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PENAEOID SHRIMP FAUNA FROM TROPICAL SEAGRASS MEADOWS: SPECIES COMPOSITION, DIURNAL, AND SEASONAL VARIATION IN ABUNDANCE

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Abstract.—The motile invertebrate epifauna of seagrass (*Thalassia testudinum*) meadows at Dorado, north coast of Puerto Rico, was sampled monthly during the day and at night for a year. The penaeoid shrimp component of the mobile epifauna was dominated by two small sicyoniids, *Sicyonia parri* (65% of N) and *S. laevigata* (21% of N). *Metapenaeopsis goodei, M. martinella,* and *M. smithi* were much less numerous. All penaeoid shrimps were collected in significantly higher numbers at night. Laboratory observations indicate that all species burrow just under the bottom during the day but are active at night. The nocturnal emergence of these penaeoids and their increased susceptibility to capture at and after dusk was documented by sampling which began before and ended after sunset; numbers of shrimp taken increased dramatically with increasing darkness. *Sicyonia parri* and *S. laevigata* showed significantly higher abundances in spring and summer months at one of two replicate sampling sites while *Metapenaeopsis* juveniles exhibited a similar pattern at both sites. There was no evidence of seasonality in *Metapenaeopsis* adults.

In recent years various investigators have conducted sampling programs in subtropical and tropical seagrass meadows dominated by turtlegrass, *Thalassia testudinum* (Bauer, in press; Greening and Livingston 1982; Gore *et al.* 1981; Heck 1976, 1977, 1979; Thorhaug and Roessler 1977; Hooks *et al.* 1976). The results of these studies on community structure show that, as in seagrass meadows in temperate areas (Heck and Orth 1980a, b; Kikuchi and Pérès 1977; Kikuchi 1966), the motile invertebrate epifauna sampled by pushnets, epibenthic dredges, otter trawls, and drop net techniques is dominated numerically by decapod crustaceans such as caridean shrimps, penaeoid shrimps, paguroid crabs, and brachyuran crabs. Kikuchi (1966, 1974) and Reid (1954) reported that decapods, e.g., shrimps, are preferred food items of fishes foraging over seagrass beds. Initially, analyses of community structure, i.e., species composition and relative abundance, were carried out on collections taken during daylight hours. More recently, Bauer (in press), Leber and Greening (ms), and Greening and Livingston (1982) have demonstrated that the *Thalassia* epifaunal community is "awake" at night; more species are collected at night and individual species abundances are significantly higher in night samples.

Penaeoid shrimps are often a numerically important component of the motile epifauna in *Thalassia* meadows (Greening and Livingston 1982; Gore *et al.* 1981; Heck 1976, 1977). In a year-long monthly sampling program conducted in seagrass beds at Dorado, north coast of Puerto Rico, penaeoids frequently comprised 10–15% of the total number of individuals in a monthly night sample (range: 1–41%).

The purpose of this report is to describe the species composition of the penaeoid fauna from these seagrass meadows, to compare estimates of abundance based on day and night sampling, and to describe seasonal variations in abundance of the numerically dominant species.

Methods

The seagrass meadows sampled were located in a cove just east of the Dorado Balneario (public beach) near Dorado (18°29′N, 66°15′W), on the north coast of Puerto Rico. These grassbeds are described by Bauer (in press); further details on study areas, methods used, and sampling information can be obtained from that report. A shallow rocky reef protects the beds from the normal 2–6′ (0.6–1.8 m) ocean swells characteristic of the north coast. The Dorado grassbeds have the form of a terrace raised approximately 1 m above the surrounding sand bottom. Two species of seagrasses, *Thalassia testudinum* and *Syringodium filiforme*, were the primary vegetation; *T. testudinum* was dominant in blade density throughout the investigation. A variety of species of attached benthic algae occurred in the grassbeds but were never extremely abundant; drift algae (e.g., Greening and Livingston 1982; Gore *et al.* 1981) were not present in noticeable quantity during the study period.

Two areas within the Dorado seagrass meadows were delimited as replicate sampling sites. The two sites were 40 m apart and almost separated by the surrounding sand bottom. The median water depth at Site 1 varied from 0.7–1.0 m (depending on tidal height) while Site 2 was somewhat shallower (0.4–0.7 m). Sediments under Site 1 were muddy sand; those at Site 2 were similar but scattered coral rubble also occurred there. These grassbeds were relatively level and free of holes so that uninterrupted runs of the pushnet could be taken.

A 0.5-m wide pushnet with a 1.0-mm mesh liner sewn into the net bag was used to sample the mobile invertebrate epifauna. A sample unit was a 10 m run so that each sample covered an area of 5 m^2. Collecting took place when the tidal level was lower than 0.2 m. A small part of Site 2 was exposed by the lowest tides; samples were not taken when this area was exposed. Night collections were usually made at new moon to first quarter or before moonrise at other lunar phases; the only quantitative field work reported here done under the light of full moon was in March 1982.

