

## DIEL AND SEASONAL VARIATION IN SPECIES COMPOSITION AND ABUNDANCE OF CARIDEAN SHRIMPS (CRUSTACEA, DECAPODA) FROM SEAGRASS MEADOWS ON THE NORTH COAST OF PUERTO RICO

*Raymond T. Bauer*

### ABSTRACT

Seagrass meadows dominated by *Thalassia testudinum* near Dorado, on the north coast of Puerto Rico, were sampled for 13 months by pushnet with a 1-mm mesh bag. Ten random samples were taken monthly both day and night at each of two replicate sites. Eighteen species of caridean shrimp were collected but 99.9% of the total abundance ( $N = 74,816$ ) was accounted for by nine species: *Latreutes fucorum* (57.0%), *Periclimenes americanus* (10.9%), *Thor manningi* (9.5%), *Alpheus normanni* (8.3%), *Hippolyte curacaoensis* (6.0%), *Latreutes parvulus* (3.1%), *Processa bermudensis* (2.3%), *Processa riveroi* (1.4%), and *Leander tenuicornis* (1.4%). Night samples were similar to day samples in overall species composition except that the day-burrowing processids were conspicuously absent from daytime collections. However, with the possible exception of *Hippolyte curacaoensis*, mean abundances of all species were consistently higher at night. Greatest night-day differences in frequency of occurrence in samples were found in the two *Processa* species, the least in leaf-inhabiting species such as *Hippolyte curacaoensis* and *Latreutes fucorum*. Laboratory observations strongly indicate that nocturnal emergence onto the surface of the seagrass beds from daytime burrows below the sediment accounts for the increased night collectability of *Alpheus normanni* and the two *Processa* species. Laboratory observations also indicate increased nocturnal activity (in the form of increased swimming) for the other species, especially *Latreutes fucorum* and *Hippolyte curacaoensis*, which may make them more susceptible to net capture at night.

Abundances of the principal (most numerous) nine caridean species were markedly seasonal, with highest abundances in late spring and summer and again in December and January, with population lows in October and November and again in February and March.

Caridean densities estimated in this study (overall, 16 shrimps/m<sup>2</sup> of sampling effort in day samples, 49/m<sup>2</sup> in night samples) are much higher than those of most previous studies in seagrasses. The small mesh net used (1 mm) probably accounts, in part, for the high abundances measured for these very small carideans; much lower densities are reported in studies using nets with larger mesh (e.g., 6-7 mm).

Seagrass meadows cover extensive areas in shallow coastal waters of the world (den Hartog, 1977) and are one of the most productive marine habitats (Thayer et al., 1975; McRoy and Helfferich, 1977). The role of seagrass beds as nursery grounds, areas where juveniles of fishes and various invertebrates feed and grow rapidly before leaving for their adult habitats, is often cited (Kikuchi and Pérès, 1977; McRoy and Helfferich, 1977; Young et al., 1976; Thayer et al., 1975; Kikuchi, 1974). Seagrass beds also serve as foraging grounds for adult fishes. Weinstein and Heck (1979) showed that adult fishes arrive at Panamanian *Thalassia* meadows at night from nearby coral reefs, presumably to forage on the abundant epifaunal invertebrates. Randall (1968) mentioned various groups of fishes, e.g., grunts (Pomadasyidae) and snappers (Lutjanidae), that feed by night over seagrass beds in the Caribbean.

The ecology of the invertebrate mobile epifauna (especially that of individual species) inhabiting seagrass meadows dominated by turtlegrass, *Thalassia testudinum*, has been little studied. The invertebrate epifauna of turtlegrass beds, like that of other seagrass meadows, may have an essential role in the transfer of

primary production, directly or indirectly, to higher trophic levels. Kikuchi (1974; 1980) and Kikuchi and Peres (1977) reviewed studies on seagrass epifauna, particularly those from temperate areas, while the review of Heck and Orth (1980a) included studies on tropical seagrass meadows. Greening and Livingston (1982), Thorhaug and Roessler (1977), Heck (1976; 1979), and Hooks et al. (1976) sampled extensively in *Thalassia* meadows in Florida, while Heck (1977) analyzed the epifaunal invertebrate assemblage from *Thalassia* meadows along the Caribbean coast of Panama. Gore et al. (1981) studied in detail the decapod crustacean epifaunal assemblage from a subtropical drift algae-seagrass habitat in Florida.

I sampled the mobile invertebrate epifauna of *Thalassia testudinum* meadows on the north coast of Puerto Rico for 13 months. In this report, I describe the species composition of the caridean shrimp component of the epifauna as well as the diel and monthly variation in shrimp abundances. The caridean shrimps are perhaps the most numerically important component of the macroepifaunal assemblage, comprising 20–90% of the total number of individuals in the monthly samples. One objective of this report is to determine if there are significant differences between abundance estimates based on day and night sampling. Although most studies on *Thalassia* epifauna have employed day sampling (Hooks et al., 1976; Heck, 1976; 1977), studies both in *Thalassia* beds (Greening and Livingston, 1982) and in other seagrass beds (Heck and Orth, 1980b; Kikuchi and Peres, 1977; Kikuchi, 1962; 1966) indicate that many epifaunal invertebrates are more abundant in night collections. In addition, in all of the studies on *Thalassia* cited above, collecting nets had a mesh size of several millimeters. However, many of the numerically abundant shrimp species that occur in *Thalassia* meadows have a small adult body size so that juveniles and small adults may pass readily through a net with such a large mesh. Therefore, another objective of this study was to estimate caridean shrimp abundances with samples taken with a fine mesh (1 mm) net.

