Pacific Science (1982), vol. 36, no. 1


# Distribution Patterns of Terrestrial Hermit Crabs at Enewetak Atoll, Marshall Islands[1]

H. M. PAGE and S. W. WILLASON[2]

ABSTRACT: Habitat utilization, population structure, and activity were investigated for members of the family Coenobitidae on three islets at Enewetak Atoll, Marshall Islands. Small *Coenobita perlatus* ( < 8.0-mm carapace length) were more abundant in the beach habitat than medium-size (8–19-mm carapace length) *C. perlatus*, *C. rugosus*, *C. brevimanus*, or *Birgus latro*. Large *C. perlatus* ( ≥ 20-mm carapace length) were present on the beach only at night and engaged primarily in reproductive behavior. *Coenobita rugosus* on the beach at night were generally females which either had recently released their eggs and larvae into the lagoon or had eggs ready for hatching on their pleopods. The size at maturity was much smaller for the *C. perlatus* population on Bokandretok as compared with populations on Ikuren and Mut. The scarcity of medium-size individuals may result from a scarcity of suitable *Turbo* shells.

TERRESTRIAL HERMIT CRABS of the genus *Coenobita* have a worldwide tropical and subtropical distribution. On atolls in the tropical Pacific, where several species have been reported (Wiens 1962), these crustaceans are major components of the terrestrial ecosystem. Their importance in removing carrion (Wiens 1962, Page and Willason, in review) and their potential impact as grazers on terrestrial vegetation have been discussed (Degener and Gillaspy 1955, Niering 1956). Seurat (1904) made casual observations on gastropod shell use, predators, food, and distribution of *Coenobita perlatus* on Mangareva. Gross (1964) provided additional observations on the distribution of *C. perlatus*, *C. brevimanus*, and the coconut crab, *Birgus latro*, while examining the osmoregulatory capability of these species at Enewetak Atoll, Marshall Islands.

Despite the observations mentioned in the above studies, no quantitative investigations of distribution and population structure have been published for Pacific island populations. The purpose of this study, conducted from 18 September to 21 October 1979 at Enewetak Atoll, was to (1) examine the relationship between habitat and species distributions and population structure and (2) examine aspects of the activity and behavior of these hermit crabs as related to their distribution.

## MATERIALS AND METHODS

### *Study Sites and Habitats*

Enewetak Atoll, located in the tropical Pacific Ocean, 11°30′ N, 162°10′ E, consists of approximately 40 small islets (total land area about 2 square miles) surrounding a central lagoon (Figure 1). Study sites were established on Ikuren and Mut, two relatively undisturbed islets in the southwest part of the atoll, and on Bokandretok, situated in the southeast about 200 m north of the inhabited islet of Enewetak. Four macrohabitats were distinguished on these islets: (1) the broad sandy beach bordering the lagoon; (2) the coral rubble and reef flat bordering the ocean; (3) the nearshore habitat dominated by the shrub *Scaevola frutescens* intermingling inshore with a tree, *Messerschmidia argentea*, morning glory, *Ipomaea* sp., and a grass, *Lepturus* sp.

[1] This research was supported by the Mid-Pacific Research Laboratory, Enewetak Atoll, Marshall Islands, and the Marine Science Institute, University of California, Santa Barbara. Manuscript accepted 25 August 1981.

[2] University of California, Marine Science Institute, Santa Barbara, California 93106.

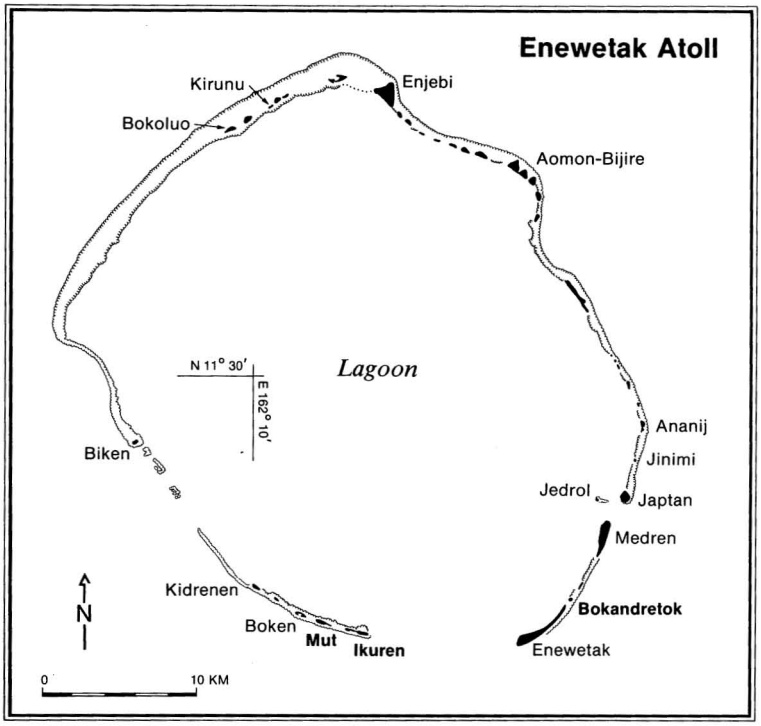



FIGURE 1. Map of Enewetak Atoll, Marshall Islands. Sampling was conducted on Ikuren, Mut, and Bokandretok islets (shown in boldface type).