Monthly day and night sampling was conducted from February 1982 to February 1983. Each month, 10 day and 10 night samples were taken at each of the two sites. A map of each site was divided into areas the size of a sample unit, 10 m × 0.5 m. These units were numbered and sample locations were chosen by using a random numbers table. In the field, one end of these randomly selected units was located by measurements from reference markers. The median speed at which the net was pushed varied from 0.7–0.9 m/sec. After a pushnet run, all material was removed from the net and placed in a plastic bag with 37–40% formaldehyde added to make an approximately 10% formalin solution. In the laboratory, animals were sorted out and placed in 70% ethanol for permanent storage.

Day samples were those taken between sunrise and sunset; night collections were conducted between sunset and sunrise. The time of day or night field work varied with low tide periods during which such work was carried out. Because of the timing of tides, three sets of samples took place across the night–day or day–night transition; since I report variations in individual sample abundance with time for these particular samples, time of field work will be given in greater detail for them. May Site 1 day samples began at 1725 Atlantic Standard Time and ended at 1925; sunset was at 1833 and darkness (when flashlight became necessary to read and record data) fell at approximately 1900. The May Site 2 night collections were from 1830 to 2000; the time of sunset and darkness was the same as for May Site 1 day. The June Site 1 night samples were from 0440 to 0555; sunrise was at 0522. In June at Site 2 there were two day (just after sunrise and during the afternoon) and no night samples. Bad weather prevented field studies in February 1982 at Site 1 and caused termination of work in July at Site 1 after only 3 samples. April Site 1 day and Site 2 night collections had to be discarded because of poor preservation.

Water temperature varied from 26–30.5°C and salinity from 34–36‰ during the study period (measured monthly during field work).

Observations on day-night activity were carried out on captive animals in recirculating aquaria with sand bottom in which *Thalassia* plants were imbedded. Shrimps were maintained under either a variable day-night light cycle which coincided with working hours or a 12 hr day:12 hr night cycle controlled by a timer. "Daylight" was fluorescent light; night observations were made under constant red light, with flashlight with and without red filter, by flash photography, or by turning on day lights during a dark cycle.

The classification of dendrobranchiate shrimps given by Pérez Farfante (1977, 1978) is followed in this report.

Results

Species composition.—Approximately 7500 dendrobranchiate shrimps were captured (Table 1). Almost all individuals were species in the superfamily Penaeoidea. Two members of the family Sicyoniidae, *Sicyonia parri* (Burkenroad) and *S. laevigata* Stimpson comprised 85.9% of the total collected (Table 1). Three *Metapenaeopsis* species (Penaeidae), *M. smithi* Schmitt, *M. martinella* Pérez Farfante, and *M. goodei* (Smith) were much less abundant (Table 1). I grouped all juvenile (without the well developed petasma or thelycum needed for species identification) *Metapenaeopsis* together; these juveniles accounted for 9.3% of the total number of shrimps. The genus *Penaeus* was represented by only 31 late postlarvae. Only four specimens of the superfamily Sergestoidea, family Sergestidae (*Lucifer faxoni* Borradaile) were taken in the samples.

Diel variation in abundance.—All penaeoid species were much more abundant in night samples than in day collections. At both sites, the mean number of *Sicyonia parri* per square meter of sampling effort was significantly higher than the day mean (95% confidence limits of day and night means do not overlap) (Fig. 1). In 3 of 13 months, no individuals of this species were captured during the day at Site 1. Estimates of monthly abundance based on night samples ranged from 1–14/m^2 (monthly means). *Sicyonia laevigata* followed a similar pattern of consistently higher mean numbers of individuals in samples taken at night (Fig. 2). On six of 27 occasions, there were no *S. laevigata* taken during daylight hours.

Table 1.—Species composition and relative abundance of dendrobranchiate shrimps from Dorado, Puerto Rico, seagrass meadows (totals of 13 months, both sites, day + night).

Rank	Species	Number collected (and % of total)
1.	*Sicyonia parri*	4827 (64.7%)
2.	*S. laevigata*	1582 (21.2%)
3.	*Metapenaeopsis* juveniles	693 (9.3%)
4.	*M. smithi*	210 (2.8%)
5.	*M. martinella*	70 (0.9%)
6.	*M. goodei*	42 (0.6%)
7.	*Penaeus* sp. (late postlarvae)	31 (0.4%)
8.	*Lucifer faxoni*	4 (0.1%)

Estimates of mean density based on nocturnal samples ranged from 0.3–3.0/m^2. Relatively few adult *Metapenaeopsis goodei, M. smithi,* and *M. martinella* occurred in the samples (Table 1). To analyze day–night variation in *Metapenaeopsis,* adults of all three species were grouped (Fig. 3). *Metapenaeopsis* adults were taken in only 1 of 27 day sampling periods. Mean abundance in night samples varied from 0.08–0.80/m^2. *Metapenaeopsis* juveniles were also primarily night collectable (Fig. 4); the mean number/m^2 in monthly night collections ranged from 0–2.4.