## METHODS

The seagrass meadows were located in a small cove just beyond the eastern end of the Dorado Public Beach, Urbanización de Mameyal, Municipio de Dorado, north coast of Puerto Rico (18°29'N, 66°15'W). The cove and its seagrass beds are protected from the often heavy open ocean swell by a series of shallow rocky reefs located roughly parallel to the shore on the seaward side of the meadows. These seagrass beds had the form of terraces raised approximately 1 m above the surrounding sand bottom. The meadows were composed of a dense mixture of *Thalassia testudinum* and *Syringodium filiforme*, with *Thalassia* the much more abundant vegetation. The presence of unattached or drift algae was not noticeable in the samples.

Two sites within the Dorado *Thalassia* meadows were chosen as replicate sampling areas. Located 40 m apart, the two sites were almost isolated from each other by the surrounding sand bottom. The median water depth varied from 0.4 m to 1.0 m during sampling which took place at lower tide periods (-0.2 m to +0.1 m). Site 1 was a triangular area 21 m × 39 m × 29 m while Site 2 was a square 20 m × 20 m. These areas, located within larger meadows, were designated as sampling sites because they were relatively free from holes and other irregularities which would interfere with continuous pushnet motion during sampling.

All samples were taken randomly. The two sites were divided on a map into strips 0.5 m × 10 m, the size of a sample unit. Each potential unit was numbered, subsequently chosen from a random numbers table, and located by measurements from reference markers. Samples were taken by a pushnet (similar to that in Manning, 1975) 0.5 m wide with a 1-mm mesh liner sewed into the net bag. After a sample was taken, all material was removed from the net and placed in a plastic bag with seawater; a 37–40% formaldehyde solution was immediately added to make an approximately 10% formalin solution. In the laboratory, animals were separated from debris and placed in 70% ethanol for permanent storage.

The field study was conducted from February 1982 through February 1983. Each month, 10 day and 10 night samples were taken at each of the two sites. Day (between sunrise and sunset) samples for both sites were taken on one date, and night (between sunset and sunrise) collections were taken

Table 1. Species composition and abundances (number of individuals collected) of caridean shrimp from Dorado, Puerto Rico, sampling Sites 1 and 2, day and night collections combined

Rank	Species	No. collected
1	<i>Latreutes fucorum</i> (Fabricius)	42,638
2	<i>Periclimenes americanus</i> (Kingsley)	8,139
3	<i>Thor manningi</i> Chace	7,087
4	<i>Alpheus normanni</i> Kingsley	6,243
5	<i>Hippolyte curacaoensis</i> Schmitt	4,506
6	<i>Latreutes parvulus</i> (Stimpson)	2,296
7	<i>Processa bermudensis</i> (Rankin)	1,721
8	<i>Processa riveroi</i> Manning and Chace	1,029
9	<i>Leander tenuicornis</i> (Say)	1,014
10	<i>Lysmata moorei</i> (Rathbun)	17
11	<i>Brachycarpus biunguiculatus</i> (Lucas)	39
12	<i>Periclimenes iridescens</i> Lebour	10
13	<i>Trachycaris restrictus</i> (A. Milne-Edwards)	9
14	<i>Gnathophyllum americanum</i> Guerin-Meneville	7
15	<i>Xiphocaris elongata</i> (Guerin-Meneville)	3
16	<i>Salmoneus</i> sp.	2
17.5	<i>Tozeuma carolinense</i> Kingsley	1
17.5	<i>Atya</i> sp.	1

on another. The median number of days between the day and night field study for a given month was three (range: 1–9). The time of sampling varied with the hours of low tides. Night collections were usually taken at periods of new moon to first quarter. The moon was between full and last quarter for the April night samples but work was completed before moonrise; the March night collections were taken under a full moon. There were three exceptions to strictly day or night samples. The May Site 1 day samples began at 1725 Atlantic Standard Time and ended at 1925 and the May Site 2 night collection began at 1830 and ended at 2000; sunset was at 1833 and darkness fell at approximately 1900. The June Site 1 night samples were from 0440 to 0555; sunrise was at 0522. In June at Site 2 there were no night collections, rather two daytime sampling periods, one just after sunrise and the other in the late afternoon (two days apart). Storms prevented field studies in February 1982, at Site 1; only 3 July Site 1 day samples were taken due to bad weather. April Site 1 day and Site 2 night collections were poorly preserved and had to be discarded.

Temperature was measured during monthly field studies and varied from lows in February of 26°C to a September high of 31°C. Salinity measurements were taken during the last six months of the study with an A&O temperature-compensated refractometer. Salinity varied between 34‰ and 36‰ and measurements to November 1983 did not vary out of that range.