(the scrub zone of Wiens 1962); and (4) the interior forest composed primarily of coconut palm, *Cocos nucifera*, and a broad-leaved tree, *Pisonia grandis*. The forest floor is covered with fallen coconut logs, husks, and other plant debris as well as coral rubble. The islet of Bokandretok is much smaller in area than Ikuren and Mut and lacks the inshore forest typical of the larger islets.

The terrestrial fauna of Enewetak is dominated by sea birds and crustaceans. Other terrestrial or semiterrestrial crustacean species encountered during this study included the brachyuran crabs *Ocypode ceratophthalma*, *O. cordimana*, *Grapsus tenuicrustatus*, *Geograpsus crinipes*, and the coconut crab, *Birgus latro* (Coenobitidae). The polynesian rat, *Rattus exulans*, was also observed.

*Species Distributions and Population Structure*

The hermit crab population was sampled by collecting all individuals within a 20-m long section of beach from the water line up to and including the wrack zone, followed by the separate collection of all individuals under a 20-m long × 8-m wide section of nearshore vegetation. Samples were taken at the same location once at 10:00 hr and once at 21:00 hr on Mut and Bokandretok and at 21:00 hr only on Ikuren. Direct sampling of *Coenobita* in the interior was not feasible due to the dense vegetation. Therefore, estimates of the species present and population characteristics in the interior were made using "bait" transects. Raw chicken legs were staked out in three transect lines 40 m apart. Each line consisted of three stations, located (A) 10 m, (B) 30 m, and (C) 50 m, from the start of the nearshore vegetation. All hermit crabs within a 1-m radius of the bait stations were collected during three visits 1 hr apart between 21:00 and 24:00 hr. Sampling was not done on the ocean side of the three study islets, because very few *Coenobita* sp. individuals were found

TABLE 1

NUMBER AND SPECIES OF *Coenobita* OBTAINED IN (a) BEACH AND NEARSHORE VEGETATION AND (b) INTERIOR FOREST "BAIT" TRANSECT SAMPLES

(a) BEACH AND NEARSHORE VEGETATION

| | BEACH | | | | NEARSHORE VEGETATION | | | |
|---|---|---|---|---|---|---|---|---|
| | Ikuren | Mut | Bokandretok | Totals | Ikuren | Mut | Bokandretok | Totals |
| Night | | | | | | | | |
| *C. perlatus* | | | | | | | | |
| Small (< 8 mm) | 101 | 84 | 106 | 291 | 38 | 55 | 57 | 150 |
| Medium (8–19 mm) | 3 | 4 | 22 | 29 | 4 | 23 | 22 | 49 |
| Large (≥ 20 mm) | 48 | 21 | 2 | 71 | 11 | 5 | 6 | 22 |
| *C. rugosus* | 11 | 29 | 5 | 45 | 21 | 42 | 110 | 173 |
| Totals | 163 | 138 | 135 | 436 | 74 | 125 | 195 | 394 |
| Day | | | | | | | | |
| *C. perlatus* | | | | | | | | |
| Small (< 8 mm) | * | 127 | 150 | 277 | * | 12 | 53 | 65 |
| Medium (8–19 mm) | | 0 | 4 | 4 | | 1 | 6 | 7 |
| Large (≥ 20 mm) | | 0 | 1 | 1 | | 19 | 1 | 20 |
| *C. rugosus* | * | 37 | 19 | 56 | * | 140 | 100 | 240 |
| Totals | | 164 | 174 | 338 | | 172 | 160 | 332 |

(b) INTERIOR FOREST "BAIT" TRANSECT SAMPLES

| | STATION | | | |
|---|---|---|---|---|
| | A (10 m) | B (30 m) | C (50 m) | Totals |
| *C. perlatus* | | | | |
| Small (< 8 mm) | 71 | 43 | 8 | 122 |
| Medium (8–19 mm) | 54 | 71 | 28 | 153 |
| Large (≥ 20 mm) | 33 | 13 | 7 | 53 |
| *C. rugosus* | 57 | 32 | 12 | 101 |
| *C. brevimanus* | 1 | 5 | 6 | 12 |
| *Birgus latro* (observed) | 3 | 13 | 12 | 28 |
| Totals | 219 | 177 | 73 | 469 |

*No data available.

there during preliminary day and night observations.