Three sets of samples were taken during the day to night or night to day transition; the changes in numbers of shrimps taken with increasing darkness or increasing light gives another view of diel variation in their collectability. Two day to night sample sets taken in May 1982, demonstrate the dramatic increase in numbers of *Sicyonia parri* and *S. laevigata* with increasing darkness (Fig. 5). The positive correlation between shrimps/sample and sample number (increasing sample number = increasing darkness) is statistically significant for both species (Table 2). Numbers of *Metapenaeopsis* adults + juveniles) per sample were positively correlated with higher sample numbers at Site 2 but not at Site 1 (Table 2). In June at Site 1, night to day collections were made and a decrease in numbers of *Sicyonia parri* and *S. laevigata* with time (higher sample numbers = increasing light) was demonstrated (Fig. 6). The negative correlation between shrimp abundance and sample number was significant for *S. parri* but not for *S. laevigata* (Table 2). *Metapenaopsis* juveniles and adults occurred in low densities during the first five samples taken before light and only 1 individual was collected in the last five pushnet runs near or after sunrise. This decline in *Metapenaeopsis* numbers was significant (Table 2).

Seasonal Variation in Abundance (Night Samples)

To look at possible differences in monthly abundances, a one-way ANOVA, using the log (x + 1) transformation, was done on monthly night mean densities for *Sicyonia parri, S. laevigata, Metapenaeopsis* adults, and *M.* juveniles for each site. Differences between individual monthly means were determined with the Student-Newman-Keuls test, using the $P = 0.05$ level of significance (Table 3).

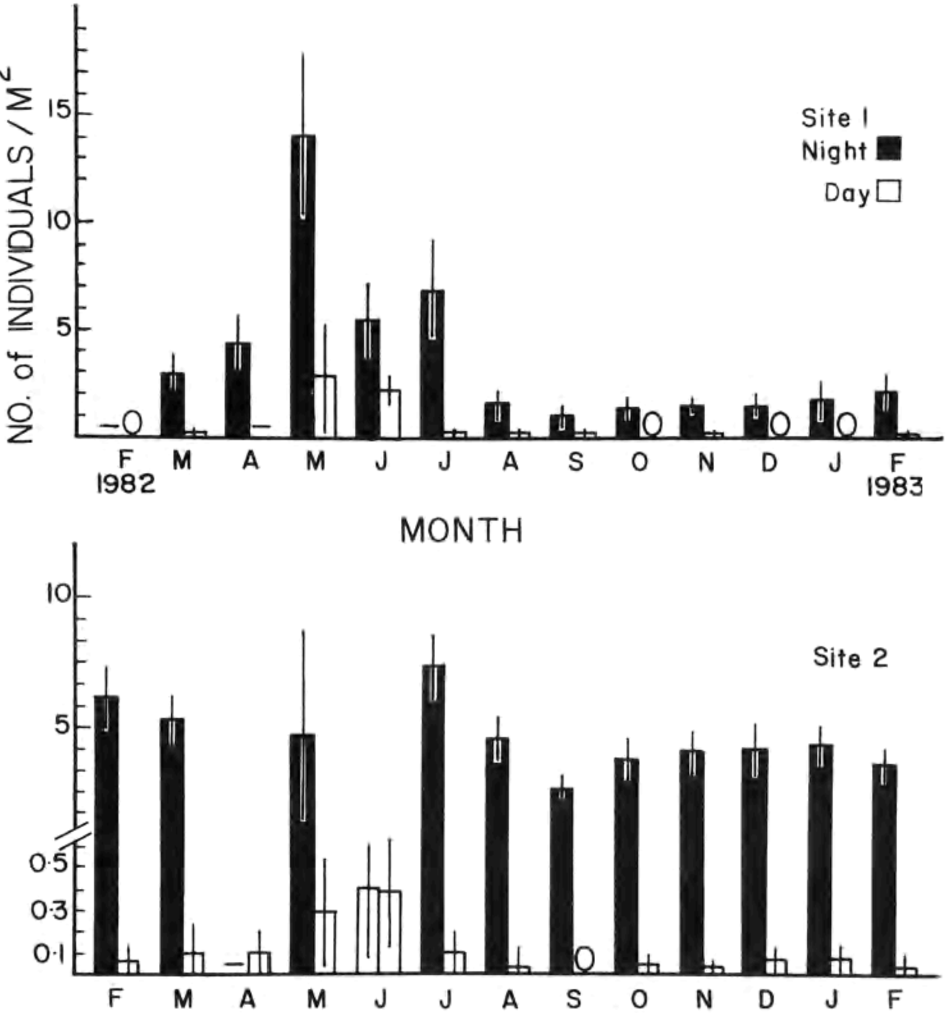

Fig. 1. Monthly day and night abundances of *Sicyonia parri.* Bars represent mean number of individuals captured per square meter of sampling effort; vertical lines are the 95% confidence limits on the means. A dash (—) signifies no sampling for that period; a zero (0) means that no individuals were taken. Black bars are night means; clear bars represent day means.

