HERMIT CRAB FAUNA FROM SEA GRASS MEADOWS IN PUERTO RICO: SPECIES COMPOSITION, DIEL AND SEASONAL VARIATION IN ABUNDANCE

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ABSTRACT

Sea grass meadows sampled monthly for one year by push net had a hermit crab fauna composed of four pagurid and four diogenid species. Three species dominated the paguroid samples: *Pagurus criniticornis* (34.2%), *Clibanarius antillensis* (30.3%), and *Cl. tricolor* (18.5%). Abundances in night samples were consistently higher than in day collections. Field observations indicate that hermit crabs on sea grass meadows congregate into clusters during the day and disperse over the meadow at night, thus accounting for increased abundances in night collections. Hermit crab species showed two seasonal peaks of abundance at this tropical location, the first in the spring or summer and the second in the winter.

In recent years, there has been a surge of interest in the faunal composition and ecology of invertebrates inhabiting sea grass meadows in the Western Atlantic, especially those meadows dominated by turtlegrass, *Thalassia testudinum* (Bauer, in press; Dugan and Livingston, 1982; Gore *et al.*, 1981; Greening and Livingston, 1982; Heck, 1976, 1977, 1979; Heck and Orth, 1980a). When samples of the motile invertebrate epifauna are taken with otter trawls, crab scrapes, push nets, and similar devices in sea grass meadows, the most abundant macroinvertebrates taken are decapod crustaceans (e.g., Dugan and Livingston, 1982; Heck, 1979; Heck and Orth, 1980a, b; Hooks et al., 1976; Kikuchi, 1966). In a yearlong sampling program in sea grass meadows on the north coast of Puerto Rico upon which the present study is based, approximately 80% (total $N = 116,982$) of the motile macroinvertebrates collected were decapods. The decapod fauna itself was dominated numerically by caridean shrimps (Bauer, in press), but hermit crabs are a characteristic and abundant component of the sea grass motile epifauna. This report describes the hermit crab fauna from these sea grass meadows, documents the marked day–night differences of numbers of hermit crabs in samples, and demonstrates the presence of seasonality in abundances of the principal species.

METHODS

Sea grass meadows were located in a cove near the public beach at Dorado, north coast of Puerto Rico (18°29'N, 66°15'W). These meadows had the form of terraces raised above the surrounding sand bottom; the sea grass vegetation was a dense mixture of *Thalassia testudinum* and *Syringodium filiforme*. A submerged rocky reef parallel to the shore and seaward of the sea grass beds protected the latter from open ocean swell. Two replicate sites, 40 m apart and nearly isolated from each other by a sandy bottom, were sampled monthly from February 1982 through February 1983. A sample consisted of a 10-m run of a 0.5-m push net lined with a 1-mm mesh; samples were taken at random within the study sites. Twenty samples were taken monthly (10 day, 10 night) at each site. Further details about the study sites and sampling methods are in Bauer (in press).

