determine juvenile and adult stages. There was no significant relationship between the proportion of ovigerous females and the physical factors of temperature, relative humidity, seawater salinity and rainfall.

RECOMMENDATION

1. The information from this study provides comparative knowledge on shell use and population ecology of *Coenobita rugosus* and other land hermit crabs and can be used as fundamental knowledge for the conservation of these animals.

2. Shell availability at the study area should be investigated in the future study to better understand on shell choices of *C. rugosus* and other hermit crabs. Although the present study was partly carried out in relation to the preliminary survey of the diversity of living gastropod molluscs in rocky pools of intertidal zone adjacent to the natural habitat of *C. rugosus* at Cape Panwa, Phuket Province (Appendix B), gastropod fauna in other habitats (e.g. coral reefs in intertidal and subtidal areas, other habitats in subtidal zones) should also be investigated.

3. Shell damage as shell condition was examined in relation to shell use by *C. rugosus* was conducted in this study. Nevertheless, other aspects of shell condition (e.g. bioerosional effects of occupied shells) should be further investigated to provide better understanding in shell use by *C. rugosus* and other land hermit crabs.

4. Shell exchange as well as related behavior of *C. rugosus* in the natural habitat should be studied to portray the pattern of shell acquisition of this land hermit crab species and to compare with those of other coenobitid crabs in different areas. This information will be important for conservationists to consider before introducing new dedicated shells into the natural habitats of hermit crabs.

5. Further experiments on shell preference by *C. rugosus* should be conducted to provide more information on shell choices of this coenobitid species in laboratory condition and to better understand on shell choices in the natural habitat.

6. Shell utilization by *C. rugosus* in the present study was investigated in order to understand resource use pattern by this species. Therefore, there should be further investigations on use patterns of other resources (e.g. habitat, food) as well as niches of this species to fulfill more understanding in life history of *C. rugosus*.

7. From the results of this study, *C. rugosus* need different types and sizes of shells to complete their life cycle. Thus, the conservation of shell diversity is required to preserve this hermit crab species. Consequently, the rate of anthropogenic overexploitation of molluscan shells, specifically gastropod species, should be decreased and controlled. Tourists should not collect gastropod shells on the beaches in order to keep these shells as homes for hermit crabs. The trades on shell collection should be controlled. In addition, the introduction of empty shells from dedication

into the natural habitats for hermit crabs by conservationists should be considered according to the information from researches on shells used by indigenous hermit crabs to avoid possibly negative effects on their populations.

8. The diversity of diets of *C. rugosus* was investigated in the present study. Nevertheless, there should be further examinations on quantitative study on diet preference and foraging behavior of *C. rugosus* to better understand in its role as generalist scavengers in coastal and insular ecosystems.

9. Further studies on reproductive behavior, fecundity, egg and larval development of *C. rugosus* should be carried out to fulfill knowledge on reproduction and recruitment of this species.

10. Several characters of the population of *C. rugosus* at Cape Panwa, Phuket Province were investigated in this study. However, other characters of the population should be further studied (e.g. color morph). The additional information will be important knowledge to more understand in adaptive mechanisms of establishment of this species in tropical habitat.

11. From the results of the present study, *C. rugosus* relies on vegetation in the natural habitat in supralittoral zone as their shelters and food resources. Therefore, the conservation of coastal habitats, specifically for the supralittoral area and its vegetation, as well as the management and controlling of the extensive tourism are primarily needed for the preservation of these crabs.

12. Land hermit crabs, including *C. rugosus*, have been caught to sell as pet animals, resulting in the decrease of their number in natural habitats. Therefore, the

trades on these crabs should be controlled. In addition, tourists should not collect these hermit crabs in natural habitats.

13. Shell utilization and population ecology should be studied in different populations of *C. rugosus* in other locations as well as other congeneric species to fulfill better understanding in life history of this animal group.