For *S. parri* at Site 1, abundances in April, May, June, and July were significantly higher than in the remaining months; at site 2, a similar pattern was not obvious (Fig. 1, Table 3). The trends in abundance of *S. laevigata* were similar to *S. parri* at Site 1, with May, June, and July means forming a group distinctly greater than the other months. Although there were significant differences at site 2 in *S. laevigata* ($P < 0.001$), groups of similar means were highly overlapping, and a pattern of highs and lows similar to Site 1 is not apparent (Table 3). Mean abundances of *Metapenaeopsis* adults were highly overlapping at Site 1 (Fig. 3, Table 3) and monthly means were not significantly different at Site 2 ($P \gg 0.10$). However, seasonal differences were present in *Metapenaeopsis* juveniles (Fig. 4, Table 3).

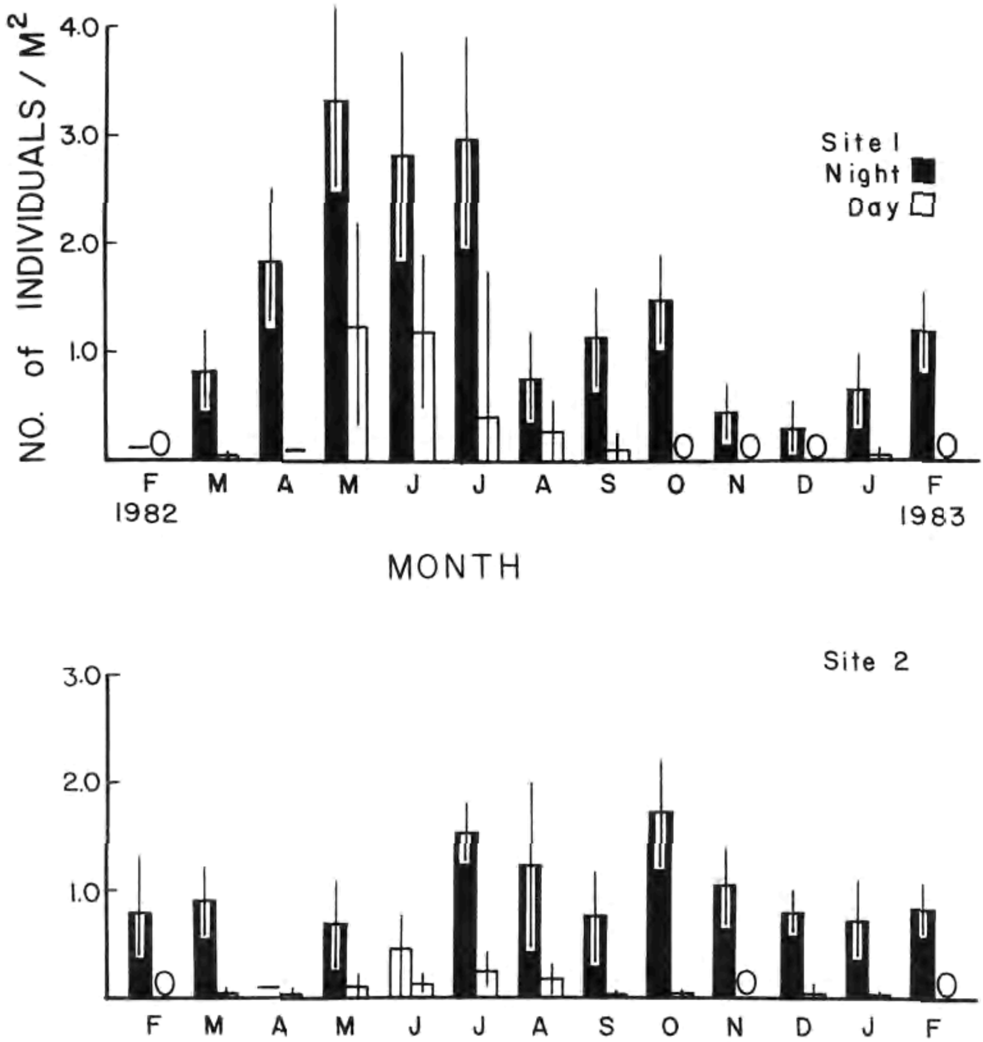

Fig. 2. Monthly day and night abundances of *Sicyonia laevigata*. Symbols same as Fig. 1.

At Site 1, May, August, and September means were significantly higher than all others; at Site 2, August, September, October were months of peak abundance.

Laboratory observations on diel activity.—Both *Sicyonia* species were nocturnally active in laboratory aquaria with sand bottom and *Thalassia*. During the daylight cycle, these shrimps remained buried just under the sandy surface. At night (complete darkness or red light) the sicyoniids emerged from the sand onto the surface of the aquarium bed; some individuals walked over the sand while many crawled up or clung to various parts of seagrass leaves. *Sicyonia* spp. could be made to burrow during a night cycle simply by turning on day (fluorescent) lights; emergence could be evoked during a day cycle within a short time by turning off lights. The few observations made on *Metapenaopsis* spp. indicated night emergence-day burrowing behavior similar to *Sicyonia* species. *Metapenaeopsis* individuals were not seen climbing seagrass leaves as did the sicyoniids.