RESULTS

In the 13 month sampling period at Dorado, Puerto Rico, 8,462 hermit crabs were collected in the 486 samples taken (Table 1). The hermit crab fauna was composed of four pagurid species, *Pagurus criniticornis, P. brevidactylus, P. stimpsoni,* and *P. marshi,* and four diogenid species, *Clibanarius antillensis, Cl. tricolor, Calcinus tibicen,* and *Dardanus venosus.* Although the total number of hermit
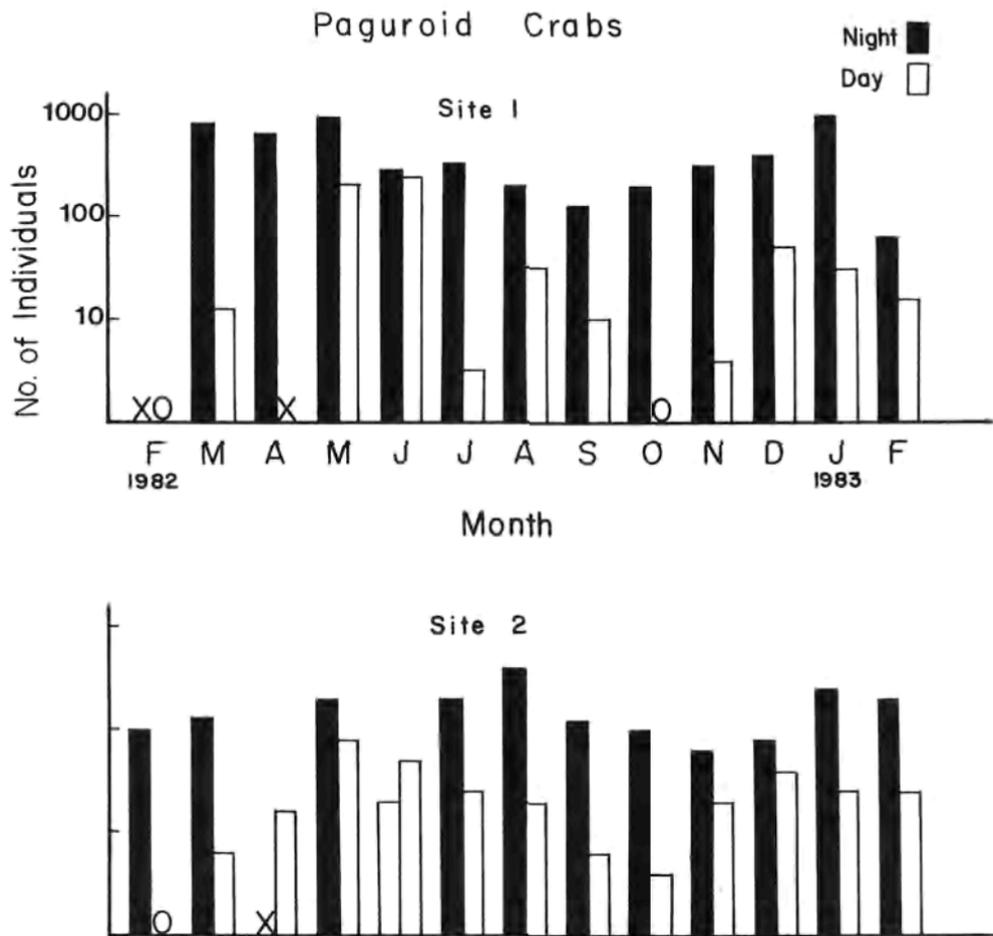
Fig. 1.   Total numbers of hermit crabs taken in monthly day (clear bars) and night (solid bars) samples at Dorado, Puerto Rico, Site 1 (above) and Site 2 (below). An "X" indicates no sample, a "O" indicates no hermit crabs were collected; at Site 2, June, there was no night sample (2 day samples). Note the logarithmic scale for numbers of individuals (same scale for both sites).

crabs at Site 1 was 2.8 times that at Site 2, the rank order of abundance was similar (positively correlated) at both sites (Spearman's rank correlation coefficient = +0.833, 0.01 > P > 0.005). Three species accounted for 83% of the total abundance: *Pagurus criniticornis* (34.2%), *Clibanarius antillensis* (30.3%), and *Cl. tricolor* (18.5%).

Hermit crabs were always more abundant (collectible) in night samples than in day collections (Fig. 1). In terms of total abundance, hermit crabs were 9.7 times (Site 1) and 6.0 times (Site 2) more numerous at night. However, the grouping of all hermit crab species together, as in Fig. 1, could mask differences among species with regard to diel variation in abundance. Night–day comparisons of abundance in monthly samples are made for each species by counting the number of months in which total night abundance for a particular species was greater than (+) or less than (−) day abundance. The few instances in which the number of individuals collected was equal in day and night collections were scored as (−). The sign test

Table 1. Species composition of the hermit crab fauna from sea grass beds at Dorado, Puerto Rico (number of individuals per site, day and night samples combined; species rank at each site in parentheses; "unidentified" not included in ranking).