Hermit crabs were identified to species (with the assistance of E. S. Reese and the Mid-Pacific Research Laboratory reference collection) and sex. The carapace length (CL) was measured to the nearest 0.1 mm, and the presence of eggs on females was recorded. The developmental state of the pleopods was noted and used as an indicator of maturity. Pleopods were classified as being (1) well developed with dark hairs, characteristic of ovigerous females; (2) medium-size without hairs; or (3) small and poorly developed. The species of gastropod shell inhabited by the crabs, identified with the aid of the Mid-Pacific Research Laboratory reference collection, was also recorded. Size frequency data were analyzed using the graphical method of Harding (1949) and Cassie (1950).

### *Activity and Reproductive Behavior*

The activity of hermit crabs on the lagoon beach was investigated by delineating a section of beach 20 m long from the water line to and including the wrack zone on Ikuren. Every 4 hr for 1–3-day periods this area was

TABLE 2

SEX RATIOS OF *C. perlatus* AND *C. rugosus*

| ISLET | BEACH | | | NEARSHORE VEGETATION | | |
|---|---|---|---|---|---|---|
| | MALES | FEMALES | RATIO ♂♂/♀♀ | MALES | FEMALES | RATIO ♂♂/♀♀ |
| *C. perlatus* | | | | | | |
| Mut | | | | | | |
| Small (< 8.0 mm CL) | 41 | 43 | 0.95 | 23 | 32 | 0.72 |
| Medium (8–19 mm CL) | 3 | 1 | 3.00 | 8 | 15 | 0.53 |
| Large (≥ 20 mm CL) | 18 | 3* | 6.00 | 3 | 1 | 3.00 |
| Bokandretok | | | | | | |
| Small (< 8.0 mm CL) | 60 | 56 | 1.07 | 36 | 33 | 1.09 |
| Medium (8–19 mm CL) | 5 | 6 | 0.83 | 8 | 4 | 2.00 |
| Large (≥ 20 mm CL) | 0 | 2 | — | 5 | 1 | 5.00 |
| Ikuren | | | | | | |
| Small (< 8.0 mm CL) | 48 | 54 | 0.89 | 26 | 12 | 2.17 |
| Medium (8–19 mm CL) | 1 | 1 | 1.00 | 1 | 2 | 0.50 |
| Large (≥ 20 mm CL) | 30 | 20 | 1.50 | 4 | 6 | 0.67 |
| *C. rugosus* | | | | | | |
| Mut | | | | | | |
| Night | 2 | 27† | 0.07 | 20 | 22 | 0.91 |
| Day | 14 | 22 | 0.64 | 63 | 67 | 0.94 |
| Bokandretok | | | | | | |
| Night | 0 | 5 | — | 63 | 43 | 1.47 |
| Day | 9 | 10 | 0.90 | 37 | 44 | 0.84 |
| Ikuren | | | | | | |
| Night | 1 | 10* | 0.10 | 13 | 11 | 1.18 |
| Day | — | — | — | — | — | — |

*$p < 0.05$ (chi-square test).
†$p < 0.001$ (chi-square test).

searched for *Coenobita*. Each individual encountered was identified to species and relative size (small, < 8.0 mm; medium, 8–19 mm; large, ≥ 20 mm). Air temperature, weather, and phase of the moon were noted. After these determinations the crabs were released. Observations were made on Ikuren and Mut on the sexual composition of aggregations of *C. perlatus* found on the beach.

## RESULTS

### *Species Distributions and Population Structure*

*Coenobita perlatus* were much more abundant than *C. rugosus* on the beach (Table 1a). Small individuals (< 8.0 mm CL, white in coloration with dark bands on the legs) were found not only under debris in the wrack zone, but frequently withdrawn into their shells exposed to the direct sun. During the night, large *C. perlatus* (≥ 20 mm CL, red in color) were also present on the beach. Medium-size *C. perlatus* (8–19 mm CL, varying in color from white to red) were much less numerous than small and large crabs on Ikuren and Mut, but were much more numerous than large individuals on Bokandretok (Table 1a). While the sex ratio of small and medium-size *C. perlatus* was 1 : 1 on the beach, significantly more large males than large females were on the beach at night on Mut (Table 2). Although not statistically significant ($p > 0.05$), a trend of more large males than large females on the beach at night on Ikuren was also evident. In contrast, virtually all *C. rugosus* on the beach at night on all islets were females (Table 2).

*Coenobita rugosus* and medium-size *C. perlatus* were found in greater relative abundance in the nearshore than in the beach habitat ($p < .001$ in all cases, chi-square test; Table 1a). Both *C. perlatus* and *C. rugosus* were frequently found aggregated around the base of *Scaevola* or *Messerschmidia*.