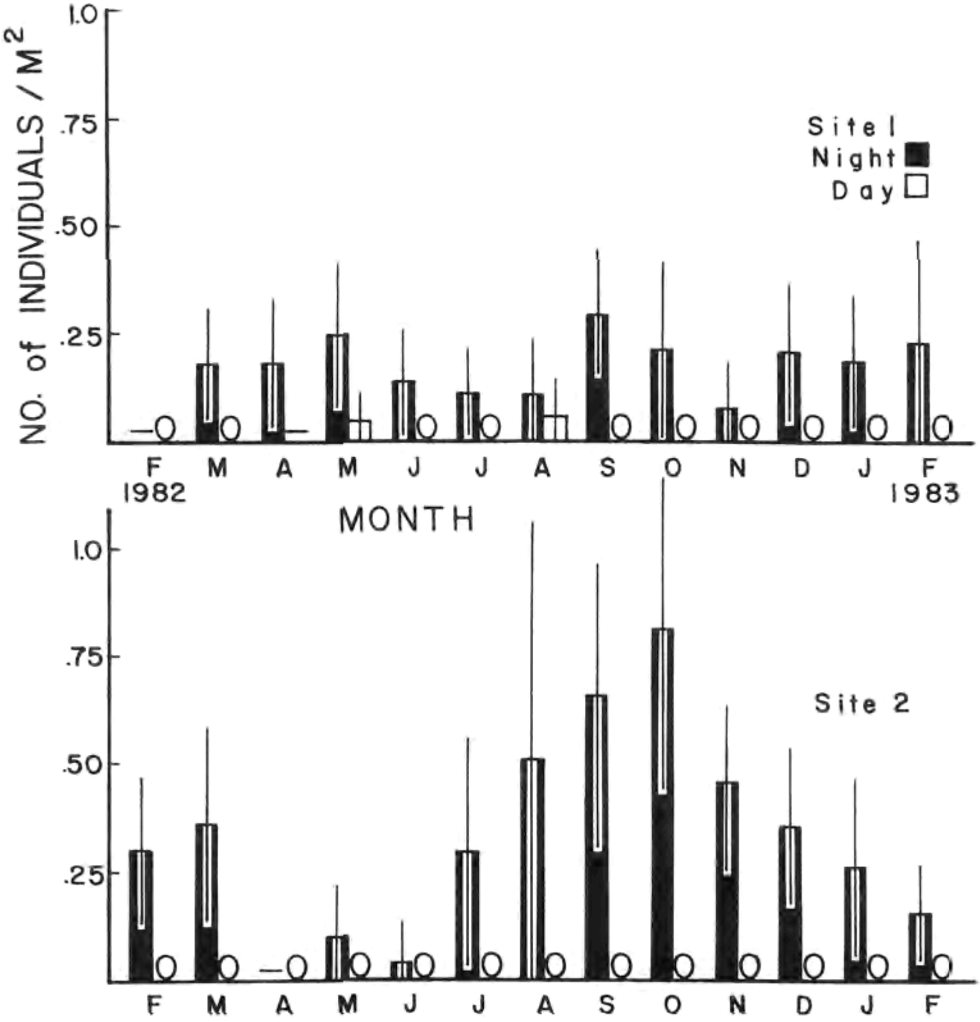

Fig. 3. Monthly day and night abundances of *Metapenaeopsis* adults (*M. goodei, M. smithi* and *M. martinella* grouped together). Symbols same as Fig. 1.

Discussion

The penaeoid shrimp fauna collected from seagrass beds at Dorado, north coast of Puerto Rico, was dominated numerically by *Sicyonia parri* and *S. laevigata*. Conspicuous by their scarcity were members of the genus *Penaeus*; of nearly 7500 penaeoid shrimps collected, only 31 *Penaeus* (late postlarvae) occurred in the samples. In other studies on seagrass mobile invertebrate epifauna, sicyoniids were quite rare or absent while either *Penaeus duorarum* (Florida) or *P. notialis* (Caribbean) was one of ten most abundant invertebrate species (Greening and Livingston 1982; Gore *et al.* 1981; Heck 1976, 1977).

If appearance in local fisheries is some indication of population abundances, then *Penaeus* spp. may be rare not only on the north coast but in other areas of Puerto Rico as well. Although Suárez Caabro (1979) does include "*Penaeus* spp."

