Reproductive Biology of Three Land Hermit Crabs (Decapoda: Anomura: Coenobitidae) in Okinawa, Japan[1]

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Abstract: Reproductive ecological research on three land hermit crabs, *Coenobita rugosus*, *C. purpureus*, and *C. cavipes*, was conducted in the southern part of Okinawa-jima island in 1985, 1986, 1987, and for a short period in 1999. Size (carapace length) of the smallest ovigerous female was 3.93 mm for *C. rugosus*, 3.83 mm for *C. purpureus*, and 9.49 mm for *C. cavipes*. Breeding season is late May to November for *C. rugosus*, late May to mid-September for *C. purpureus*, and mid-May to late August for *C. cavipes*. Some females of all three species probably produced at least two broods during the breeding season. The smallest males in which spermatophores were present in dissected vas deferens were 4.24 mm for *C. rugosus* and 4.94 mm for *C. purpureus*. *Coenobita cavipes* females produced more, smaller eggs in comparison with *C. purpureus*. My observations suggest that coenobitid crabs living in areas with a low supply of shells or with poor shells reproduce at smaller sizes, as is the case in marine hermit crabs. Time of onset of larval release by *C. rugosus*, with its protracted breeding season, varied according to the seasonal shift in time of sunset. The period during which females of *C. rugosus* released larvae was about 2 hr in spring tides but was much longer (3 to 5 hr) during neap tides. Larger females of *C. purpureus* occupied shells derived from the land snail *Achatina fulica;* smaller ones used shells from the marine snail *Lunella granulata*. Use of mutually exclusive larval release sites by the larger and smaller females of *C. purpureus* remained unchanged over 13 yr, from 1986 to 1999. This behavioral difference may be related to the differences in their habitats (i.e., inland versus shore) and to the route traveled by the larger crabs in reaching the sea from inland sites.

Six coenobitid crab species, *Coenobita violascens* Heller, *C. brevimanus* Dana, *C. perlatus* H. Milne Edwards, *C. cavipes* Stimpson, *C. purpureus* Stimpson, and *C. rugosus* H. Milne Edwards, have been reported from the Ryukyu Islands, Japan. Of these, *C. violascens*, *C. brevimanus*, and *C. perlatus* are restricted to the southern Ryukyus, including Ishigaki-jima Island and Iriomote-jima Island (Nakasone 1988*a*). Three species are widely distributed on the islands of Okinawa Prefecture, namely the small species *Coenobita rugosus* and the larger species, *C. purpureus* and *C. cavipes*. *Coenobita rugosus* usually inhabits the shore, whereas *C. purpureus* and *C. cavipes* both live from the shore to 600 m or more inland. Small individuals of *C. purpureus* are commonly found at the shore, but the larger ones are less common there. Both *C. rugosus* and small *C. purpureus* occur sympatrically on most islands of the Ryukyus, but little work has been done on their ecology because of the confusion of their taxonomy.

It is well known that land hermit crab females migrate to the shore to release their larvae in the sea, but ecological information on their reproduction is scanty or fragmentary for the coenobitid species (Yamaguchi 1938, Degener and Gillaspy 1955, Vogel and

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Kent 1971, Ball 1972, De Wilde 1973, Page and Willason 1982, Wolcott 1988, Brodie 1999).

In Japan, coenobitid crabs have been used as pets for children, having been introduced to the mainland from the Bonin Islands. Because of their endangerment in the Bonin Islands, all coenobitid crabs in Japan were recognized as a natural monument on 12 November 1970, to promote their conservation. This study was carried out to obtain ecological data for conservation under the permission of the Agency for Culture Affairs, Ministry of Education, Science, Sports, and Culture of Japan.

Extensive observations on the reproductive behavioral ecology of *C. cavipes*, *C. purpureus*, and *C. rugosus* have been made in the southern part of Okinawa during the course of ecological and distributional studies of land hermit crabs in Okinawa Prefecture. The purpose of this paper is to clarify the following aspects of these three species: (1) population structure and breeding season; (2) changes in time at onset of larval release and seasonal changes in the number of larval release females (i.e., females with eggs ready to be released); (3) body size at sexual maturity; and (4) egg size.

MATERIALS AND METHODS

Monthly samples were taken on the shore of Hyakuna and Shimoda, located on the east side of Tamagusuku village; the southern part of Okinawa-jima island; and on the shore of Kudaka-jima island about 5.3 km distant from the coast of Azama, Chinen Cape. The monthly samples were acquired during the periods December 1985 to November 1986 and April to November 1987, using two pitfall traps (21 by 13.5 by 14 cm) buried to the same level as the substratum. Chicken feed (ca. 80 g) was put in each trap to attract the hermit crabs. The traps were set by 1800 hours at the same site every month, and the crabs trapped were gathered not later than 0830 hours the next day. These traps were set twice a month, in the first part and the latter part of each month. They were placed in vegetation communities that included *Hibiscus tiliaceus* L., *Ipomoea pes-caprae* (L.) Br. subsp. *brasiliensis* (L.) Ooststr., *Scaevola taccada* (Gaertn.) Roxb., *Argusia argentea* (L. fil) G. Murata, and *Pandanus odoratissimus* L. fil, although the composition of the vegetation differed at individual sites. Because larger crabs were rarely caught in the pitfall traps, additional random sampling in the study area was done by hand. The specimens of *C. cavipes* examined for breeding season studies were provided by a pet trader who had permission from the Agency for Culture Affairs to collect land hermit crabs.

The sample specimens were all frozen for later examination. After thawing, the species of shells inhabited by the crabs were determined. The crabs were then removed by hand or forceps from their shells (the shell was cracked with a hammer if necessary), and the species and sex of the crabs were determined. Intact shells were returned to suitable habitat for potential reuse by other crabs. Carapace length (anterior calcified part) was measured to the nearest 0.01 mm with vernier calipers. All females and some males caught in 1987 were dissected to determine the presence of mature oocytes and spermatophores, respectively.

It was difficult to identify the species or sex of some crabs less than 2.50 mm in length, but for most specimens it was possible to determine species and sex by means of the existence of a black band or stripe on the lower surfaces of the eyestalks (see Nakasone 1988*a*) and gonopores on the coxae of the third pereiopods. The smaller individuals of *C. purpureus* lacked a black band, but those of *C. rugosus* generally had the black band. Adults of both species are easy to distinguish by color differences.