Behavioral observations were made on shrimps maintained in recirculating saltwater aquaria in a room with a 12-h day and 12-h night cycle; day illumination was provided with fluorescent lights. Night observations were made under red light, by using flashlights at periodic intervals, and by photographs made using a flash unit.

## RESULTS

*Species Composition and Relative Abundance.*—In the 13 months of sampling (486 samples) at the two Dorado *Thalassia* sites, nearly 75,000 caridean shrimps were collected. Among these carideans are representatives of 18 species, 15 genera, and 6 families (Alpheidae, Atyidae, Gnathophyllidae, Hippolytidae, Palaemonidae, Processidae) (Table 1). Nine of the 18 species account for 99.9% of all individuals: the hippolytids *Latreutes fucorum* (57.0%), *L. parvulus* (3.1%), *Thor manningi* (9.5%), and *Hippolyte curacaoensis* (6.0%); the palaemonids *Periclimenes americanus* (10.9%) and *Leander tenuicornis* (1.4%); the processids *Processa bermudensis* (2.3%) and *P. riveroi* (1.4%); and the alpheid *Alpheus normanni* (8.3%). Four very small juveniles of *Xiphocaris elongata* and *Atya* sp. were collected; these atyid species are freshwater as adults.

In terms of overall individual abundances Sites 1 and 2 differed greatly; the

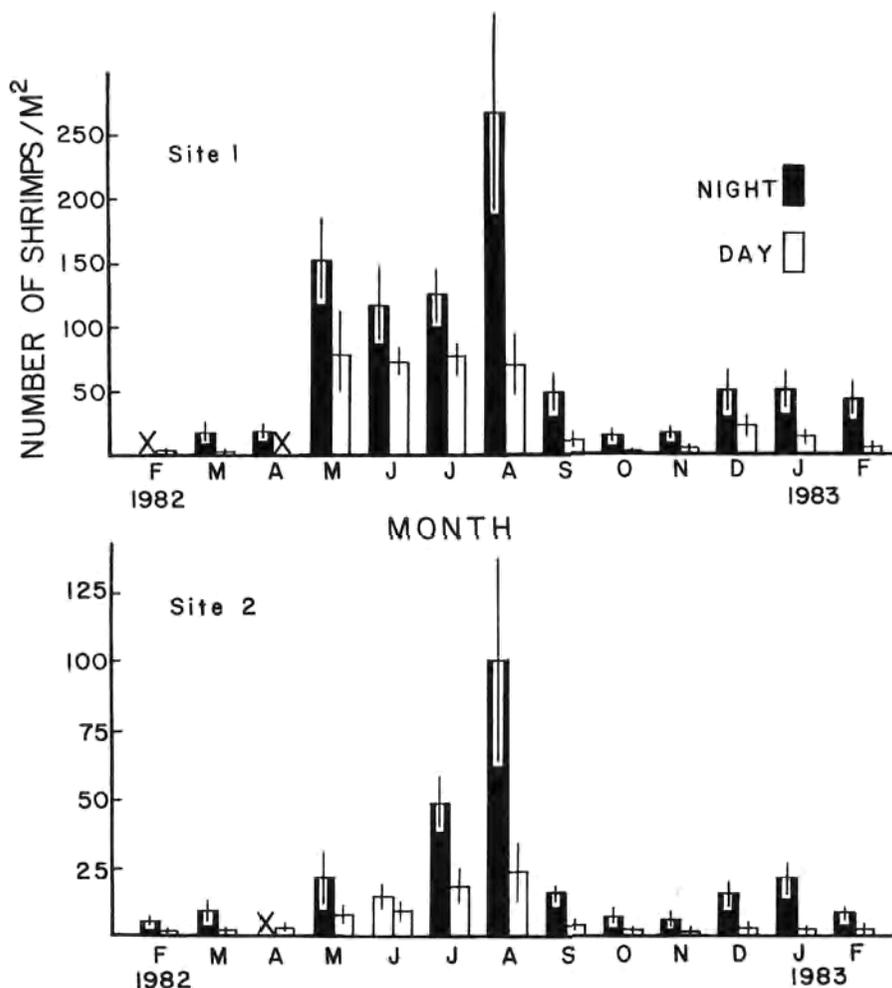


Figure 1. Comparison of monthly night (solid bars) and day (clear bars) abundances of caridean shrimps at Sites 1 and 2. Bars represent mean number of shrimps captured per square meter of sampling effort (area swept by pushnet); 95% confidence intervals on means are given. An "X" indicates no sample.

total number of caridean shrimps at Site 1 was 57,706 but only 17,089 at Site 2. *Latreutes fucorum*, *Periclimenes americanus*, *Alpheus normanni*, *Thor manningi*, and *Processa bermudensis* were the species primarily responsible for the much higher (3.38 $\times$ ) abundance at Site 1. However, the two sites were quite similar in the relative abundance of the numerically important species. When the rank order of abundance of the principal (most numerous) nine species is compared between Site 1 and Site 2 (using the more representative night collections, see below), there is substantial agreement at the two sampling sites (Spearman rank correlation coefficient  $r = +0.883$ ;  $0.001 < P < 0.005$ ).