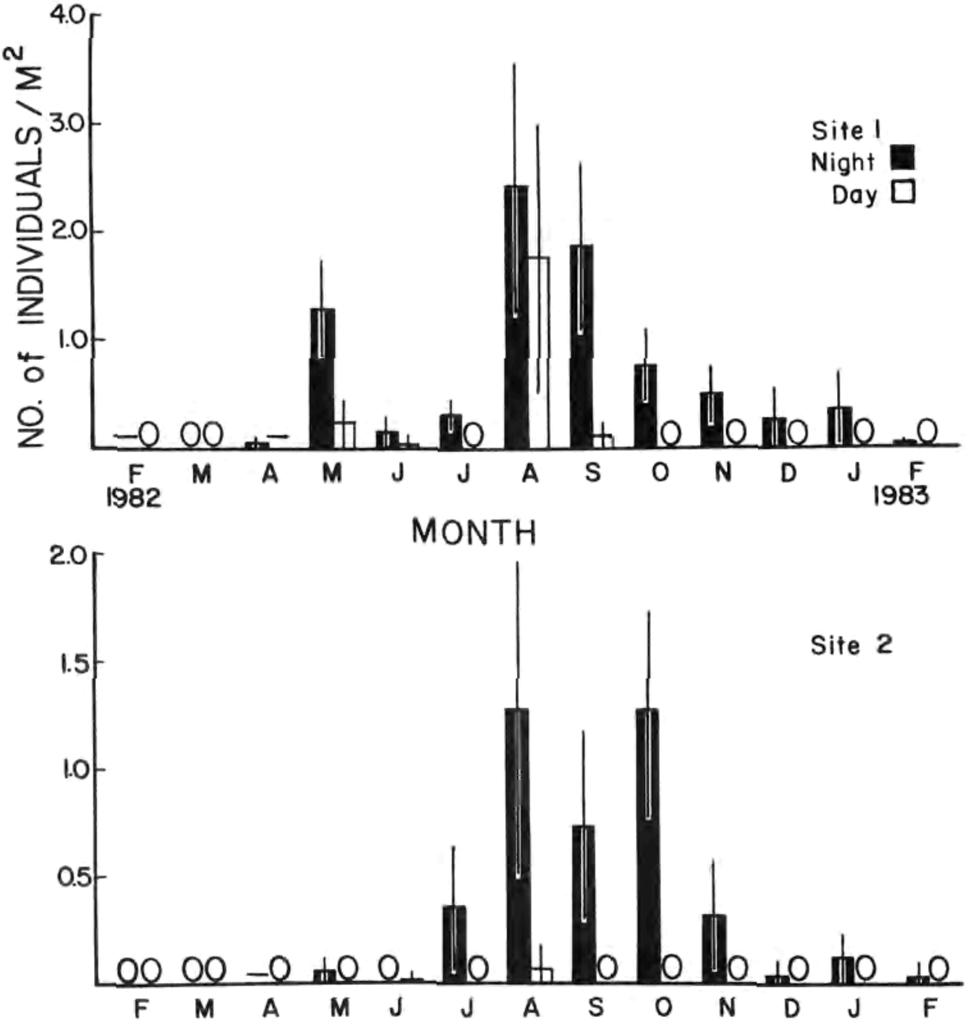

Fig. 4. Monthly day and night abundances of *Metapenaeopsis* juveniles. Symbols same as Fig. 1.

in the list of 130 species taken in local fisheries of Puerto Rico, no further information is given by him. Furthermore, Weiler and Suárez Caabro (1980) do not list penaeoids in their report on species composition and catch records of Puertorican fisheries. An occasional local fishery for *Penaeus* spp. is known from southwest Puerto Rico (Laguna Joyuda, Boquerón) (Roger Zimmerman, pers. comm.). Three species, *P. schmitti, P. subtilis,* and *P. notialis,* contribute to this fishery (Allan Stoner, pers. comm.). I have collected only a very few specimens of *Penaeus* spp. in other seagrass beds on the north coast (Luquillo platform, Condado Lagoon). Schmitt (1935) collected a few specimens of *Penaeus brasiliensis* on the north coast. In summary, shrimps of the genus *Penaeus* do occur in Puerto Rico but there is no indication of large populations. Brackish water mangrove areas and seagrass meadows are available as juvenile habitats on the north coast and the rest of the island. The factor or combination of factors which