The samples from the interior of Ikuren resembled the beach and nearshore samples from Ikuren and Mut in the bimodal size frequency distribution of *Coenobita perlatus* (Figure 2), but differed in both the larger mean size of males and females in the first mode ($p < 0.001$, *t*-test) and the smaller mean size of males in the second mode ($p < 0.001$, *t*-test). The paucity of medium-size *C. perlatus*, apparent in the beach and nearshore habitats, was also evident in the interior. Medium-size *C. perlatus* comprised 40 percent (71 of 177) of the sample at 30 m and 38 percent (28 of 73) at 50 m inshore (Table 1b).

Although *Coenobita rugosus* individuals found in the interior were larger than those found in the beach and nearshore habitats, the size frequency distribution of this species differed greatly from that of *C. perlatus* (Figure 2). The maximum size of *C. rugosus* was 8–9 mm CL and the size distribution of mature individuals overlapped that of immature *C. perlatus*.

On Bokandretok, large *C. perlatus* individuals were scarce (Table 1a). In addition, while the smallest female with well-developed pleopods was about 12 mm CL and the smallest ovigerous female was > 20 mm CL on Ikuren and Mut, a significantly higher ($p < 0.001$, chi-square test) proportion of females 4–8 mm CL had type 1 pleopods on Bokandretok (Figure 2). Three small individuals (4 mm CL, white in color) were carrying eggs there.

*Coenobita brevimanus* and the coconut crab, *Birgus latro*, were found primarily in the interior (Table 1b). *Coenobita brevimanus* individuals were quite rare (only 17 individuals were found); hence the population structure of this species could not be estimated. The size of sampled *C. brevimanus* ranged from 8.5 mm to 17.5 mm CL.

### *Activity and Reproductive Behavior*

The number of hermit crabs on the beach was correlated with time of day, presence of a full moon, and the amount of cover or wrack present. In the absence of a full moon, large and small *Coenobita perlatus*, hidden during the day, moved onto the beach between 19 : 00 and 20 : 00 hr (Figure 3). Small individuals appeared first, were present in greater numbers, and remained on the beach longer than large individuals.