Species	Site 1	Site 2	Percentage of total number
Pagurus criniticornis (Dana, 1852)	2,449 (1)	445 (3)	34.2
Clibanarius antillensis Stimpson, 1862	2,023 (2)	541 (2)	30.3
Cl. tricolor (Gibbes, 1850)	939 (3)	624 (1)	18.5
Pagurus stimpsoni (A. Milne Edwards and Bouvier, 1893)	444 (4)	37 (6)	5.7
P. brevidactylus (Stimpson, 1859)	219 (5)	258 (4)	5.6
Calcinus tibicen (Herbst, 1791)	126 (6)	257 (5)	4.5
Pagurus marshi Benedict, 1901	3 (7)	7 (7)	0.08
Dardanus venosus (H. Milne Edwards, 1848)	0 (8)	1 (8)	0.01
"Unidentified" (crushed, appendages missing, small juveniles, megalopa, etc.)	43	47	1.1

(Tate and Clelland, 1957) was used to test the one-sided hypothesis that the median of the monthly night minus day abundances was not greater than zero; less formally stated, the hypothesis was that the number of hermit crabs collected in night samples was not consistently greater than that in day collections. In most cases, this hypothesis is rejected ($P < 0.05$). The two exceptions were *Calcinus tibicen* at Site 1 and *Pagurus stimpsoni* at Site 2.

From the data given above on diel variation in hermit crab collectibility with a push net in a sea grass habitat, it is obvious that night collections are more representative of hermit crab abundances than day samples. Therefore, in the following results on seasonality of species abundances, only data from night samples were used. Estimates of monthly mean density (night) for the six most abundant species are given in Figs. 2, 3. To analyze for differences among monthly means, a one-way ANOVA was done on $\log_{10} (x + 1)$ transformed data, where x is the number of individuals per m^2 of sampling effort. The Student-Newman-Keuls test was used to determine differences between specific means. For most species, the null hypothesis of no difference between means is rejected (Table 2).