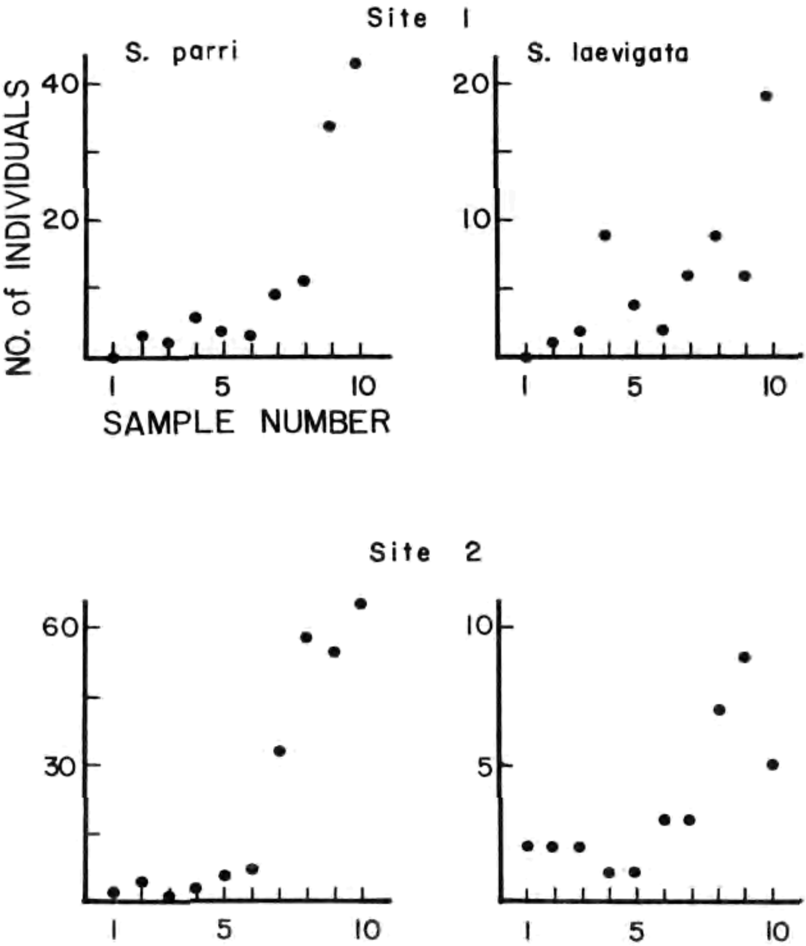

Fig. 5. Increase in numbers of *Sicyonia parri* and *S. laevigata* taken with increasing darkness (higher sample numbers) in collections beginning before and ending after sunset (May 1982).

prevent the occurrence of large populations of *Penaeus* spp. around Puerto Rico are not known; on the north coast, the narrowness of the insular shelf (a few kilometers) could be one possible factor.

Both the *Sicyonia* and the *Metapenaeopsis* species from the Dorado seagrass beds were nocturnally active. The laboratory observations indicated that, in the presence of daylight, *S. parri, S. laevigata,* and *Metapenaeopsis* species burrow just under the bottom sediments. In darkness they emerge from daytime hiding places to walk over the bottom and, in the species of *Sicyonia,* to climb up the seagrass blades. Field evidence confirms the nocturnal activity of these species. The numbers of *Sicyonia* spp. taken in night collections were always much higher than in the day; the nighttime presence of these shrimps on the seagrass beds and especially their habit of climbing seagrass leaves makes them susceptible to push-net capture at night. Their emergence from day burial at dusk is confirmed by samples begun before and terminating after sunset; the increase in numbers of

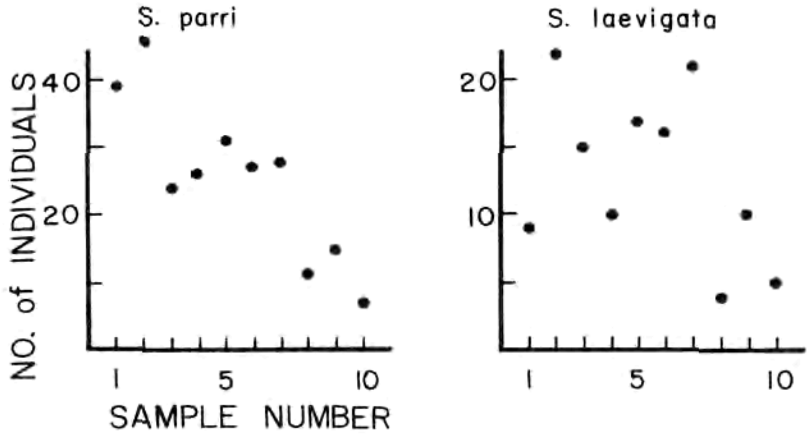

Fig. 6. Decline in numbers of *Sicyonia parri* and *S. laevigata* taken with increasing light (higher samples numbers) in collections beginning before and ending after sunrise (June 1982, Site 1).

sicyoniids per sample with increasing darkness was dramatic. Their return to beneath the surface at dawn was documented by the capture of fewer and fewer individuals with increasing light in collections that took place over the night–day transition. That the sicyoniids were actually burying themselves in the seagrass meadow sediments (instead of migrating elsewhere or avoiding the net during the day) is confirmed by some day observations in which I dug and screened bottom sediments from the seagrass beds; sicyoniids occurred beneath the surface in these sediments. Both laboratory and field evidence show that *Metapenaeopsis* spp. are active at night and burrow during the day.

Several investigators have made observations on the nocturnal behavior of

Table 2.—Correlations of number of individuals/sample and sample number (≈increasing time) in collections beginning before and ending after sunset or sunrise. The Spearman rank correlation coefficient (r_s) is calculated for the possible correlation for each species or group. The probability is given for the one-sided hypothesis: no positive correlation (day to night samples) or no negative correlation (night to day). The null hypothesis is rejected when $P < 0.05$. (S) = significant test; (NS) = nonsignificant.

Species	r_s	Probability
	May Site 1 (day to night)	
Sicyonia parri	+0.918	<0.001 (S)
S. laevigata	+0.797	$0.005 > P > 0.001$ (S)
Metapenaeopsis spp.	+0.312	>0.10 (NS)
	May Site 2 (day to night)	
Sicyonia parri	+0.912	<0.001 (S)
S. laevigata	+0.788	$0.005 > P > 0.001$ (S)
Metapenaeopsis spp.	+0.670	$0.025 > P > 0.01$ (S)
	June Site 1 (night to day)	
Sicyonia parri	−0.770	$0.01 > P > 0.005$ (S)
S. laevigata	−0.360	>0.10 (NS)
Metapenaeopsis spp.	−0.684	$0.025 > P > 0.01$

Table 3.—Comparison of monthly mean abundances (night samples). Months are listed in order of increasing means. Vertical lines join months whose means are not significantly different (Student-Newman-Keuls test, $P > 0.05$). There were no significant differences between means for *Metapenaeopsis* adults at Site 1 (one-way ANOVA, $P \gg 0.10$). Months of zero abundance are not listed below. (*S.* = *Sicyonia*; *M.* = *Metapenaeopsis*).