Egg sizes were determined based on ocular micrometer measurements of 10 non-eyed and 10 eyed eggs from individual pleopods of each sampled female. The sample for non-eyed eggs consisted of pleopods from five individuals of *C. rugosus* (body length 5.81–8.65 mm), seven of *C. purpureus* (body length 8.08–18.25 mm), and three of *C. cavipes* (body length 11.37–15.29 mm). Sizes of eyed eggs were determined from six individuals of *C. rugosus* (body length 6.82–12.58 mm), six of *C. purpureus* (body length 10.83–17.03 mm), and four of *C. cavipes* (body length 12.87–17.23 mm). The *t*-test and Welch's test (t') were used to analyze the data for differences in egg size (length) between species.

For the study of reproductive behavior, two sites on the Hyakuna coast at which larval release females (females with eggs ready to be released) were frequently seen were selected as study sites A and B. Observations were carried out at these sites to determine the time of larval release and the variation in number of larval release females of each species. Females returning from the shore after releasing their larvae were collected every 5 min at these sites. The species and numbers of females collected were recorded before release of the specimens. This procedure was repeated from sunset until larval release females became scarce. The sites were about 52 m apart, located about midway between the Shimoda and Hyakuna sampling areas. The survey at sites A and B was conducted by two or three persons with electric flashlights during the spring tide, semimonthly from early June through early December 1987. Additional work at sites A and B was done for a short period during the breeding season in 1999 to extend the observations of differential use of sites A and B by large and small females of *C. purpureus* females.

RESULTS

Population Size Structure

Ceonobita rugosus was much more abundant than *C. purpureus* at Hyakuna, but both species were abundant at Shimoda and Kudaka-jima. The size-frequency distributions of females of *C. rugosus* and *C. purpureus* from the Kudaka-jima populations are presented in Figures 1 and 2, respectively. The decline in number of individuals trapped during winter was due to the inactivity of the crabs. Both sexes of *C. rugosus* of 6–8 mm carapace length were found in large numbers throughout the year in the Shimoda and the Hyakuna populations. Individuals of both sexes less than 5 mm in length were most frequent from May to October at Kudaka-jima and from June to October at Hyakuna. The minimum size of ovigerous *C. rugosus* females was 4.77 mm at Hyakuna and 4.96 mm at Shimoda in 1986, and 5.32 mm at Hyakuna in 1987. The maximum size was 8.75 mm at Hyakuna and 9.20 mm at Shimoda in 1986, and 12.81 mm at Hyakuna in 1987. In the Kudaka-jima population of *C. rugosus* both sexes ranged mostly from 3 to 7 mm (for females see Figure 1). Ovigerous females were found from early June, although they may appear from late May as in the 1987 Hyakuna population samples. Ovigerous females ranged in size from 3.93 to 12.58 mm.

Because of the small sample size of *C. purpureus* from Hyakuna, those crabs were not included in the analysis of population structure. In the Shimoda population most individuals of both sexes ranged from 3 to 7 mm. Crabs less than 5 mm appeared mostly from April to October. Ovigerous females were 6.21–18.26 mm in length in the Hyakuna population and 6.20–15.95 mm long in the Shimoda population. The Kudaka-jima population of *C. purpureus* consisted mostly of males 4–6 mm long and females 3.5–7.0 mm long (Figure 2); ovigerous females were 3.83–17.29 mm long. Crabs less than 5 mm were found mostly from April to October.

Based on specimens of *C. cavipes* collected in 1986 and 1987 from Hyakuna, ovigerous females range from 9.49 to 19.14 mm in length. Sample sizes for this species were insufficient to warrant further analysis of the data.

Breeding Season

Ovigerous individuals of *C. rugosus* were found from 9 June to 27 November 1986, but were also observed from 27 May in the 1987 samples. Therefore, the breeding season ranges from at least late May to late November (Figure 3), but may vary from year to year. Most *C. rugosus* females were ovigerous from July to August. Of 45 nonovigerous females captured on 19 May 1987, 15 (33.3%) had mature oocytes. Ovigerous females (10.8%, 9 of 83) were first found in the samples on 27 May, of which five had eyed eggs.

