

JEMBE 01815

## Pattern of reproduction and recruitment in two sicyoniid shrimp species (Decapoda: Penaeoidea) from a tropical seagrass habitat

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(Received 21 October 1991; revision received 12 March 1992; accepted 20 March 1992)

**Abstract:** The temporal pattern of breeding and recruitment was analyzed in populations of two species of penaeoid shrimp, *Sicyonia parri* (Burkenroad) and *S. laevigata* Stimpson, sampled for a 13-month period from seagrass meadows in a tropical locality, Puerto Rico. The reproductive condition of females was assessed by observing the degree of ovarian maturity and the presence or absence of sperm masses in the seminal receptacles. Adult females with "mature" ovaries were found in nearly all months of the year in both species, and a high proportion of adult females were inseminated during all months of the sampling period. Recruitment, estimated by changes in the proportion of individuals in juvenile size classes of monthly population samples, took place throughout the year and was highly correlated between the two species, with the highs and lows of recruitment indicating an episodic rather than a seasonal pattern. Comparisons of sicyoniid recruitment with that of caridean shrimps sampled from the same seagrass meadows suggest that different factors affected recruitment in the two groups. Comparisons of reproductive patterns of *S. parri* and *S. laevigata* with those of sicyoniid species from other latitudes suggest continuous reproduction, on the population level, in tropical sicyoniids and increasing restriction and seasonality of breeding periods in *Sicyonia* species from higher latitudes.

**Key words:** Sicyoniid shrimp; Penaeoid; Recruitment; Reproduction; Tropical

### INTRODUCTION

One goal in studies on reproductive ecology of benthic invertebrates is to make and test generalizations about latitudinal variation in patterns of reproduction and recruitment. Such paradigms are useful for generating hypotheses about the specific environmental stimuli (proximate factors) and selective pressures (ultimate factors) that are responsible for breeding and recruitment patterns observed, as well as for making predictions about possible changes in reproduction and recruitment due to natural fluctuations or anthropogenic alterations in these factors. The commonly accepted model is that reproduction and recruitment of near-shore, benthic invertebrates with planktonic larvae are continuous throughout one year in tropical areas, becoming more

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Contribution 31 of Center for Crustacean Research.

restricted during the year with increasing latitude (Orton, 1920; Thorson, 1950; Giese & Pearse, 1974; Grahame & Branch, 1985). Seasonal change in water temperature has been identified as perhaps the most important factor that triggers the onset of the reproductive period in species that breed seasonally, although variations in salinity, photoperiod, and food supply available to the reproductive adult may be critical proximate factors in reproduction (Sastry, 1983). The ultimate factor accounting for seasonality of breeding seasons and subsequent recruitment at higher latitudes was hypothesized by Thorson (1950) to be the seasonal periodicity of larval food, i.e., planktonic productivity, although a variety of other factors have been suggested (Scheltema, 1986; Roughgarden et al., 1988). Sastry (1983) reviewed literature on crustacean reproduction and concluded that there is a tendency for more extended reproductive seasons with decreasing latitude, although many exceptions were noted. Year-round breeding in benthic invertebrates with planktotrophic larvae might be expected in tropical areas where high, relatively constant water temperatures prevail and where larval food supplies from primary and secondary plankton production may be available throughout the year, especially near shore (e.g., Longhurst & Pauly, 1987).

It is becoming more apparent that it is difficult to make ecological generalizations that include different habitats and phylogenetically diverse groups of organisms (Hairton, 1989; Pearse et al., 1991). For example, Pearse et al. (1991) have shown that classically held views on the timing and mode of reproduction in antarctic benthic invertebrates have not stood up under the test of empirical studies on an increased number of species. Bauer (1989) found that, although breeding (embryo production) was continuous throughout the year in nine species of caridean shrimp inhabiting a tropical seagrass meadow, recruitment was best described as episodic rather than seasonal or continuous. In studying reproductive pattern, perhaps the most constructive approach would be to compare temporal variation in breeding and recruitment within and among different taxa at the same location and also among species of the same taxa at different sites and latitudes.

The objectives of this report are (1) to describe the month to month variation during 1 year in reproduction and recruitment in *Sicyonia parri* (Burkenroad) and *S. laevigata* Stimpson (Decapoda, Penaeoidea), shrimps that broadcast fertilized eggs directly into the water for embryonic and larval development; (2) to compare reproductive and recruitment patterns of these *Sicyonia* spp. with that reported by Bauer (1989) for nine species of shrimp (Decapoda, Caridea), from the same locale, that incubate embryos prior to hatching into the plankton as advanced larvae; and (3) to contrast temporal variation in reproduction and recruitment of these tropical *Sicyonia* spp. with that of other *Sicyonia* spp. studied in subtropical and temperate zone locations.