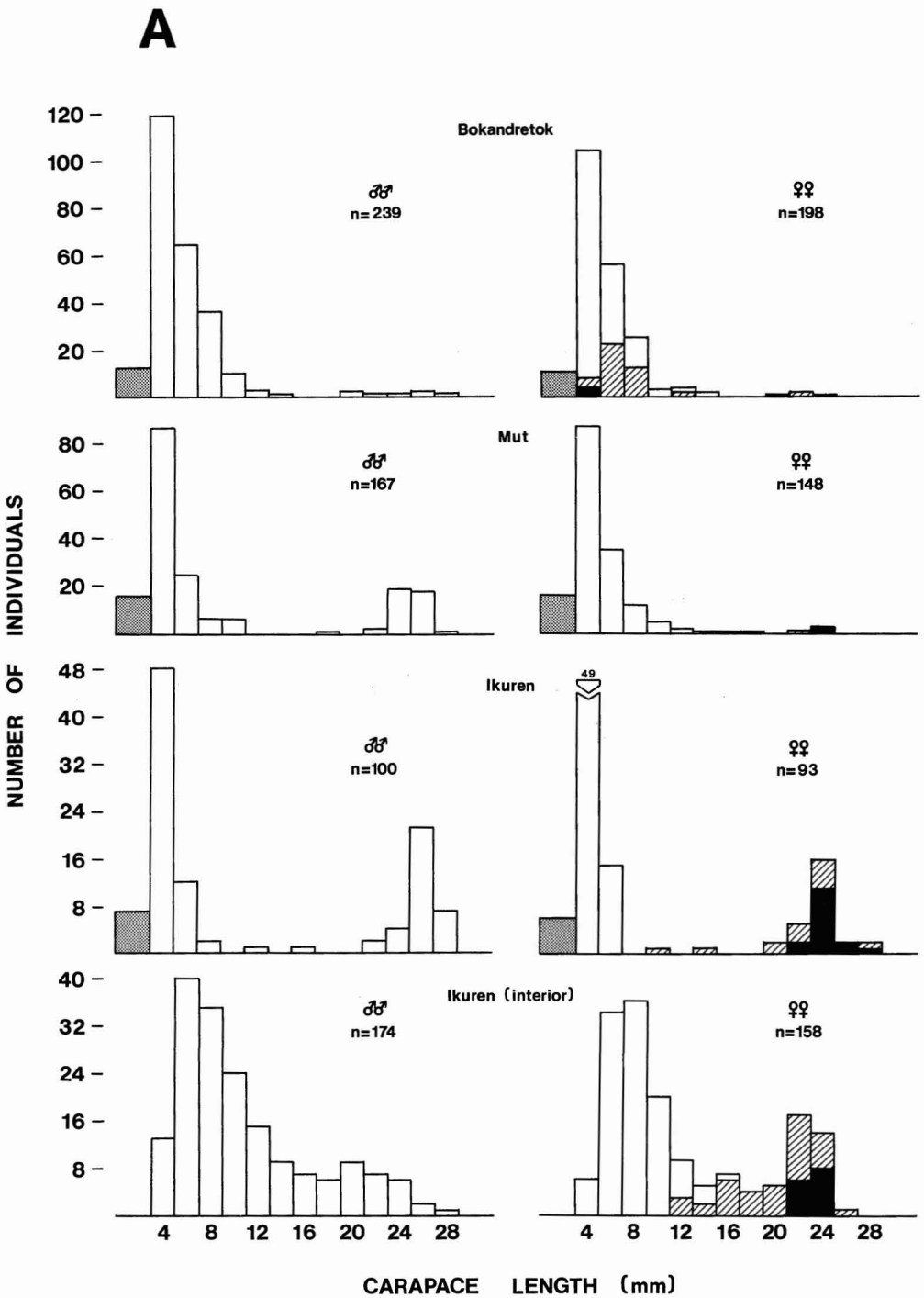
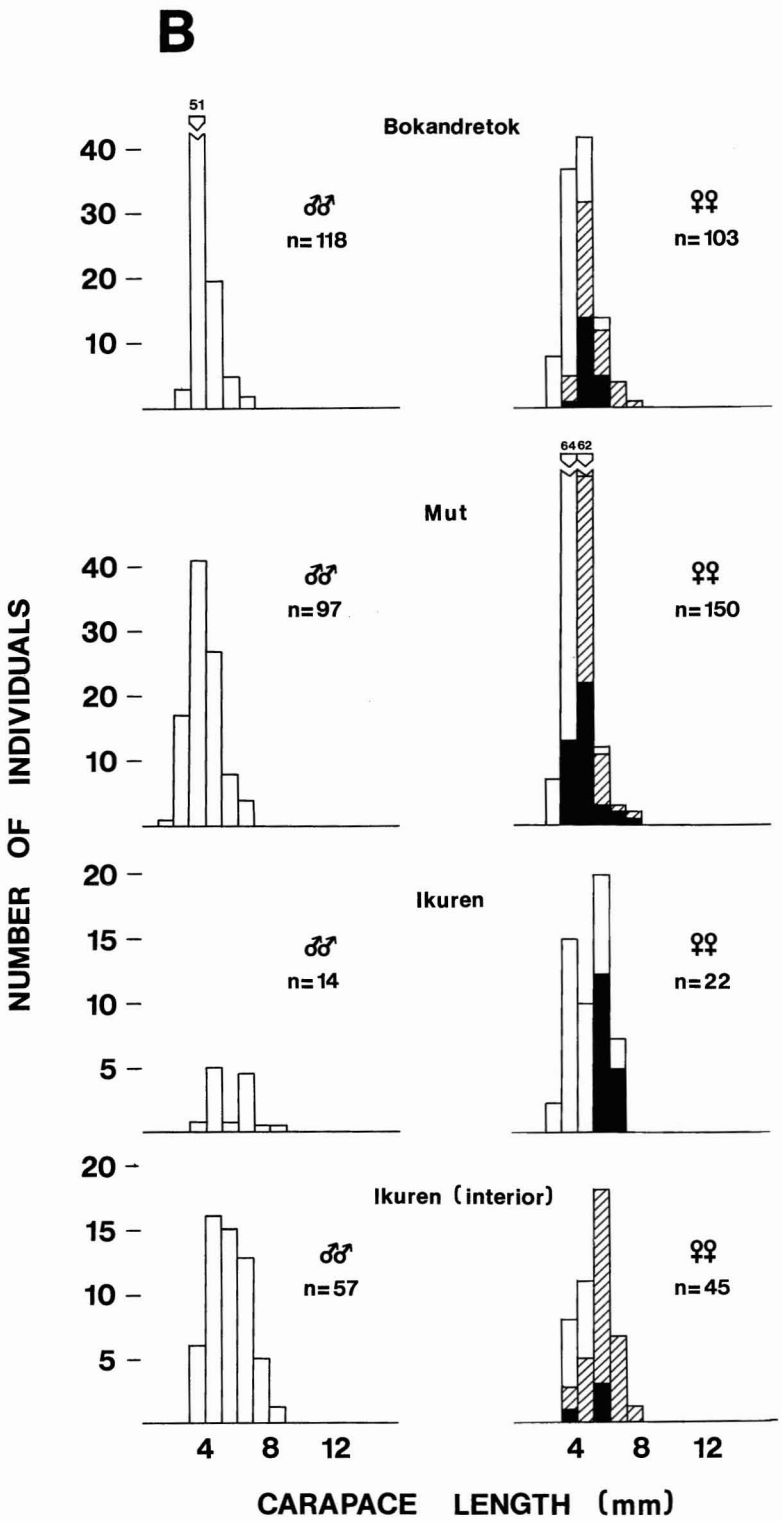



FIGURE 2. Size frequency distributions for male and female (A) *C. perlatus* and (B) *C. rugosus* from the beach–nearshore habitat and from the interior. Day and night samples combined. Stippled bar, unsexed crabs ( < 2.0 mm CL), assuming a 1 : 1 sex ratio; hatched bar, females with type 1 pleopods, including ovigerous females; solid bar, ovigerous females; white bar, total crabs.