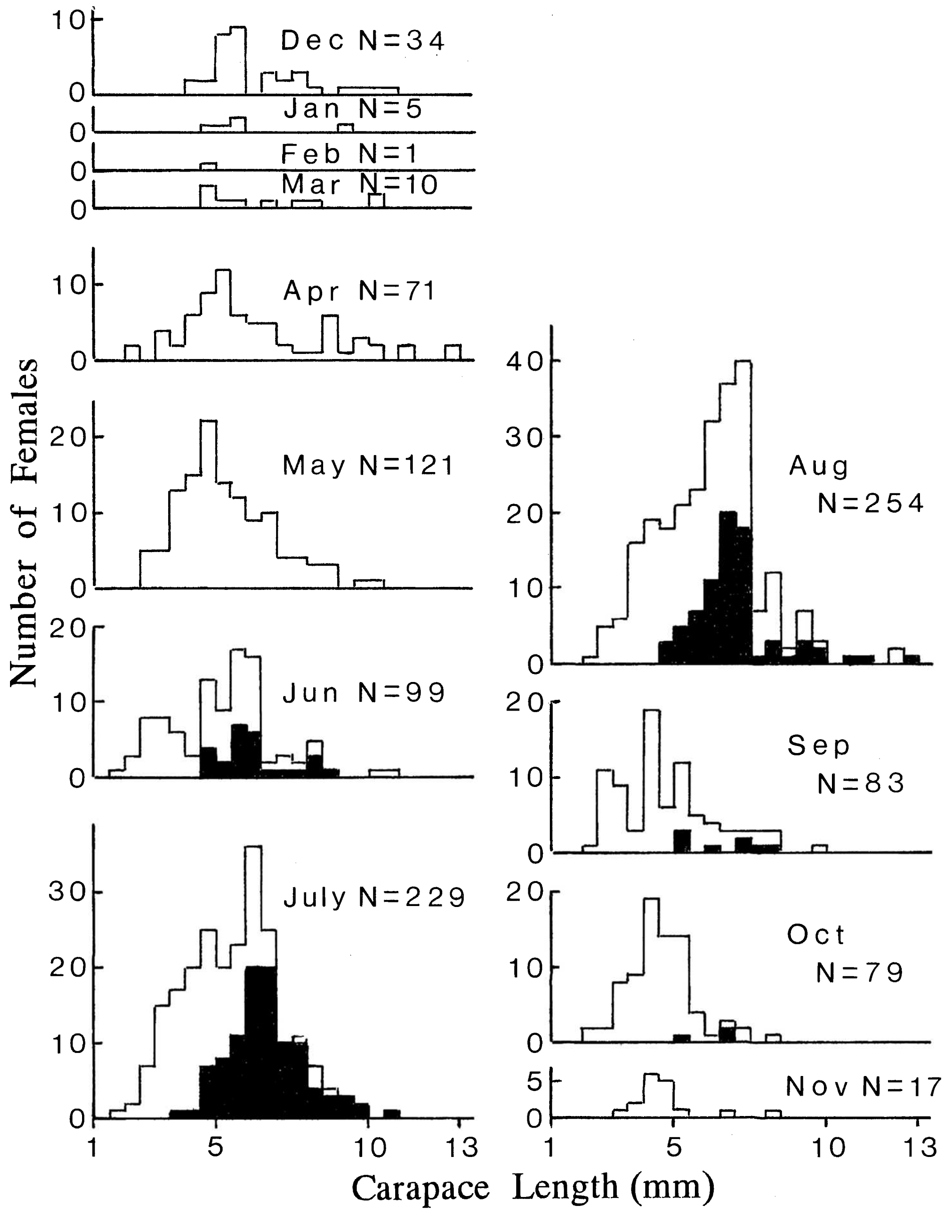

FIGURE 1. Size-frequency distribution of *C. rugosus* females sampled from December 1985 to November 1986 on Kudaka-jima Island; data for ovigerous females in black.

Of 65 females collected randomly at site B on 14 June, three had just released their larvae, as suggested by the presence of membranes from hatched zoeae still attached to the well-developed pleopodal hairs.

Ovigerous females of *C. purpureus* were found from 9 June to 16 September 1986 and from 27 May 1987 in the Shimoda population, and from 25 May 1986 in the Kudaka-jima population. Thus, the breeding season ranges from late May to mid-September (Figure 3). Although ovigerous females were

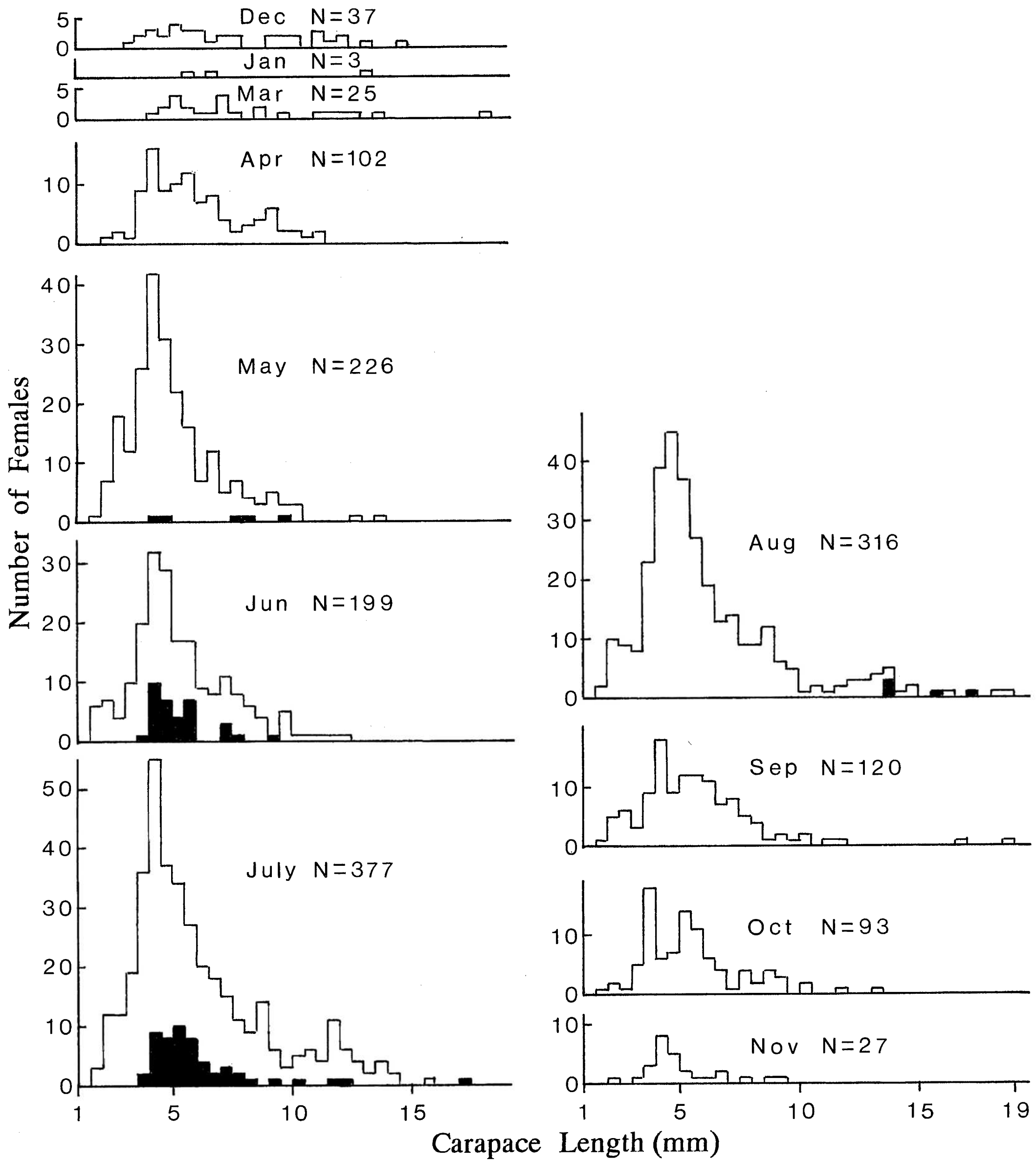

FIGURE 2. Size-frequency distribution of *C. purpureus* females sampled from December 1985 to November 1986 on Kudaka-jima Island; data for ovigerous females in black.

not found in the samples on 19 May, 10 of 45 (22.2%) sampled on 27 May were ovigerous, with non-eyed eggs. Females released their larvae at study sites A and B as shown in Figures 4 and 5.