The preceding analysis was made to detect possible seasonal differences in abundance of each hermit crab species. The results of the Student-Newman-Keuls tests (Table 2) generally yield, for each species, large groups of means that are not statistically different, and overlap between groups is high. However, in Figs. 2, 3 and in Table 2, there seem to be common trends in abundance at both sites among species. At Site 1, monthly night means tend to be high in winter and spring, and low in summer and autumn; at Site 2, the first peak of abundance appears in the summer months but there is a similar winter increase (Figs. 2, 3). This suggests that, at each sampling site, the abundances of the various hermit crab species varied in common, i.e., population highs and lows occurred at about the same time of year. To test this hypothesis, a Kendall Concordance test was performed on the ranks of the monthly night means of hermit crab species. Within a species, means were ranked from lowest to highest; the summed ranks of all species for each month are illustrated in Fig. 4. For Site 1, the concordance coefficient W = 0.64 and the probability of no concordance (W = 0) is <0.005; for Site 2, W = 0.55 and P (W = 0) is <0.005. This analysis supports the observation that the hermit crab fauna as a whole exhibited a spring and a winter peak in abundance at Site 1, while at Site 2 the first peak occurred later during the summer.
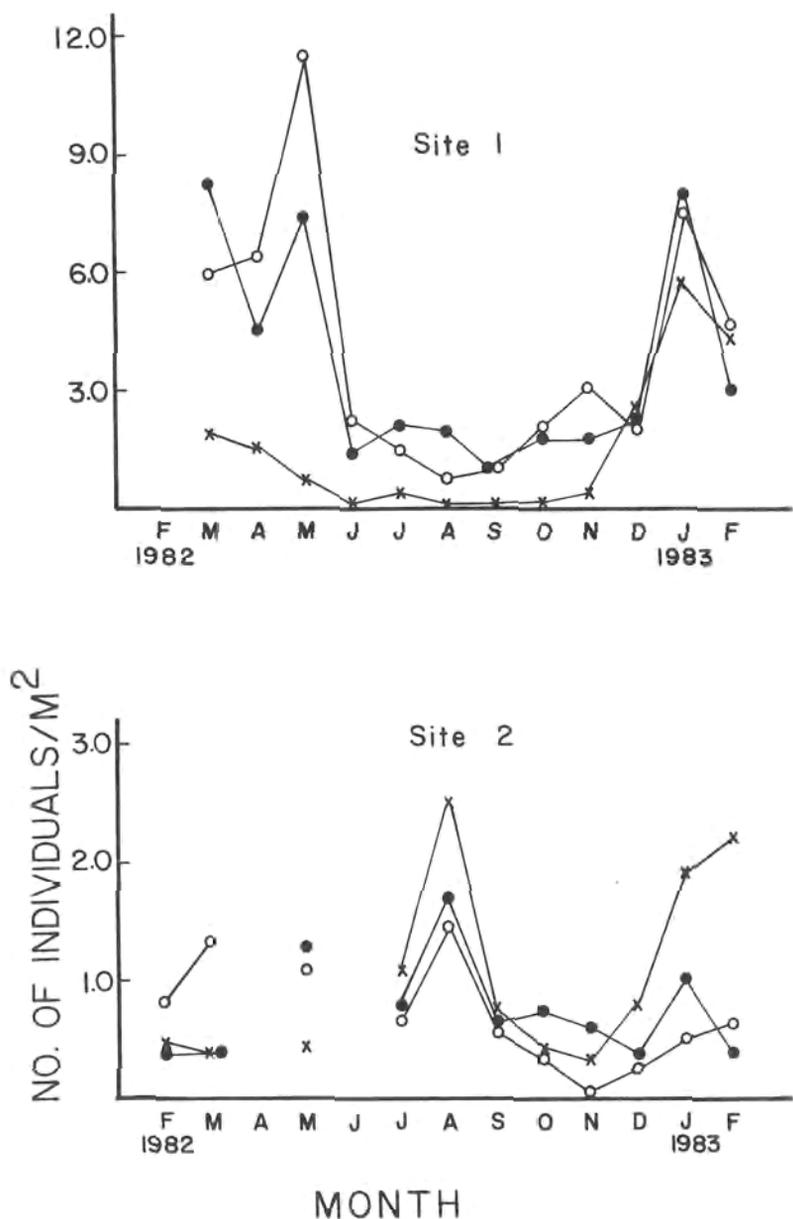
Fig. 2. Mean abundances (number of individuals per m² of sampling effort) of *Pagurus criniticornis* (open circles), *Clibanarius antillensis* (solid circles), and *Cl. tricolor* ("x") from night samples at Site 1 (above) and Site 2 (below). For clarity of presentation, estimates of variation on the mean are not illustrated. See Table 4 which shows which means are significantly different in each species. There was no February night sample at Site 1 in 1982 and none in April and June at Site 2.
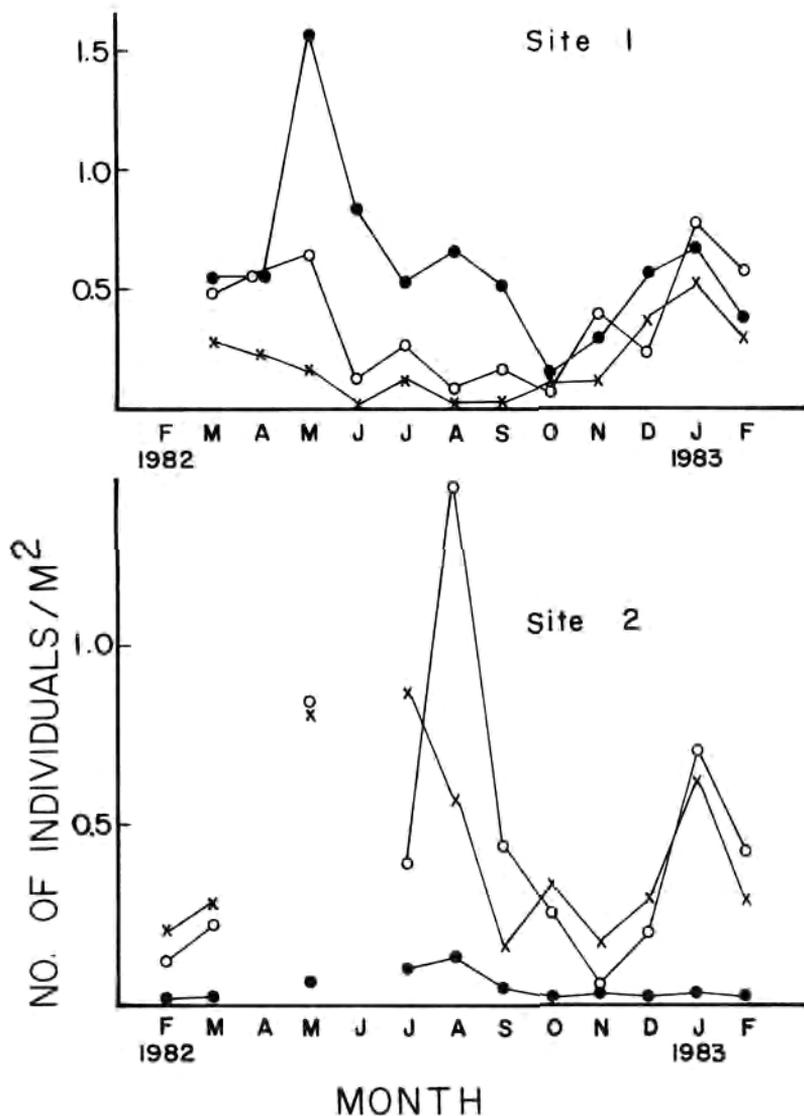
Fig. 3.   Mean abundances (number of individuals per m² of sampling effort) of *Pagurus brevidactylus* (open circles), *P. stimpsoni* (solid circles), and *Calcinus tibicen* ("x") from night samples at Site 1 (above) and Site 2 (below). For clarity of presentation, estimates of variation on the mean are not illustrated. See Table 4 which shows which means are significantly different in each species. There was no February night sample at Site 1 in 1982 and none in April and June at Site 2.