*Diel Variation in Species Composition and Abundance.*—At both sites, the total abundance in night samples was approximately three times that in day collections

Table 2. Comparison of paired monthly night and day mean abundances of the principal caridean shrimp species. For each species, the number of months is given in which the night mean was greater than (+) or less than (-) the day mean. The one-sided hypothesis tested (sign test) was that the median of monthly night minus day mean abundance was not greater than zero, i.e., night means were not consistently greater than day means. S = significant,  $P < 0.05$ ; NS = nonsignificant,  $P > 0.05$

Species	Site 1	Site 2
<i>Latreutes fucorum</i>	11 (+), 0 (-); S	11 (+), 0 (-); S
<i>Latreutes parvulus</i>	11 (+), 0 (-); S	11 (+), 0 (-); S
<i>Thor manningi</i>	11 (+), 0 (-); S	11 (+), 0 (-); S
<i>Alpheus normanni</i>	11 (+), 0 (-); S	11 (+), 0 (-); S
<i>Leander tenuicornis</i>	11 (+), 0 (-); S	9 (+), 1 (-); S
<i>Periclimenes americanus</i>	11 (+), 0 (-); S	10 (+), 0 (-); S
<i>Processa riveroi</i>	11 (+), 0 (-); S	11 (+), 0 (-); S
<i>Processa bermudensis</i>	11 (+), 0 (-); S	11 (+), 0 (-); S
<i>Hippolyte curacaoensis</i>	7 (+), 4 (-); NS	10 (+), 1 (-); S

(Site 1 night:day abundance = 3.15; Site 2 night:day = 2.83). In terms of species composition, the two *Processa* species were noticeably absent from day samples. The hippolytid *Lysmata moorei* and the palaemonid *Brachycarpus biunguiculatus* were seldom found (Table 1) but, when collected, occurred only in night samples.

Night mean abundances of carideans were significantly higher than day abundances throughout the year at both sites (Fig. 1). However, data which groups all carideans could be dominated by the few most numerous species; the day-night differences in abundance of individual species are important and must be considered. Therefore, the difference between paired monthly night and day mean abundance was calculated for all principal species at both sites. A positive difference indicates that the night mean was higher than the day mean for a particular month; a negative difference results from a higher daytime abundance. The number of occurrences of positive or negative differences is given for each species in Table 2. The sign test (Tate and Clelland, 1957) was used to calculate the probability of the one-sided hypothesis: the median of the night-day differences in monthly mean abundance is not greater than zero (positive). For all species at both sites, except *Hippolyte curacaoensis* at Site 1, the null hypothesis is rejected ( $P < 0.05$ ) and the alternative hypothesis that night-day differences in abundance are positive is accepted.

Another way to view night-day differences in collectability of the various shrimp species is to examine frequency of occurrence. For each species, the difference between night and day sample frequency (proportion of samples with at least one individual) for a particular month was calculated. The median difference for each species at each site is shown in Table 3. Larger positive values indicate higher frequency of occurrence at night. Values approaching zero indicate equal frequency of occurrence day and night. Negative values would indicate higher frequency in day collections. In Table 3, the species are ranked from highest to lowest median night-day difference in sample frequency. *Processa riveroi* and *P. bermudensis* are species at one extreme, i.e., species which are most frequently collected at night but are rare in day samples. At the other extreme are *Latreutes fucorum* and *Hippolyte curacaoensis* in which frequency of occurrence (but not necessarily abundance) was similar in night and day samples.

Three sets of samples which, because of the timing of low tide, were not taken exactly between sunrise and sunset (day) or sunset and sunrise (night). These collections give a view of variation in caridean abundances during the transition

Table 3. Median and 95% confidence intervals of the difference (night frequency of occurrence minus day frequency) for monthly collecting periods. Larger values indicate higher frequency at night while values approaching zero show species with similar frequency of occurrence night and day. Species are ranked from greatest (most "night-collectable") to least night-day difference in frequency.

Rank	Species	Median (95% C.L.) of (night frequency minus day frequency)
Site 1		
1	<i>Processa bermudensis</i>	0.9 (0.9-1.0)
2	<i>Processa riveroi</i>	0.7 (0.4-1.0)
3	<i>Thor manningi</i>	0.5 (0.0-0.7)
4	<i>Latreutes parvulus</i>	0.4 (0.1-0.7)
5.5	<i>Alpheus normanni</i>	0.3 (0.0-0.9)
5.5	<i>Leander tenuicornis</i>	0.3 (0.0-0.7)
7	<i>Periclimenes americanus</i>	0.1 (0.0-0.6)
8.5	<i>Latreutes fucorum</i>	0.0 (0)
8.5	<i>Hippolyte curacaoensis</i>	0.0 (0.0-0.1)
Site 2		
1	<i>Processa riveroi</i>	1.0 (0.7-1.0)
2.5	<i>Processa bermudensis</i>	0.7 (0.4-1.0)
2.5	<i>Alpheus normanni</i>	0.7 (0.0-0.8)
4	<i>Latreutes parvulus</i>	0.6 (0.1-1.0)
5.5	<i>Thor manningi</i>	0.2 (0.0-0.5)
5.5	<i>Periclimenes americanus</i>	0.2 (0.0-0.4)
7	<i>Leander tenuicornis</i>	0.15 (0.1-0.6)
8	<i>Latreutes fucorum</i>	0.1 (0.0-0.6)
9	<i>Hippolyte curacaoensis</i>	0.0 (0.0-0.2)