S. parri	*S. laevigata*	*M.* juveniles	*M.* adults
		Site 1	
Sept	Dec	Feb 83	—
Oct	Nov	April	
Aug	Jan	June	
Dec	Aug	Dec	
Nov	March	July	
Jan	Sept	Jan	
Feb 83	Feb 83	Nov	
March	Oct	Oct	
April	April	May	
June	June	Sept	
July	July	Aug	
May	May		
		Site 2	
Sept	May	Feb 83	May
May	Jan	Dec	Feb 83
Feb 83	Sept	May	Jan
Oct	Feb 82	Jan	July
Nov	Dec	Nov	Feb 82
Dec	Feb 83	July	March
Jan	March	Sept	Dec
Aug	Nov	Aug	Aug
March	Aug	Oct	Nov
Feb 82	July		Sept
July	Oct		Oct

various penaeoid species. Cobb *et al.* (1973) reported that *Sicyonia brevirostris* were much more abundant at night and that gut content analyses also indicated nocturnal activity. Pérez Farfante (1971) noted that the few data available indicated that *Metapenaeopsis goodei*, *M. smithi*, and *M. martinella* were night active. Several *Penaeus* spp., e.g., *P. aztecus* and especially *P. duorarum* make shallow day burrows which they leave at night (Wickham and Minkler 1975; Pérez Farfante 1969; Fuss 1964; Williams 1958). Light intensity has been shown to be the most important factor mediating activity in these *Penaeus* species (Bishop and Herrnkind 1976; Wickham and Minkler 1975; Fuss and Ogren 1966). In the laboratory, I could cause emergence of *Sicyonia* spp. during the day by simply turning off the lights for 20–30 minutes. When lights were turned on again, the shrimps began burrowing within a very few minutes.

Seasonal variations in abundance of *Sicyonia* and *Metapenaeopsis* spp. were not as notable as those of the nine most numerous caridean species from the same meadows (Bauer, in press). The carideans had marked population highs in late spring and summer with a smaller peak in December and January; abundance peaks and troughs were very highly correlated statistically. Seasonal differences in abundance were found in *Sicyonia parri* and *S. laevigata* at Site 1, with significantly higher densities in late spring and summer months; this pattern was not apparent at Site 2. When sorting the samples from the field, it was obvious that large numbers of *Sicyonia* juveniles arrived at the seagrass meadows in May and June, perhaps accounting for higher *Sicyonia* abundances in that period. These observations need to be verified by size-frequency analysis of monthly collections (now in progress). *Metapenaopsis* adults showed little seasonal variation in numbers. However, recruitment of *Metapenaeopsis* juveniles was not continuous; sharp increases in numbers occurred from August and September or October at both sites.

Penaeoid species were less abundant than caridean shrimps at the Dorado seagrass meadows. *Sicyonia parri* total abundance was a little higher than that of *Hippolyte curacaoensis*, the fifth ranked caridean; *S. laevigata* was intermediate in total captured between the seventh and eight ranked carideans, *Processa bermudensis* and *P. riveroi*, respectively (Bauer, in press). *Metapenaeopsis* spp. were comparatively rare. I consider the *Sicyonia* night abundances reported here to be good estimates of population densities. *Sicyonia* spp. are heavily armored, robust, benthic species; I know of no reports of night swimming away from the bottom for *Sicyonia* spp. In addition, the small mesh (1 mm) used in the pushnet assured that the small adults and juveniles were taken. *Sicyonia parri* and *S. laevigata* are small sicyoniids (maximum sizes given in Williams 1984). Juveniles and small males with 2–4 mm carapace length were at times quite numerous; shrimps of this size can easily slip through the 6–7 mm mesh of trawls and scrapes generally used in seagrass sampling studies (e.g., Greening and Livingston 1982; Heck 1976, 1977, 1979). Bauer (in press) also found that densities of carideans (similar in size or smaller than sicyoniids) estimated by fine mesh pushnet samples were much higher than in studies using trawls or scrapes with larger mesh and equal to caridean densities taken by drop net (Gore *et al.* 1981).

Metapenaeopsis abundances might be underestimated in pushnet samples, even those taken at night. Wheeler (1937, cited in Pérez Farfante 1971) reported that *M. goodei* was collected near the water surface at night. If this is normal behavior (i.e., not a case of shrimps being attracted by a bright artificial light) and members of these species do swim off the bottom at night, then estimates of abundance would be in error.

In summary, penaeoid shrimps of the genera *Sicyonia* and *Metapenaeopsis* are very nocturnal and therefore susceptible to pushnet capture at night. Quantitative sampling for analysis of community structure or life history must take place at night to include these species and to estimate their relative abundances and densities. In addition, a small mesh net should be used in collecting to include the juveniles and small adults of these penaeoids.

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