DISCUSSION

The hermit crab fauna at Dorado, Puerto Rico, was numerically dominated by *Pagurus criniticornis, Clibanarius antillensis,* and *Cl. tricolor.* In other systematic sampling studies in Florida sea grasses (e.g., Greening and Livingston, 1982; Gore *et al.,* 1981; Heck, 1976; Hooks *et al.,* 1976), the most abundant hermit crab (and

Table 2. Comparison of monthly abundance means (night samples) of different hermit crab species. A one-way ANOVA on $\log_{10}(x + 1)$ transformed data (number of individuals/m² sampling effort) was used to calculate the probability of the hypothesis that there was no significant difference among monthly means in each species at a given site. The probability of the null hypothesis is given below each species. The Student-Newman-Keuls test was used to determine differences among specific means; monthly means (listed in order of increasing size) joined by the same vertical line are not significantly different at the 0.05 confidence level. *Cl. tri.*, *Clibanarius tricolor*; *Cl. ant.*, *Cl. antillensis*; *C. tib.*, *Calcinus tibicen*; *P. crini.*, *Pagurus criniticornis*; *P. brev.*, *P. brevidactylus*; *P. stim.*, *P. stimpsoni*. All abbreviations for months signify 1982 samples except for J83 (January, 1983) and F83 (February, 1983). There was no February night sample at Site 1 in 1982 and none in April and June at Site 2.