B
51
Bokandretok
♂♂
n=118
♀♀
n=103
64 62
Mut
♂♂
n=97
♀♀
n=150
Ikuren
♂♂
n=14
♀♀
n=22
Ikuren (interior)
♂♂
n=57
♀♀
n=45
NUMBER OF INDIVIDUALS
CARAPACE LENGTH (mm)

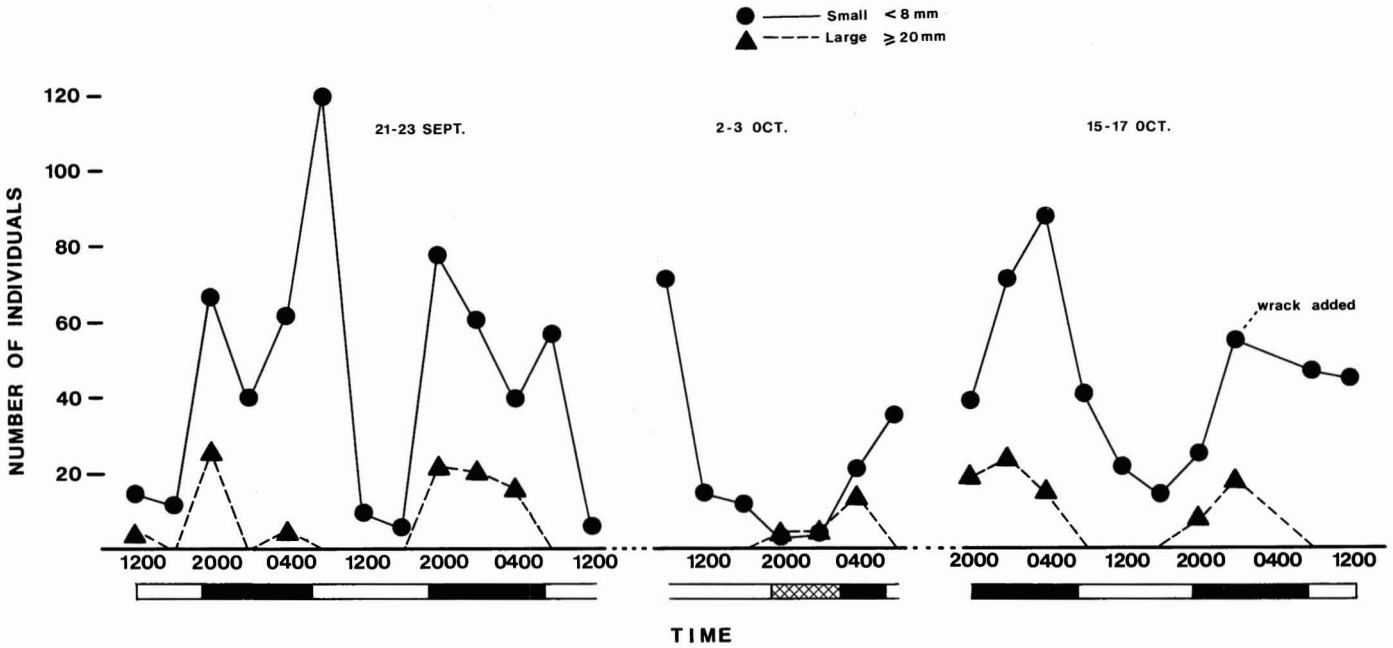



FIGURE 3. Activity of *C. perlatus* on a 20-m section of beach on Ikuren. Dark bar denotes night; hatched bar presence of a full moon.

TABLE 3

SEX RATIO AND REPRODUCTIVE CONDITION OF FEMALE *C. perlatus* IN MATING AGGREGATIONS ON THE BEACH AT NIGHT ON MUT ISLET

| TYPE OF AGGREGATION | | CONDITION OF FEMALE | | |
|---|---|---|---|---|
| RATIO: MALE/FEMALE | NUMBER OF AGGREGATIONS | GRAY EGGS | MATTED PLEOPODS* | SPERMATOPHORE ATTACHED |
| 1/1 | 8 | 3 | 2 | 3† |
| 2/1 | 7 | 3 | 4 | |
| 3/1 | 2 | 1 | 1 | |

*Female just released larvae.
†Two females had gray eggs, one had matted pleopods.