In the samples of *C. cavipes* collected from the Hyakuna area and given to us by a pet trader, ovigerous females were found from 11 May to 2 August 1987. On 11 May, 3 of 34 (8.8%) of the females had non-eyed eggs, and

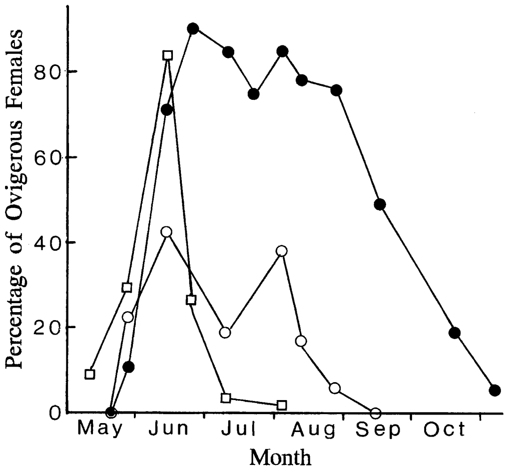

FIGURE 3. Percentage of ovigerous females of coenobitid crabs in monthly samples. Open squares, *C. cavipes;* open circles, *C. purpureus;* closed circles, *C. rugosus.*

on 27 May, 7 of 24 (29.7%) of the females had non-eyed eggs. Of 25 females sampled on 14 June, 21 (84%) had eyed eggs (Figure 3). At site A, two females on 14 June and 170 on 25 June released their larvae into the sea (Figure 4).

Locations and Timing of Larval Release

Larval release females approached the surf slowly. Some females actively entered the sea, but others waited on the sand or small rocks for the surf to reach them. They released their larvae into the water by extending and retracting a large portion of their body in and out of their shell. After releasing the zoeae, instead of turning around the females simply walked backward until they reached a spot with no wave action and then walked forward. This backward motion probably offers less resistance to the backwash compared with forward movement.

Females that released their larvae at coastal study sites A and B at Hyakuna were observed closely. Only the larger females of both *C. purpureus* (>9 mm, mostly >11.5 mm) and *C. cavipes* (9.49 to 18.89 mm, mostly >12 mm) released their larvae at site A (Figures 6 and 7, respectively). Site B, on the other hand, was used by females of *C. rugosus* (small species) and by mostly smaller females of *C. purpureus* (large species) for release of larvae, although a few large females (>11.5 mm) of both *C. purpureus* ($n = 3$) and *C. cavipes* ($n = 1$) also released larvae at site B. Thus, with few exceptions, larger and smaller females of *C. purpureus* compose two cohorts that utilize separate larval release sites. Most large females of *C. cavipes* released their larvae at site A. Both study sites were small, sandy beaches where wave action is moderately reduced by rocks and/or reefs. Large females of *C. purpureus* and *C. cavipes* at site A occupied shells derived from the land snail *Achatina fulica*, whereas smaller females of *C. purpureus* and females of *C. rugosus* at site B used shells from the marine snail *Lunella granulata*.

Larval release activities at sites A and B occurred from mid-June to late August 1987 or early September 1986 for *C. cavipes* and *C. purpureus*, and from late June to late October or even until late November (1986) for *C. rugosus* (Figures 4, 5). At site A the times of larval release by both *C. cavipes* and larger *C. purpureus* females ranged from about 1940 hours (after sunset) to 2130 hours in spring tides. At site B the times of larval release by smaller *C. purpureus* and *C. rugosus* ranged from about 1930 to 2130 hours during spring tide for the period mid-June to late August, after which site B was almost completely occupied by *C. rugosus*. The times of larval release by *C. rugosus* ranged from about 1930 to 2130 hours in late August and from about 1820 to 2030 hours in late October (Figure 5). Thus, the onset of larval release by *C. rugosus* females varied according to time of sunset. Larval release females were also numerous at mid- and neap tides. However, the periods during which larval release females were observed at neap tides were much longer (by about 2 hr) than at the spring and mid-tides (Figure 8). The changes in percentage of larval release females at sites A and B are illustrated in Figure 9. The larval release phase of all three species extended until at least early September, but at site A females of *C. cavipes* became dominant after 25 July, and at site B females of *C. rugosus* became dominant after 20 August.