#### MATERIALS AND METHODS

Populations of nocturnally active shrimps living in seagrass meadows at a site near Dorado, north coast of Puerto Rico (18° 29' N, 66° 15' W) were sampled monthly for

13 months with 1-mm mesh push nets (Bauer, 1985). Specimens of *S. parri* and *S. laevigata* were sorted out from samples preserved in 10–15% seawater formalin and stored in 70% ethyl alcohol. Observations on reproductive condition and measurements for size-frequency distributions were done on an approximate maximum of 300 individuals·species<sup>-1</sup>·mo<sup>-1</sup> from night samples ( $n = 20 \cdot \text{mo}^{-1}$ , February 1982 through February, 1983). Numbered samples from each month were chosen at random until the total number of individuals of each species exceeded 300. When the total monthly sample abundance for a species was less than 300, measurements and observations were made on all individuals collected in that month.

Breeding condition of females was determined by observation on degree of ovarian development in females. A dissection into the dorsal surface of the first abdominal segment of all females exposed the posterior lobes of the ovary which were examined at 25× magnification with a stereomicroscope. Ovaries were scored on the basis of relative size and color as “immature” (dominated by non-vitellogenic oocytes) and “mature” (dominated by postvitellogenic oocytes). Ovaries categorized as “immature” varied from thin, transparent strands to thicker but colorless cords above and around the hindgut in the first abdominal segment. “Mature” ovaries were much larger and thicker and varied in color from yellow to a deep orange in alcohol. Prior to staging ovarian condition in females used in monthly population samples, the oocyte composition of visually staged ovaries was analyzed from a preliminary sample of inseminated *S. parri* females ranging in size from 5.4 to 8.0 mm carapace length (median = 6.5 mm), 20 with ovaries staged as “immature” and 12 with ovaries classified as “mature”. A smear from a sample of each ovary was made, and the size (maximum diameter) and frequency of oocytes in different degrees of development was measured. The classification of oocyte developmental stages was modified from that of Cobb et al. (1973) for *S. brevistris*: *undeveloped* [small cells with nucleus occupying most of cell, surrounding cytoplasm clear; mean diameter =  $32.4 \pm 0.6 \mu\text{m}$  (SE),  $n = 213$ ], *developing* (“early developing” of Cobb et al., 1973, larger relative area of somewhat granulate cytoplasm; mean diameter,  $71.4 \pm 1.2 \mu\text{m}$ ,  $n = 221$ ), and *postvitellogenic* (included both “developed” and “ripe” stages of Cobb et al., 1973; large cells with cytoplasm full of yolk granules; mean diameter =  $147.5 \pm 3.5 \mu\text{m}$ ,  $n = 165$ ).

Observations were taken on another indicator of female breeding activity, insemination. The presence or absence of sperm masses in the seminal receptacles was recorded in all females. All males were checked for presence or absence of fusion of petasomal (gonopodal) endopods, the indicator of male sexual maturity in penaeoid shrimp, including sicyoniids (Kennedy et al., 1977).

In addition to observations on reproductive condition, the size of all individuals was recorded, using carapace length (C.L.), defined as the distance from the posterior edge of the eye orbit to the posterior mid-dorsal edge of the carapace. Individuals that were so small that sex could not be determined (0.5–1.0 mm C.L.) were not included in the size frequency diagrams given below separately for males and females but were included in measures of recruitment.

In this study, recruitment refers to the arrival and entry of postlarval individuals from the plankton into the benthic population of the species. Recruitment was estimated by the variations in the proportion of the population sample in the smaller size classes of combined male/female size frequency distributions which included specimens that were too small to be sexed. The total range and number of 0.25-mm size classes in the size frequency distributions for the entire sampling period were determined for each species. Monthly recruitment was defined by calculating the percentage of the population sample in the lower 25% of all possible size classes, as in Bauer (1989) for caridean shrimp. Thus, for the purposes of calculating a measure of recruitment, all individuals smaller than 3 mm C.L. were considered as juveniles. This figure corresponds well to the size at which both males and females attain the characteristics used to define sexual maturity, being slightly lower than the minimum sizes of "adult" females (given below in Results) and slightly larger than the smallest male with a fused petasma (2.6 and 2.2 mm C.L. in *S. parri* and *S. laevigata*, respectively).