Cl. tri.	Cl. ant.	C. tib.	P. crini.	P. brev.	P. stim.
Site 1					
Sep	Sep	Jun	Aug	Aug	Oct
Jun	Aug	Aug	Sep	Oct	Nov
Aug	Oct	Sep	Jul	Jun	F83
Oct	Jun	Oct	Dec	Sep	Sep
Jul	Nov	Jul	Jun	Jul	Jul
Nov	Jul	Nov	Oct	Dec	Mar
May	Dec	May	Nov	Nov	Apr
Apr	F83	Apr	F83	Mar	Dec
Mar	May	Mar	Mar	Apr	J83
Dec	Apr	F83	Apr	F83	Aug
J83	Mar	Dec	J83	May	Jun
F83	J83	J83	May	J83	May
(<0.0001)	(<0.0001)	(>0.10; ns)	(<0.0001)	(<0.005)	(<0.005)
Site 2					
May	Dec	Sep	Nov	Nov	Feb
Nov	Feb	Nov	Dec	Feb	F83
Mar	Mar	Feb	Oct	Dec	Mar
Oct	F83	Mar	Jan	Mar	Oct
Feb	Sep	F83	Sep	Oct	Dec
Sep	Nov	Dec	F83	F83	Nov
Jul	Jul	Oct	Jul	Jul	J83
Dec	Oct	Aug	Feb	Sep	Sep
J83	J83	May	May	May	May
F83	May	J83	Aug	J83	Jul
Aug	Aug	Jul	Mar	Aug	Aug
(<0.0005)	(0.025 > P > 0.01)	(<0.005)	(<0.0005)	(<0.001)	(>0.10; ns)

often the most abundant decapod) reported was *Pagurus bonairensis*. However, the "*P. bonairensis*" of these reports probably represents more than one species. Lemaitre *et al.* (1982) consider *P. bonairensis* a synonym of *P. stimpsoni*, one of the less abundant species in the Dorado meadows. Garcia-Gomez (1982) points out that in Florida waters, hermits described in ecological studies as *P. bonairensis* are a mixture of *P. maclaughlinae* with a smaller proportion of *P. bonairensis* (=*P. stimpsoni*). Thus, the *Pagurus* component of the hermit crab fauna at Dorado, Puerto Rico, is a similar mixture of one *Pagurus* species (*P. criniticornis*) with *P. stimpsoni* and also *P. brevidactylus*. The major difference between Florida (subtropical) sea grass meadows and my tropical sites is the abundance of the diogenids *Clibanarius antillensis* and *Cl. tricolor* at the Puerto Rico sites. These diogenids are common in the rocky intertidal in Puerto Rico as in Florida (Provenzano, 1959; Bach *et al.*, 1976), but in meadows around Puerto Rico extend down into sea grass habitats as well. Differences in relative abundances of the various hermit
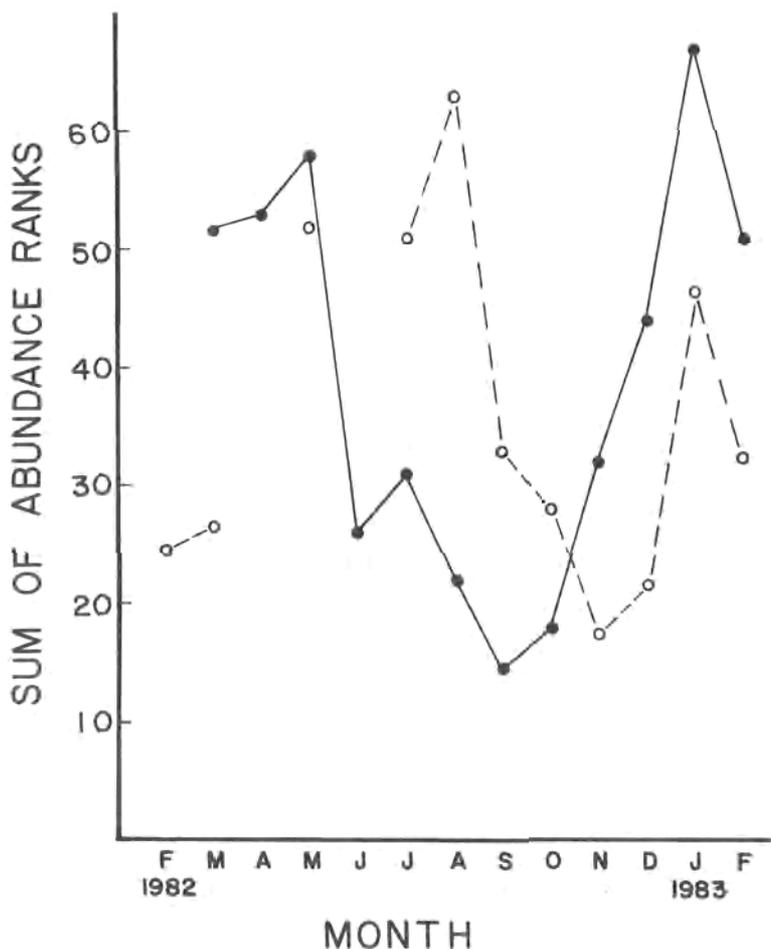
Fig. 4. Joint variation in abundances of the six most numerous hermit crab species. The monthly means of abundance from night samples were ranked in each species. The sum of ranks of all species for each month is illustrated above for Site 1 (solid circles) and Site 2 (open circles). There was no February night sample at Site 1 in 1982 none in April and June at Site 2.