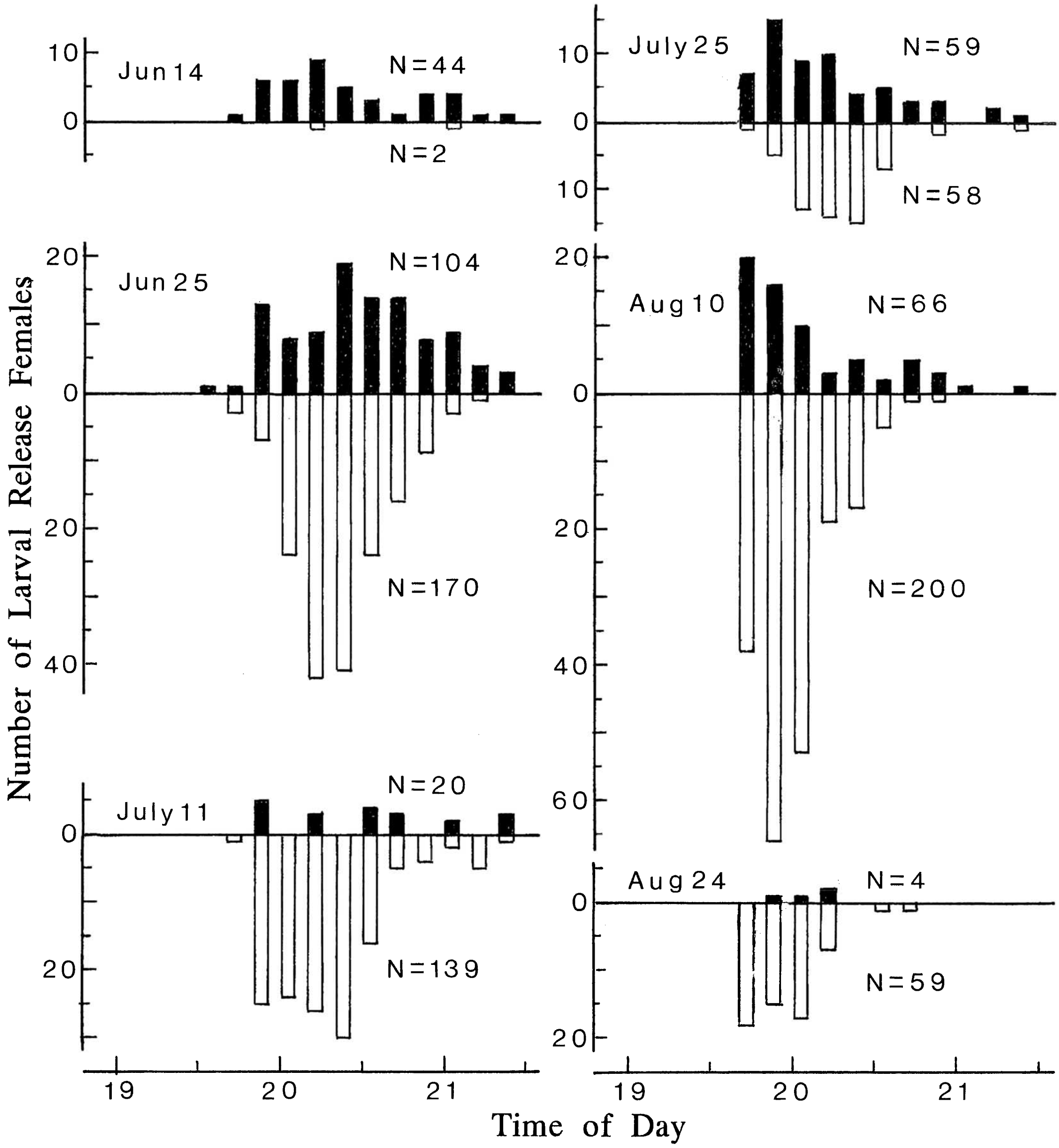

FIGURE 4. Variation in the number of larval release females with time of day and month of year at study site A during spring tides in 1987. Closed bars, *C. purpureus;* open bars, *C. cavipes.*

Body Size at Sexual Maturity and Number of Broods

Mature females were determined by the presence of embryos deposited on pleopods. The smallest individuals of *C. rugosus* and *C. purpureus* bearing eggs were 4.77 and 6.21 mm long, respectively, in the samples from Hyakuna, 4.96 and 6.20 mm from Shimoda, and 3.93 and 3.83 mm from Kudaka-jima. Thus, the smallest ovigerous females of both species on Kudaka-jima were smaller

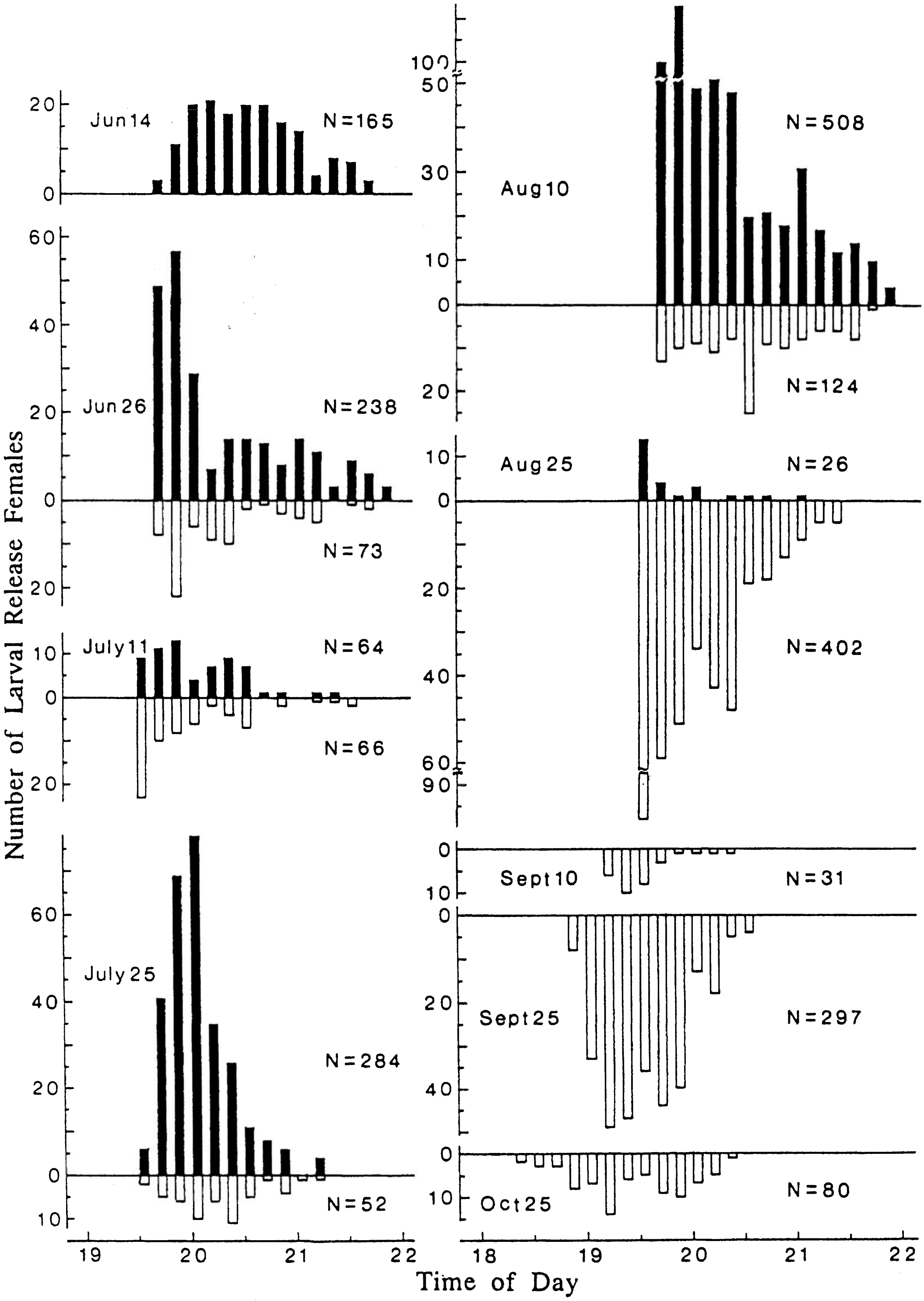

FIGURE 5. Variation in the number of larval release females with time of day and month of year at study site B during spring tides in 1987. Closed bars, *C. purpureus;* open bars, *C. rugosus.*