A full moon greatly inhibited hermit crab activity; emergence time was postponed from 19:00 to 20:00 hr until the moon had set the following morning (about 04:00 hr) on 2–3 October (Figure 3).

At 24:00 hr on 16 October, we artificially increased the amount of wrack on the beach by adding logs, rocks, and coconut husks. The number of small hermit crabs on the beach during the following midday (12:00 hr) was at least twice that found at the same time on previous days (Figure 3).

The large *Coenobita perlatus* on the beach at night moved in and out of the wave wash, engaged in courtship behavior, and foraged. Some of the animals active in the wave wash were females with matted pleopods on which an occasional unhatched egg was still attached. These crabs apparently had released their hatching larvae in the water. Other crabs may have replenished their shell water in the lagoon. Aggregations of two or more crabs on the beach were frequently observed. These contained only one female with one or more males (Table 3). Actual mating was possible before the release of larvae, as evidenced by the two females with gray eggs (zoea larvae enclosed by the egg membrane) and attached spermatophores (Table 3). Mating occurs ventral to ventral with both crabs about three-quarters out of their shells, and the spermatophores are transferred by means of the modified pereiopods of the male (E. S. Reese, personal communication).

*Coenobita rugosus* individuals were rarely present on the beach. Inspection of 12 randomly selected *C. rugosus* found within the 20-m area at 20:00 hr on 2 October revealed all to be females; seven had brown eggs with eye-spots.

### *Shell Resource Utilization and Availability*

A detailed treatment of the patterns of shell resource utilization will be given in Willason and Page (in review). *Coenobita* sp. at our study sites occupied 69 species of gastropod shells. The number of shell species used decreased dramatically with increasing crab size so that virtually 100 percent of the *C. perlatus* individuals > 12 mm CL were either in *Turbo setosus* or *T. argyrostomus* shells (Willason and Page, in review). Sixty-four percent of the *Turbo* shells occupied by medium-size *C. perlatus* ($n = 88$) were worn and pitted apexes derived from larger shells. Only 14 percent were small intact *Turbo* shells in good condition. Ninety percent of the *Turbo* shells used by large *C. perlatus* ($n = 39$) were in good condition.

A 300-m section of lagoon beach and cobble on Ikuren was searched for empty *Turbo* shells; 51 shells were found: 7 were in good condition, 17 possessed one hole, and 27 either possessed two holes or were in other ways severely damaged. The average aperture width of the *Turbo* shells in good condition and those with one hole was $28.3 \pm 4.0$ mm ($n = 24$). The average aperture width of *Turbo* shells used by large *Coenobita perlatus* was $35.2 \pm 1.9$ mm ($n = 104$). The size range of *Turbo* shells used by medium-size individuals

ranged from 15-mm aperture width for a crab of 8-mm CL to 27-mm aperture width for a crab of 19-mm CL (estimated from a regression of *Turbo* aperture width on crab carapace length, $r = 0.97$, $n = 90$). Thus, the empty *Turbo* shells found during the search were not suitable for most medium-size crabs.

## DISCUSSION

Hermit crab utilization of the beach, nearshore, and interior habitats varied with species, time of day, presence of moonlight, amount of wrack on the beach, size, sex, and reproductive condition of mature individuals. Our data support observations by Seurat (1904) on *Coenobita perlatus* at Mangareva and by Gross (1964) on the broad distribution of *C. perlatus*. The smallest crabs were closest to the beach, while large individuals were present on the beach as well as in the interior. The association of the small *C. perlatus* primarily with beach and nearshore habitat may be linked with the shell water requirements of this species. *Coenobita perlatus* prefers seawater over fresh water when filling its shell (Gross and Holland 1960) and usually has field blood serum concentrations hypertonic to seawater (Gross 1964). Two explanations for their distribution appear possible: (1) small individuals may need to replenish their shell water from the lagoon more frequently than medium and large individuals; and (2) small crabs possess more rigid osmoregulatory requirements than large individuals, utilizing only seawater to fill their shells.

The presence of large individuals on the beach was mainly associated with the reproductive behavior of this species. Deposition of zoea into the lagoon by brooding females and courtship–mating were the principal activities observed. Medium-size, not yet mature, individuals were most numerous in the interior and rarely found on the beach.