crab species among areas are apparently highly related to interactions among shell supply, shell utilization patterns, and competition for shells (e.g., Bach *et al.*, 1976; Bertness, 1980, 1981a, b, c, 1982; Hazlett, 1981). Variation in the intensity and kind of predation pressure might also explain variation in the species composition of the hermit crab fauna between subtropical and tropical sites. For example, Engstrom (1984) found that differences in fish predation between a tropical (Belize) and subtropical (Florida) area accounted for changes in the bathymetric distribution (intertidal versus extension into the shallow subtidal) of a xanthid crab.

The number of hermit crabs taken in night samples is significantly higher than in day collections. I frequently observe in sea grass meadows that, during the day, solid objects such as pieces of coral rubble are studded with shells containing inactive hermit crabs. At night, these aggregations of hermit crabs disperse, and

structures such as rocks and coral rubble are vacant. Dispersed active hermits would be more susceptible to push net capture (unless the net "captures" a day aggregation center, which occasionally happens). This day–night behavioral difference probably accounts for the increased night abundances in samples. The daytime hermit crab congregations might also be located among rhizomes below the surface of the bed, along the margins of the bed (where extensive cavities formed by exposed rhizomes are created), or in other areas inaccessible to the push net. As discussed in Greening and Livingston (1982) and Bauer (in press), the nocturnal activity of hermit crabs and other sea grass crustaceans (caridean and penaeoid shrimps) is probably an adaptation for avoiding predation by visually hunting fishes.

Another, less likely possibility explaining day–night differences in abundance is that the hermit crabs make daily migrations between the sea grass meadows and other habitats, e.g., the nearby rocky reef. However, at the Dorado sites, the hermits would have to cross at least several meters of sandy bottom to reach nearby rocky areas. Heck and Thoman (1981) have shown that exposed decapods (including hermit crabs) are much more vulnerable to predation on unvegetated subtidal areas than in sea grass meadows. In addition, Hazlett (1983) has shown that *Clibanarius tricolor* and *Calcinus tibicen,* two of the hermits from the Dorado sites, show high site attachment and do not make large daily movements.

At my study sites, peaks of abundance of hermit crabs occurred in spring (Site 1) and summer (Site 2) and again in winter (both sites) at this tropical location. Monthly variation in abiotic factors such as water temperature (26–31°C) and salinity (34–36‰) was slight at these meadows. Bauer (in press) described similar patterns in the nine most abundant caridean species, and life history studies (in progress) indicate that recruitment of juveniles of both the carideans and the penaeoids *Sicyonia parri* and *S. laevigata* is highly seasonal and corresponds to the abundance peaks. Similar analyses might show seasonal recruitment of juveniles for the hermit crab fauna at Dorado, Puerto Rico. An understanding of seasonality in abundance, reproduction, and recruitment in hermit crabs will require further study. Bertness (1981d, e, f), Fotheringham (1976, 1980), and Hazlett (1981), among others, have shown that reproduction and recruitment depend on a complicated set of factors relating to shell supply and adequacy, while Bertness (1981e) has also suggested the possible effect of variations in the planktonic (larval) environment on recruitment in the tropics.

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