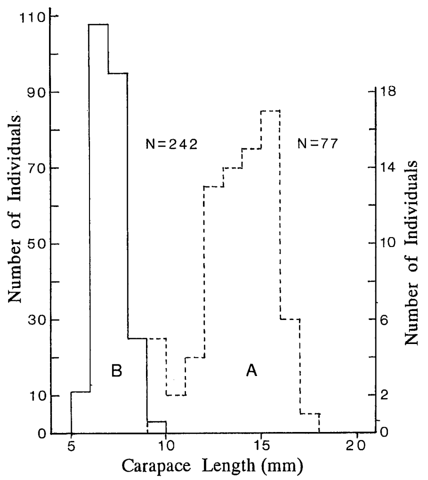

FIGURE 6. Size-frequency distribution of larval release females of *C. purpureus* at study sites A (broken lines, right y-axis) and B (solid lines, left y-axis).

than those at both Hyakuna and Shimoda. The smallest female *C. cavipes* releasing larvae at site A was 9.49 mm.

Mature males were determined by the presence of spermatophores in dissected vas deferens. The vas deferens was thick and large for the period from spring to autumn, but was thin and small in winter. However, in

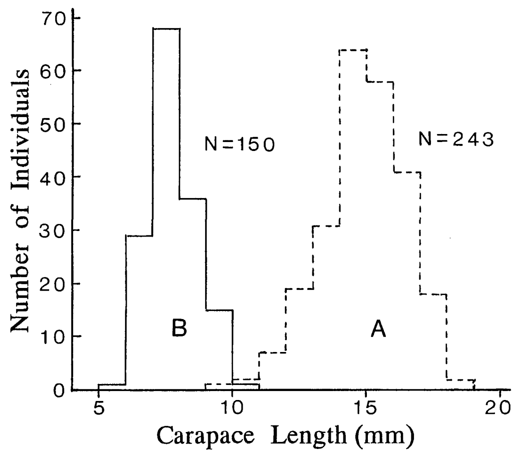

FIGURE 7. Size-frequency distribution of larval release females of *C. cavipes* at study site A (broken lines) and of *C. rugosus* at site B (solid lines).

winter the vas deferens contained spermatophores arranged in a band. In *C. rugosus*, the smallest male that had spermatophores was 4.24 mm long; in *C. purpureus* the smallest mature male was 4.94 mm.

Dissected females of all three species of crabs studied often had both brooded embryos and mature oocytes. The percentages of females with both embryos and oocytes varied throughout the reproductive season, but reached 15.8% in late June in *C. purpureus*, 28.6% in early June in *C. cavipes*, and 83.3% in late July in *C. rugosus*. Furthermore, of the crabs collected randomly after releasing larvae at sites A and B, the frequency of females with mature oocytes reached at least 80% at some time during the reproductive period of each species. Mature oocytes were found from early June to early October in *C. rugosus*, late June to late July in *C. purpureus*, and early June to late June in *C. cavipes*. These observations suggest that some females of all three species produce more than one brood during the breeding season.

Egg Size

The mean egg sizes on the first pleopod in each species are presented in Table 1. Data for the other pleopods are not presented because preliminary analysis and testing failed to reveal significant variation in egg size among pleopods of the same species. There were significant differences between species in the mean length of non-eyed eggs (*C. rugosus* versus *C. purpureus*: $t' = 76.395$, $df = 13$, $P < 0.001$; *C. rugosus* versus *C. cavipes*: $t' = 8.721$, $df = 14$, $P < 0.001$; *C. purpureus* versus *C. cavipes*: $t' = 7.539$, $df = 10$, $P < 0.001$), but there were no significant differences between species in the mean length of eyed eggs (*C. rugosus* versus *C. purpureus*: $t' = 2.051$, $df = 11$, $P > 0.05$; *C. rugosus* versus *C. cavipes*: $t = 0.411$, $df = 18$, $P > 0.05$; *C. purpureus* versus *C. cavipes*: $t' = 1.732$, $df = 12$, $P > 0.05$). Thus, when non-eyed eggs became eyed eggs they attained nearly the same size in all three species. There were no significant differences between non-eyed and eyed eggs in mean length in *C. purpureus* ($t = 1.444$, $df = 18$, $P > 0.05$), whereas there

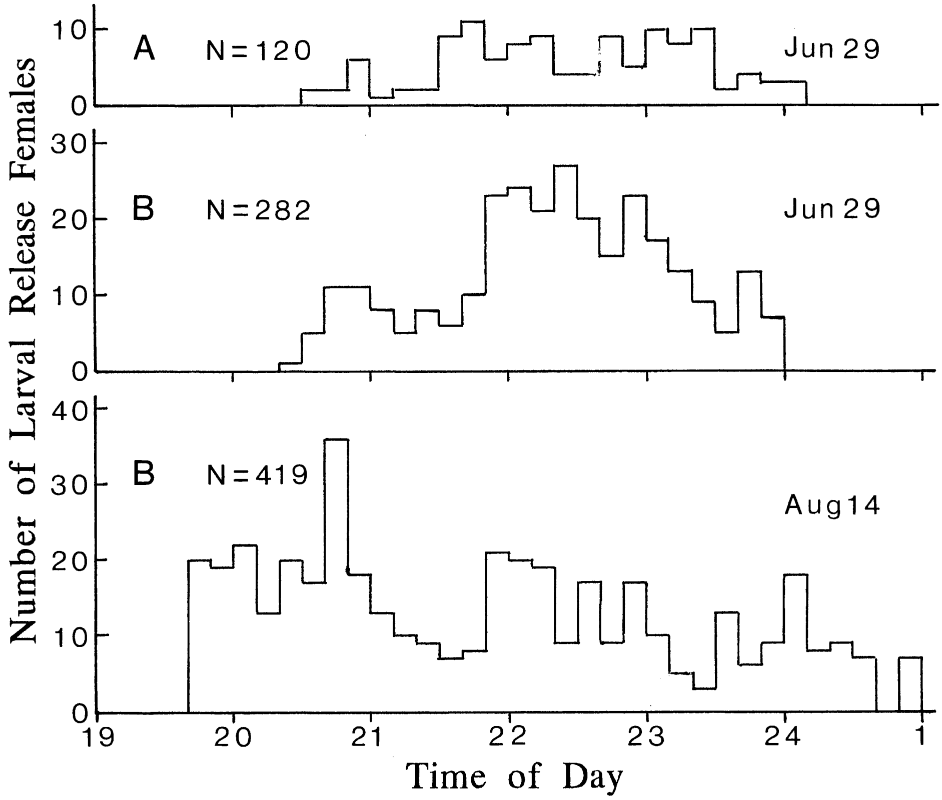

FIGURE 8. Variation in the number of larval release females of coenobitid crabs at study sites A and B during neap tides in 1986. *Top*, data for *C. cavipes* and *C. purpureus* at site A, pooled for 29 June; *middle*, data for *C. purpureus* and *C. rugosus* at site B, pooled for 29 June; *bottom*, data for *C. purpureus* and *C. rugosus* at site B, pooled for 14 August.