between day and night or vice versa. A striking increase in the numbers of carideans with increasing darkness (=higher sample number) can be observed at dusk (Fig. 2a and b). A decline in total caridean numbers was observed in dawn samples (Fig. 2c). Such a plot of grouped data can be dominated by the most abundant species; variations in abundance of individual species must be analyzed. For each species, a possible correlation between increasing or decreasing abundance with time was calculated using the Spearman rank correlation coefficient. For samples beginning before and ending after sunset, given the previous data on night-day differences in abundance, a positive correlation or increase in shrimp numbers with the onset of darkness was hypothesized; for the samples which began at night but progressed past sunrise, a negative correlation between abundance and sample number was expected.

Table 4 shows that increases in abundance with increasing darkness during the dusk collections are statistically significant for all species except *Hippolyte curacaoensis* (May Site 1) and *Latreutes fucorum* (May Site 2). The June Site 1 night collections were taken during the transition from night to day. In this case, a decline in abundance with time (increasing light) was expected. Although the correlation between abundance and time (sample number) was negative for all species, the correlation was statistically significant only in *Latreutes fucorum*, *Alpheus normanni*, *Periclimenes americanus*, and *Processa riveroi* (Table 4).

*Seasonal Variations in Abundance.*—Peak numbers of carideans occurred from May–September 1982, with a decline to lows in October and November; a secondary high occurred in December and January, with a drop in February 1983, back to the previous February and March levels (Fig. 1). Grouping all species could mask the variation in abundance of individual species when, as in this assemblage, a few species were much more numerous than the others. Kendall's

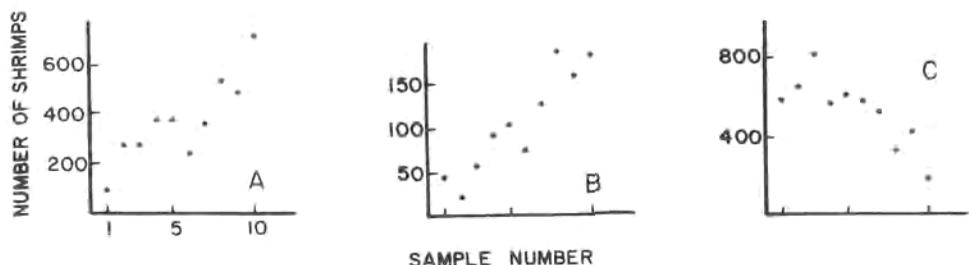


Figure 2. Changes in the number of carideans captured per sample in collections beginning before and terminating after sunset (A, May Site 1; B, May Site 2) or before and after sunrise (C).

coefficient of concordance,  $W$ , was calculated to determine if population abundances of the 9 most abundant species had varied together, i.e., did population highs and lows take place at about the same time for most species? The monthly mean night densities of each species were ranked for the entire year of sampling. For each month, the ranks of all species were summed (Fig. 3) to determine if there was substantial agreement among monthly abundances. The chi-square given in Tate and Clelland (1957: 76-77) was used to calculate the probability that the coefficient of concordance ( $W$ ) is equal to zero, i.e., the null hypothesis of no concordance. At Site 1,  $W = 0.38$ ,  $\chi^2$  (11 df) = 37.6,  $P \ll 0.005$ ; at Site 2,  $W = 0.53$ ,  $\chi^2$  (10 df) = 47.7,  $P \ll 0.005$ . At both sites, there is a statistically significant concordance among species in their peaks and valleys of abundance.

*Laboratory Observations on Microhabitat and Diel Activity.*—Qualitative observations on diel variation in activity and microhabitat preferences of the principal species have yielded the following information. *Hippolyte curacaoensis*, *Latreutes fucorum*, and *L. parvulus* are species which mainly rest on *Thalassia* or *Syringodium* leaves during the day. In the dark, *L. fucorum* and *H. curacaoensis* often rise off the leaves and swim among them. Both *Processa* species are very nocturnal, lying buried under the bottom sediments during the day; at night, they emerge onto the surface. When lights are turned on in the laboratory, these shrimps immediately bury themselves. *Alpheus normanni* construct burrows in which they usually remain during the day but from which they emerge at night. *Periclimenes americanus*, *Leander tenuicornis*, and *Thor manningi* occur both on the seagrass leaves and on the bottom; qualitative day-night differences in activity are not obvious although quantitative observations may reveal them.

## DISCUSSION

In the tropical *Thalassia testudinum* seagrass meadows investigated, caridean shrimps were much more numerous in night collections than in day samples. For all the nine most numerous species (except *Hippolyte curacaoensis* at one site), monthly mean night abundances were consistently higher than the corresponding day means. The number of carideans increased dramatically after darkness in samples begun before and extending beyond sunset.