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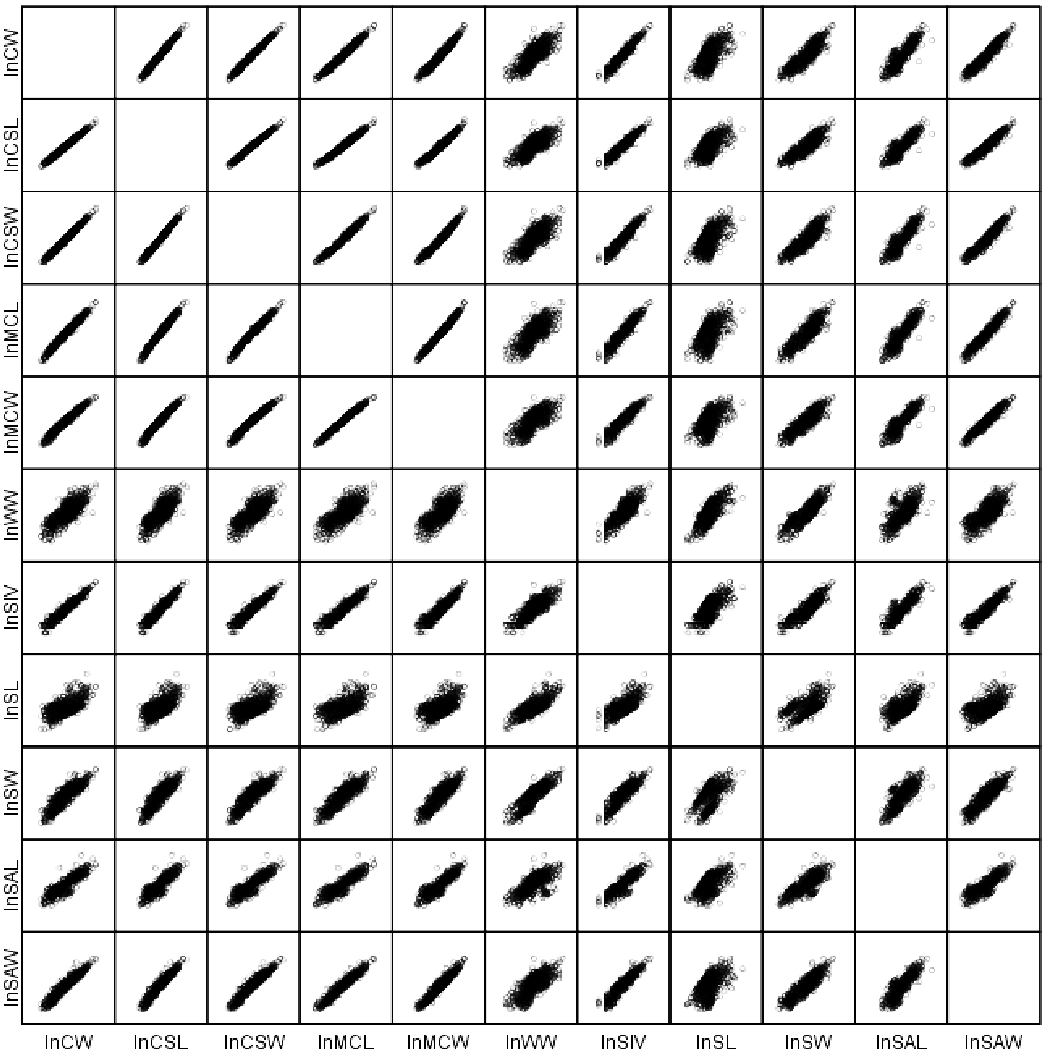
APPENDIX

Appendix A

Scatter plot matrix between transformed values of characters of hermit crab *Coenobita rugosus* and the inhabited shells sampled. 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.



Appendix B

The list of living gastropod molluscan species in rocky pools of intertidal zone adjacent to the natural habitat of *Coenobita rugosus* at Cape Panwa, Phuket Province from April 2011 to March 2012.

Family	**Scientific name**
Cerithiidae	*Clypeomorus batillariaeformis* Habe & Kosuge, 1966
Littorinidae	*Littorina scabra* (Linnaeus, 1758)
Muricidae	*Thais hippocastanum* (Linnaeus, 1758)
Neritidae	*Nerita albicilla* Linnaeus, 1758
	Nerita chamaeleon Linnaeus, 1758
	Nerita polita Linnaeus, 1758
Turbinidae	*Turbo cinereus* Born, 1778

VITA

Mr. Thanakhom Bundhitwongrut was born on February 11, 1974 in Bangkok. He graduated in bachelor degree of Fisheries from Faculty of Fisheries, Kasetsart University in 1995. During his undergraduate study between 1993 and 1994, he was granted the Scholarship for Outstanding Award on Educational Excellence. From 1995 to 1996, he worked at Biological Resources Section, Natural Resources and Environmental Management Division, Office of Environmental Policy and Planning, Ministry of Science, Technology and Environment. Between 1996 and 1997, he worked for Aquatic Animal Examining Section at Don Muang Airport Terminal, Fisheries Resources Conservation Division, Department of Fisheries, Ministry of Agriculture and Cooperatives. From 1997 to 1999, he worked at Natural History Research Division, Ecology and Environmental Center, Natural History Museum, National Science Museum, Ministry of Science, Technology, and Environment. He obtained his master degree in Zoology from Department of Biology, Faculty of Science, Chulalongkorn University in 2001. His master research was partly financially supported by Biodiversity Research and Training Program (BRT T_144017). Prof. Dr. Tab Nilanidhi Foundation granted the Outstanding Award on MSc. (Zoology) Course of Chulalongkorn University for him in 2002. After pursuing his master degree, he worked for Crustacean Section, Natural History Research Division, Ecology and Environmental Center, Natural History Museum, National Science Museum, Ministry of Science and Technology between 2002 and 2003. Since 2003, he has worked at Department of Aquaculture, Faculty of Fisheries, Kasetsart University as a permanent lecturer. During working at the university, he was awarded the Outstanding Teaching Award of Faculty of Fisheries in 2005. He was allowed to take a leave of absence to pursue his doctoral degree in Biological Science Program, Department of Biology, Faculty of Science, Chulalongkorn University in 2009. His doctoral research project was financially supported by Thai Government Science and Technology Scholarship (NSTDA).