were significant differences between non-eyed and eyed eggs in mean length in *C. rugosus* ($t = 3.881$, $\mathrm{df} = 18$, $P < 0.002$) and *C. cavipes* ($t' = 12.324$, $\mathrm{df} = 12$, $P < 0.001$). The difference between length and width was larger in eyed eggs than in non-eyed eggs. Thus, the eggs tended to become longer and more slender in shape as their development progressed.

DISCUSSION

Considering both the chronology of larval release and the occurrence of ovigerous females, it appears that the basic breeding season is similar for *C. purpureus* and *C. cavipes* (i.e., from late May to late August), although ovigerous females of *C. purpureus* may be found into mid-September. By comparison, the breeding season of *C. rugosus* is somewhat longer, extending from late May to November.

Females of all three crab species in this study released their larvae directly into the seawater. However, according to De Wilde (1973), females of *C. clypeatus* do not enter the water; they drop or fling their eggs onto the wet rocks and the larvae are washed into the sea during high tide. Brodie (1999) showed that females of *C. compressus* release hatching larvae into the swash zone and the zoeal larvae are washed by the receding tide from the swash zone. Thus, it appears that the larval release behavior of *C. clypeatus* and *C. compressus* differs from that of the three species included in my study, but these dif-

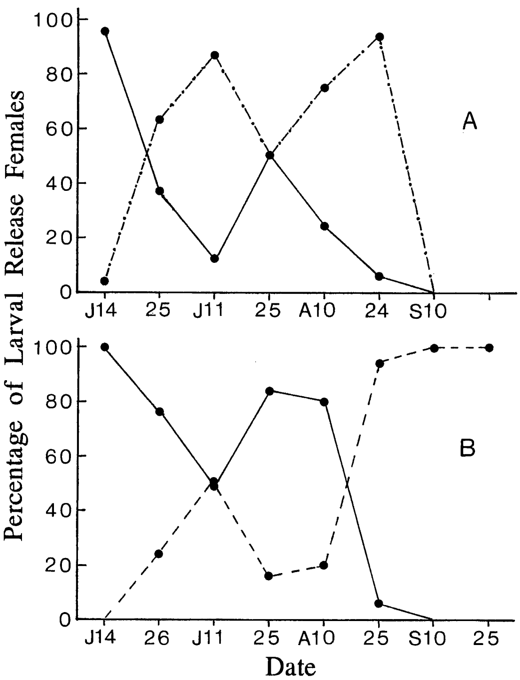

FIGURE 9. Seasonal variation in the number of larval release females of coenobitid crabs at study sites A and B. For study site A: solid line, *C. purpureus;* broken line, *C. cavipes;* for study site B: solid line, *C. purpureus;* broken line, *C. rugosus.*

ferences in behavior may be related to topographical differences at the larval release sites. Sites A and B of this study agree with the general observation that larval release sites are protected by rocks and/or reefs from wave action (Yamaguchi 1938).

All large females of both *C. cavipes* and *C. purpureus* observed at study site A occupied shells derived from the terrestrial snail *Achatina fulica.* Thus, it seems likely that they traveled from inland to site A to release their larvae. The use of different larval release sites by larger and smaller females of *C. purpureus* remained unchanged over 13 yr from 1986 to 1999; this may be related to the differences of inland and shore habitats, and to the route traveled by larger crabs from inland.

It was found that onset of larval release by *C. rugosus,* a species with a long breeding season, varied according to time of sunset (Figure 5). The period during which larval release females were observed was about 2 hr in spring tides, but was much longer (3 to 5 hr) during neap tides (Figure 8). Thus, it appears that the period of time during which larval release females are observed is related to tide level.

As described earlier, the smallest ovigerous females of *C. rugosus* and *C. purpureus* on Kudaka-jima (3.93 and 3.83 mm, respectively) were smaller than those at Hyakuna (4.77 and 6.21 mm) and Shimoda (4.96 and 6.20 mm). Hermit crabs on Kudaka-jima were often found occupying old shells with broken apertures, high degrees of abrasion, and with one or more holes, and some crabs also occupied plastic bottle caps instead of shells (Nakasone 1987). Thus, the hermit crabs on Kudaka-jima were inhabiting poor shells or substitutes for shells. My observations suggest that coenobitid crabs living in areas with a low supply of shells or with shells of poor quality reproduce at smaller sizes, as is the case in marine hermit crabs (Markham 1968, Fotheringham 1976*a,b,* Bertness 1981*a,b*).

The smallest ovigerous females collected in this study were 3.93 mm long for *C. rugosus* and 3.83 mm for *C. purpureus* from

TABLE 1

Comparison of Non-Eyed and Eyed Egg Sizes (Mean ± SD in mm) on the First Pleopod among Three Species of *Coenobita*

	Size of Non-eyed Eggs		Size of Eyed Eggs	
Species	Length	Width	Length	Width
C. rugosus	0.658 ± 0.045	0.616 ± 0.041	0.736 ± 0.040	0.641 ± 0.040
C. purpureus	0.747 ± 0.092	0.715 ± 0.098	0.816 ± 0.110	0.699 ± 0.121
C. cavipes	0.508 ± 0.025	0.473 ± 0.028	0.745 ± 0.052	0.659 ± 0.043

Kudaka-jima, compared with 3.98 mm for *C. rugosus* and 3.05 mm for *C. purpureus* from Yaeyama (Shimamura 1987). The smallest *C. cavipes* ovigerous female collected at site A was 9.49 mm, but Shimamura (1987) found ovigerous females of this species as small as 8.84 mm in samples from Yaeyama. It seems likely that most *C. rugosus* and *C. purpureus* females do not reach sexual maturity until they are more than 4 mm in length. Some females of both *C. rugosus* and *C. purpureus* may lay eggs during their second year of life, judging from the size-frequency distributions (Figures 1, 2) and sizes of glaucothoes (Nakasone 1988*b*). This conclusion was also reached by Shimamura (1987). Similarly, De Wilde (1973) reported that *C. clypeatus* matures in the second year of life. Because of the small sample size, it was uncertain whether females of *C. cavipes* reach sexual maturity at sizes less than 8.84 mm. The results of observations on spermatophores show that *C. rugosus* and *C. purpureus* males may not reach sexual maturity until they attain sizes over 4.30 and 5.00 mm, respectively.