The increased collectability of shrimps at night could be due to nocturnal activity with concomitant susceptibility to net capture, to net avoidance in day samples, or to migrations onto the beds at night from other areas. Laboratory observations strongly indicate that at least some of the species are much more active at night and thus more accessible to net capture. *Processa riveroi* and *P. bermudensis* are

Table 4. Correlations of numbers of individuals and sample number (increasing time) in 3 collections transitional between night and day or day and night. The Spearman rank correlation coefficient ( $r_s$ ) is given for the possible correlation between abundance and sample number for each species. The probability of the one-sided hypotheses: no positive correlation (day to night samples) or no negative correlation (night to day) is given. Probabilities  $<0.05$  are considered significant, i.e., the null hypothesis is rejected

Species	$r_s$	Probability	Significance
May Site 1 (day to night)			
<i>Latreutes parvulus</i>	+0.648	0.01 $< P < 0.05$	+
<i>Latreutes fucorum</i>	+0.927	$<0.001$	+
<i>Processa riveroi</i>	+0.809	0.001 $< P < 0.005$	+
<i>Processa bermudensis</i>	+0.936	$<0.001$	+
<i>Thor manningi</i>	+0.939	$<0.001$	+
<i>Hippolyte curacaoensis</i>	-0.491	$>0.10$	-
<i>Alpheus normanni</i>	+0.718	0.01 $< P < 0.025$	+
<i>Periclimenes americanus</i>	+0.761	0.001 $< P < 0.005$	+
<i>Leander tenuicornis</i>	+0.776	0.001 $< P < 0.005$	+
May Site 2 (day to night)			
<i>Latreutes parvulus</i>	+0.912	$<0.001$	+
<i>Latreutes fucorum</i>	+0.285	$>0.10$	-
<i>Processa riveroi</i>	+0.958	$<0.001$	+
<i>Processa bermudensis</i>	+0.718	0.01 $< P < 0.025$	+
<i>Thor manningi</i>	+0.894	$<0.001$	+
<i>Hippolyte curacaoensis</i>	+0.876	$<0.001$	+
<i>Alpheus normanni</i>	+0.930	$<0.001$	+
<i>Periclimenes americanus</i>	+0.603	0.025 $< P < 0.05$	+
<i>Leander tenuicornis</i>	+0.782	=0.005	+
June Site 1 (night to day)			
<i>Latreutes parvulus</i>	-0.239	$>0.10$	-
<i>Latreutes fucorum</i>	-0.903	$<0.001$	+
<i>Processa riveroi</i>	-0.821	0.001 $< P < 0.005$	+
<i>Processa bermudensis</i>	-0.521	0.05 $< P < 0.10$	-
<i>Thor manningi</i>	-0.139	$>0.10$	+
<i>Hippolyte curacaoensis</i>	-0.024	$>0.10$	-
<i>Alpheus normanni</i>	-0.588	0.025 $< P < 0.05$	+
<i>Periclimenes americanus</i>	-0.648	0.01 $< P < 0.05$	+
<i>Leander tenuicornis</i>	-0.518	0.05 $< P < 0.10$	-

quite infrequent in day samples and not available for day capture because of daytime burrowing habits. *Alpheus normanni*, like the processids, is nocturnal and generally stays below the meadow surface in burrows during the day. The grass shrimps *Latreutes fucorum* and *Hippolyte curacaoensis* cling to seagrass leaves during daylight hours but swim more frequently at night (unpublished student project). The frequency of occurrence of these shrimps in samples is similar day and night but their abundance is much higher in night samples. Their night swimming behavior may make them more susceptible to net capture; visual avoidance of the pushnet during the day is a possibility. *Leander tenuicornis*, *Periclimenes americanus*, and *Thor manningi* apparently occur above the sediment surface and among seagrass leaves day and night; night swimming and/or daytime net avoidance might account for their higher night abundances. Daily migrations to and from the meadows seem an unlikely explanation for day-night differences in abundance for these species. Seagrass meadows are previously recorded habitats for most of these species (Chace, 1972; Williams, 1984). Although abundances are higher at night, at least some of each species can be