Virtually no information is available in the literature on the biology of *Coenobita rugosus* from the tropical Pacific region. This species has been reported on the beach at night in large numbers at Sar Uanle, Somalia (Vannini 1975), Aldabra Atoll in the Indian Ocean (Grubb 1971), and Kikai Island (Yamaguchi 1938). By contrast, few *C. rugosus* were on the beach at night at Enewetak and were primarily females carrying late embryos or with matted pleopods indicating recent release of larvae into the lagoon. This suggests either that earlier investigators observed primarily females or that *C. rugosus* exhibits behavioral differences at other locations. At Enewetak *C. rugosus* may fill its shell with lagoon water less frequently than *C. perlatus*. Vannini (1975) reported that the *C. rugosus* at Sar Uanle, Somalia, could absorb water from the wet sand. It is also possible that *C. rugosus* may remain in close proximity to a food source associated primarily with the nearshore vegetation.

*Coenobita brevimanus* individuals were not common, and most were found in the interior. Gross (1964) observed *C. brevimanus* in the interior and reported that this species has lower blood serum concentrations and shell water of much lower salinity than *C. perlatus*. He proposed that *C. brevimanus* uses pools of standing fresh water available in the interior as a water source. A physiological requirement for fresh water could account for the presence of this species inland.

Two hypotheses could explain the bimodal population structure of *Coenobita perlatus* on Ikuren and Mut islets. First, the modes could represent recruitment, or "year," classes. This explanation would require a new recruit to increase in body weight over 1000-fold in 1 yr. Unfortunately, no recruitment or growth data are currently available for *Coenobita*. The second explanation is that the size distribution of empty shells is responsible for the bimodal population structure of *C. perlatus* on Ikuren and Mut and for the absence of medium and large *C. perlatus* individuals on Bokandretok. Available evidence for marine hermit crabs shows that shell size influences growth (Bertness 1981, Fotheringham 1976, Markham 1968). If the same principle applies to terrestrial hermit crabs, a lack of available medium-size shells could inhibit the growth of smaller individuals through the medium-size classes. Two lines of evidence support this hypothesis. First, most medium-size individuals were occupying shells derived from

large *Turbo argyrostomus*, indicating that shells in good condition of the proper size may not be available. Second, empty small and large shells were more abundant than medium-size shells. The relative absence of medium and large *C. perlatus* individuals and the presence of small mature crabs on Bokandretok appears consistent with a shell limitation hypothesis. No large shells were found in the sampled areas or through extensive search of other areas. If, however, shell availability were in total responsible for the small mature individuals on Bokandretok, one might expect to observe some ovigerous small *C. perlatus* on Ikuren and Mut. None were found. This suggests that some other factor, perhaps food availability, may influence the size at maturity. Since Bokandretok is small and lacks the lush, more diverse flora found on the other two islets, less food may be available.

ACKNOWLEDGMENTS

We thank A. Kuris, E. S. Reese, A. Wenner, R. Haley, J. O'Brien, T. Mickel, and P. Van Wyk for critically reading the manuscript. We also thank T. Shields, M. DeGruy, G. Long, and K. Mitchell for providing technical assistance while at Enewetak. E. S. Reese provided access to his collections, support, and useful discussion.

## LITERATURE CITED

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

CASSIE, R. 1950. The analysis of polymodal frequency distributions by the probability paper method. N. Z. Sci. Rev. 8:89–91.

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

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

GROSS, W. 1964. Water balance in anomuran land crabs on a dry atoll. Biol. Bull. 126:54–68.

GROSS, W., and P. HOLLAND. 1960. Water and ionic regulation in a terrestrial hermit crab. Physiol. Zool. 33:21–28.

GRUBB, P. 1971. Ecology of terrestrial decapod crustaceans on Aldabra. Phil. Trans. R. Soc. (B) 260:411–416.

HARDING, J. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U.K. 28:141–153.

MARKHAM, J. 1968. Notes on growth patterns and shell-utilization of the hermit crab *Pagurus bernhardus* (L.). Ophelia 5:185–205.

NIERING, W. 1956. Bioecology of Kapingamarangi, Caroline Islands: Terrestrial aspects. Atoll Res. Bull. 49:1–32.

PAGE, H., and S. WILLASON. In review. Feeding patterns of terrestrial hermit crabs at Enewetak Atoll.

SEURAT, L. 1904. Observations biologiques sur les cenobites (*Cenobita perlata*, Edwards). Bull. Mus. Hist. Nat., Paris 10:238–242.

VANNINI, M. 1975. Researches on the coast of Somalia. The shore and dune of Sar Uanle. 5. Description and rhythmicity of digging behavior in *Coenobita rugosus* Milne-Edwards. Monitore Zool. Ital. (N. S.) Suppl. 6:233–242.

WIENS, H. 1962. Atoll environment and ecology. Yale University Press, New Haven.

WILLASON, S., and H. PAGE. In review. Patterns of shell resource utilization by terrestrial hermit crabs at Enewetak Atoll, Marshall Islands.

YAMAGUCHI, S. 1938. Spawning and development of *Coenobita rugosus*. Bull. Sci. Kyushu Univ. 8:163–175.