The percentage of females with both brooded embryos and mature oocytes was 83.3% in late July for *C. rugosus*, about 80% in July for *C. purpureus*, and 85.7% in late June for *C. cavipes*. These observations indicate that some females of these three species may produce at least two broods during the breeding season. Moreover, some females of *C. rugosus*, a species with a protracted breeding season, may even produce a third brood, as is also the case with *C. clypeatus* (De Wilde 1973).

Non-eyed eggs of *C. cavipes* were the smallest among the three species. The eyed eggs in *C. rugosus* were not significantly different in size from those of *C. cavipes*. However, the larval size at hatch in *C. rugosus* was significantly larger than that in *C. cavipes* (Nakasone 1987). This suggests that egg size may increase more rapidly in *C. rugosus* than in *C. cavipes* just before hatching. *Coenobita cavipes* produced more, smaller eggs compared with *C. purpureus*, and the size of larvae at hatch was the smallest among the three species studied (Nakasone 1987, 1988*b*), a common reproductive strategy (i.e., the combination of small egg size and large numbers of eggs).

As mentioned in the Results, the large females of both *C. cavipes* and *C. purpureus* that released their larvae at site A occupied the shells of the giant land snail *Achatina fulica*. The shells of this land snail are light and large, very suitable for large crabs inhabiting inland sites. It is known that the growth and egg production of marine and especially land hermit crabs are affected by the weight of the shell occupied (Bertness 1981*b*, Osorno et al. 1998). The large but light shells of *A. fulica* have a high internal volume/weight ratio (see Osorno et al. 1998). By occupying these light shells, large females of both *C. purpureus* and *C. cavipes* may reduce the energetic cost of carrying a shell (Herreid and Full 1986), and its large size provides sufficient space for larger clutch sizes. According to the Energy Savings Hypothesis proposed by Osorno et al. (1998), the large females of *C. cavipes* and *C. purpureus* may be able to compensate for the energy expended during locomotion from inland sites to the seashore by utilizing large but lightweight shells such as those provided by *A. fulica*.

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Literature Cited

Ball, E. E. 1972. Observations on the biology of the hermit crab, *Coenobita compressus* H. Milne Edwards (Decapoda; Anomura) on the west coast of the Americas. Rev. Biol. Trop. 20:265–273.

Bertness, M. D. 1981*a*. Pattern and plasticity in tropical hermit crab growth and reproduction. Am. Nat. 117:754–773.

———. 1981*b*. The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). Crustaceana (Leiden) 40:197–205.

Brodie, R. J. 1999. Ontogeny of shell-related behaviors and transition to land in the terrestrial hermit crab *Coenobita compressus* H. Milne Edwards. J. Exp. Mar. Biol. Ecol. 241:67–80.

Degener, O., and E. Gillaspy. 1955. Canton Island, South Pacific. Atoll Res. Bull. 41:1–51.

De Wilde, P. A. W. J. 1973. On the ecology of *Coenobita clypeatus* in Curacao with reference to reproduction, water economy and osmoregulation in terrestrial hermit crabs. Stud. Fauna Curacao Other Carribb. Isl. 44:1–138.

Fotheringham, N. 1976*a*. Effects of shell stress on the growth of hermit crabs. J. Exp. Mar. Biol. Ecol. 23:299–305.

———. 1976*b*. Population consequences of shell utilization by hermit crabs. Ecology 57:570–578.

Herreid, C. F., II, and R. J. Full. 1986. Energetics of hermit crabs during locomotion: The cost of carrying a shell. J. Exp. Biol. 120:297–308.

Markham, J. C. 1968. Notes on growth-patterns and shell-utilization of the hermit crab *Pagurus bernhardus* (L.). Ophelia 5:189–205.

Nakasone, Y. 1987. Ecological studies of land hermit crabs in the southern part of Okinawa Island. Pages 16–60 *in* AMAN, a report on the distribution and ecology of land hermit crabs in Okinawa Prefecture. Okinawa Prefectural School Board. [in Japanese.]

———. 1988*a*. Land hermit crabs from the Ryukyus, Japan, with a new species from the Philippines (Crustacea, Decapoda, Coenobitidae). Zool. Sci. (Tokyo) 5:165–178.

———. 1988*b*. Larval stages of *Coenobita purpureus* Stimpson and *C. cavipes* Stimpson reared in the laboratory and survival rates and growth factors of three land hermit crab larvae (Crustacea: Anomura). Zool. Sci. (Tokyo) 5:1105–1120.

Osorno, J. L., L. Fernandez-Casillas, and C. Rodriguez-Juarez. 1998. Are hermit crabs looking for light and large shells?: Evidence from natural and field induced shell exchanges. J. Exp. Mar. Biol. Ecol. 222: 163–173.

Page, H. M., and S. W. Willason. 1982. Distribution patterns of terrestrial hermit crabs at Eniwetok Atoll, Marshall Islands. Pac. Sci. 36:107–117.

Shimamura, K. 1987. Ecological studies of land hermit crabs in the Yaeyama Islands. Pages 61–118 *in* AMAN, a report on the distribution and ecology of land hermit crabs in Okinawa Prefecture. Okinawa Prefectural School Board. [in Japanese.]

Vogel, H. H., and J. R. Kent. 1971. A curious case: The coconut crab. Fauna (Oslo) 2:4–11.

Wolcott, T. G. 1988. 3: Ecology. Pages 55–96 *in* W. W. Burggren and B. R. McMahon, eds. Biology of the land crabs. Cambridge University Press, Cambridge.

Yamaguchi, S. 1938. Spawning and development of *Coenobita rugosus*. Bulteno Scienca 8:163–177, pls. 2,3. Imperial University of Kyushu. [in Japanese with English summary.]