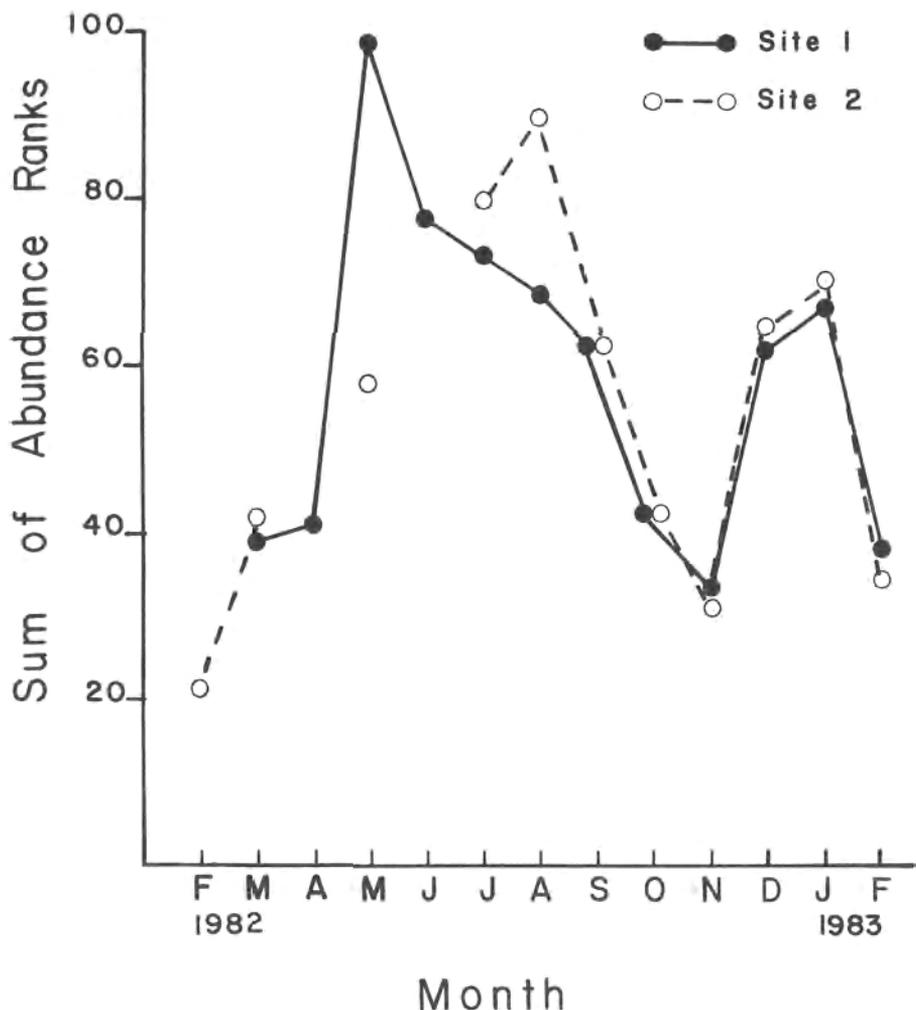


Figure 3. Monthly variation in abundance for the principal nine caridean species as measured by monthly sum of ranks from Kendall Concordance Test. Monthly mean night abundances of each species were ranked from lowest to highest; sum of ranks of all species for individual months is plotted. Site 1, solid dots; Site 2, open circles.

collected from the meadows during the day either by net (e.g., *L. fucorum*, *Thor manningi*) or by sorting through meadow sediments or among seagrass rhizomes (the processids and the alpheid). Movement away from the cover of the seagrass bed would most likely expose these shrimps to increased predation (Coen et al., 1981; Heck and Thoman, 1981).

It seems obvious that, for these caridean species in these seagrass beds, abundance estimates should be based on night sampling. Night collections should at least be part of studies on seagrass epifaunal community structure because caridean and other decapod shrimps are the numerically dominant or one of the numerically important components in these habitats (Greening and Livingston, 1982; Gore et al., 1981; Heck and Orth, 1980b; Heck, 1979; Kikuchi and Pérès, 1977; Hooks et al., 1976). Greening and Livingston (1982) found that, when benthic algae were

very abundant on a seagrass bed, some nocturnal species took refuge in them and were thus captured in day samples which scraped up the algae. Preliminary sampling in a specific area might reveal which species are better captured in day or night samples or which are equally accessible day and night. However, if a study is not focused on a specific organism but the entire caridean or other decapod crustacean segment of the epifaunal assemblage, night sampling seems necessary.

The apparent nocturnal activity of the principal caridean shrimp species in *Thalassia* seagrass beds in northern Puerto Rico and elsewhere is very likely a means by which these small shrimps avoid visually hunting diurnal fish predators. Greening and Livingston (1982) reviewed the evidence from previous studies that support this hypothesis. Several studies have indicated that shrimps and other crustaceans are important food items of fishes living on or foraging over seagrass beds (Adams, 1976; Goldman and Talbot, 1976; Kikuchi, 1966; 1974; Randall, 1967). The nocturnal behavior of these seagrass invertebrates does not protect them completely. The nocturnal and presumed feeding activity of many carnivorous fishes on seagrass beds or other habitats is well known (Hobson, 1965; 1975; Goldman and Talbot, 1976; Weinstein and Heck, 1979).

The abundances of all the principal caridean species showed marked seasonal variation. Variation in water temperature was not marked at this tropical location (26–31° C); caridean abundances show no obvious correlation with the temperature variation that did occur. Although not measured for the entire year, there is no evidence for pronounced salinity variations at the study sites. The strong fluctuations in population abundance of the caridean shrimps may be related to life history phenomena (e.g., seasonal recruitment), variations in predation pressure, or other biological factors. Life history studies (in progress) and qualitative observations on the samples indicate that strong seasonal pulses of recruitment did take place at the study sites; however, analysis of these shrimps' life history patterns is needed before speculating further. Gore et al. (1981) found that, although there was some evidence for seasonal recruitment, the marked variation in decapod species abundances in a subtropical drift-algae seagrass system was related to periodic increases in the quantity of drift algae. The seagrass meadows studied here on the north coast of Puerto Rico were, qualitatively, clean of drift algae. The pronounced seasonal variation in caridean abundances observed by me does not support the hypothesis of Heck and Orth (1980a) that the fluctuations of population abundance are low in tropical seagrass epifaunal invertebrate species.

The caridean shrimp densities from these tropical *Thalassia* beds appear very high compared to those reported in other studies. In fact, such densities are probably not unusual in tropical seagrass meadows and very likely are a result of adequate sampling with a fine mesh (1 mm) net. Collections at other areas along the north coast (Luquillo Platform, Isla Piñero) give a similar magnitude in caridean abundance. The body sizes of the numerically abundant caridean species in these tropical meadows are quite small (Williams, 1984, and Chace, 1972, for maximum body sizes of species discussed in this study). These small species (especially juveniles and smaller adults) can easily slip through the 6–7-mm mesh of nets often used which may account for the 1–4 orders of magnitude difference between densities reported here and in other studies (Greening and Livingston, 1982; Heck, 1976; 1977; 1979; Thorhaug and Roessler, 1977). Gore et al. (1981), using a drop net with seining by a 3-mm mesh net in a subtropical drift algae-seagrass habitat, reported densities which are the same order of magnitude as those observed in this investigation. An anonymous reviewer suggested that the high densities observed at the Puerto Rican sites might be due to their shallow depth which could prevent predatory fish from foraging there. In reality, these

meadows are not particularly shallow for *Thalassia* meadows; sampling had to be at low tide periods because at other times the water was too deep for pushnet sampling. While fish predators were not specifically monitored, there was no depth or temperature barrier to carnivorous fish from nearby rocky reefs. Predatory fish were collected both in the samples and observed on the meadows at other times by snorkeling or scuba. The striking decline in shrimp abundances in the fall from summer highs may well be due to predation on juveniles recruited in the summer (observations from life history studies in progress).

It is certainly true that in any net sampling one will capture more small organisms with a finer mesh. However, in studies of *Thalassia* invertebrate macroepifauna, carideans are considered numerically important species in the analysis of community structure. The large mesh net used in such studies might miss a large segment of the caridean populations so that their abundance relative to larger invertebrates would be underestimated. However, it should also be pointed out that, at least in some, if not all, of these studies, fish were being captured which would not be well sampled by a pushnet with fine mesh. For future studies on seagrass mobile epifaunal invertebrate community structure and especially for life history studies on caridean shrimp populations in seagrass beds, field studies which include nocturnal collecting with a small mesh net are recommended.

Kikuchi and Peres (1977) noted the similarities or parallelism in caridean faunas from seagrass beds in different geographic areas. Similar taxonomic groups (families, genera) appear to inhabit equivalent microhabitats within seagrass meadows. In the *Thalassia* beds investigated here, as in the temperate seagrass beds studied by Kikuchi (1962) and Ledoyer (1969) (cited in Kikuchi and Pérès, 1977), there are leaf-inhabiting shrimp of the genera *Hippolyte* and *Latreutes*. The most abundant shrimp taken at the Puerto Rican sites, *Latreutes fucorum*, is often considered to be an associate of *Sargassum*. This alga was not seen at the study sites. Both Chace (1972) and Williams (1984) noted that, although *Sargassum* is certainly a habitat of *L. fucorum*, this shrimp is commonly found in seagrass meadows. A similar situation occurs in the western North Pacific where *L. acicularis* is abundant not only in *Sargassum* (Mukai, 1971) but also in *Zostera* seagrass meadows (Kikuchi, 1962). *Tozeuma carolinense*, a grass shrimp, is listed as one of the most abundant epifaunal invertebrates in studies on West Atlantic seagrass beds (Greening and Livingston, 1982; Heck, 1979); however, it was virtually absent from the meadows sampled in this study. The hippolytids *Heptacarpus* spp. and *Eualus* spp., from two principally North Pacific genera often abundant in *Zostera* meadows, are not present in western Atlantic or Caribbean sites. However, the small morphologically similar hippolytid *Thor* may be their ecological equivalent in *Thalassia* beds. Completely nocturnal processid shrimps are a component of both temperate and tropical seagrass meadows (in this study, *Processa* spp.; in Greening and Livingston, 1982, *Ambidexter symmetricus*). Palaemonid shrimps are an important faunal element of seagrass beds; at the Puerto Rican sites, *Periclimenes americanus* and *Leander tenuicornis* represent the palaemonids. In temperate seagrass beds, night active, day burrowing crangonid shrimps can be abundant (Kikuchi, 1962; Heck and Orth, 1980b). The Crangonidae are a primarily temperate and boreal family not represented in tropical and subtropical *Thalassia* beds. The nocturnal *Alpheus normanni* is abundant at the Puerto Rican meadows and it and other alpheids are often common on subtropical and tropical seagrass beds.

The diurnal and nocturnal microhabitats, as well as the feeding habits, life history, and productivity of most of these often very abundant shrimps are poorly

known. Further studies on these aspects of their biology are necessary to determine their ecological role in seagrass communities.

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ADDRESS: *Department of Biology, University of Puerto Rico, Río Piedras, Puerto Rico 00931.*