In order to compare the pattern of recruitment of these penaeoid shrimps with that reported for caridean shrimp taken in the same collections (Bauer, 1989), the monthly values for "percent recruitment" for *S. parri* and *S. laevigata* were ranked within each species for the period of the study (excluding February, 1982, for which no data was available for carideans in Bauer, 1989). The monthly ranks for the two species were summed for each month. These sicyoniid monthly sum of ranks were then themselves ranked over the period March 1982 through February 1983. Similarly, the monthly recruitment ranks of each of the nine caridean species reported in Bauer (1989) were summed for each month and then ranked over the same time period for comparison of caridean recruitment pattern with that of the sicyoniid species.

## RESULTS

### OOCYTE COMPOSITION OF OVARIAN STAGES

Ovaries classified as "immature" were almost completely dominated by undeveloped and developing oocytes; very few postvitellogenic oocytes were observed in ovaries staged visually as immature (Fig. 1). In "mature" ovaries, postvitellogenic oocytes were most frequent, but there were substantial proportions of undeveloped and developing oocytes in these ovaries as well (Fig. 1). The oocyte composition of ovaries staged as immature and mature in *S. laevigata* was qualitatively very similar to that described above for *S. parri*.

### BREEDING INDICES

Two separate indices of breeding intensity of females were calculated for each month and species: (a) percentage of adult females inseminated and (b) percentage of adult females with mature ovaries. Minimum "adult" or sexually mature female size might

## IMMATURE OVARY

## MATURE OVARY

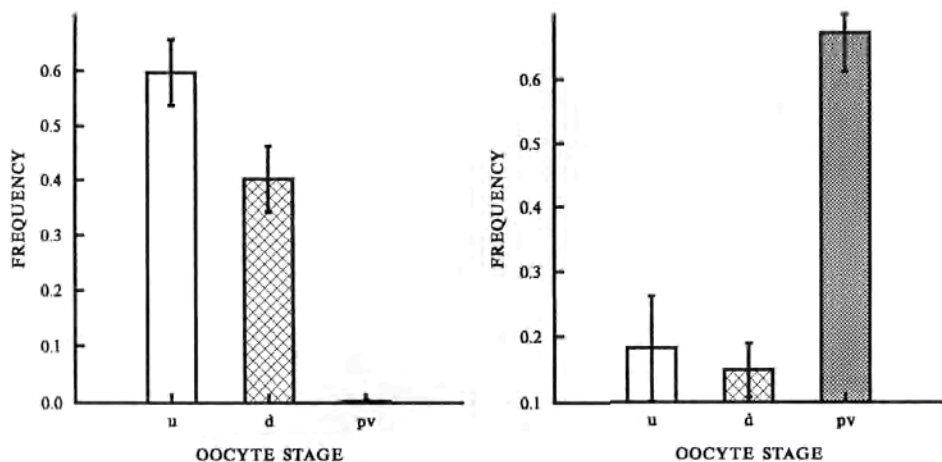


Fig. 1. The frequency (mean, standard error bars) of oocyte types in immature ( $n = 20$ ) and mature ovaries ( $n = 12$ ) of *Sicyonia parri* from ovarian smears (no. of oocytes per sample, 16–119, median = 38). u, undeveloped; d, developing; pv, postvitellogenic oocytes.

be defined as the size of the smallest female with either breeding characteristic. However, relatively few females were found inseminated at sizes much smaller than the overwhelming majority. Use of the size of these “precocious” females to define the size at which females are considered capable of being inseminated would artificially lower the values for “percentage of adult females inseminated”, especially during those months in which large numbers of small juvenile females entered the population. Similar to Ellis (1983), we viewed the size class distribution of all inseminated and uninseminated females (Fig. 2) and defined the lower size limit of sexually mature (in terms of insemination) as the size class at which the ratio of inseminated to uninseminated females reached or was closest to 1:1. Calculations for percent inseminated were accordingly based on females  $\geq 3.75$  mm C.L. in *S. laevigata* and  $\geq 4$  mm C.L. in *S. parri*. These size limits included 96.2% and 96.6% of all inseminated females in *S. laevigata* and *S. parri*, respectively.

In defining the size group of females used in calculations of “percentage of adult females with mature ovaries”, there was no problem with “precocious” females (Fig. 3). The smallest females with mature ovaries occurred in the same size class used as the lower size limit for calculations of “percentage inseminated” in *S. laevigata* and in one size class larger in *S. parri*. All females equal to or larger than these sizes composed the size group on which calculations of “percentage of adult females with mature ovary” were made.

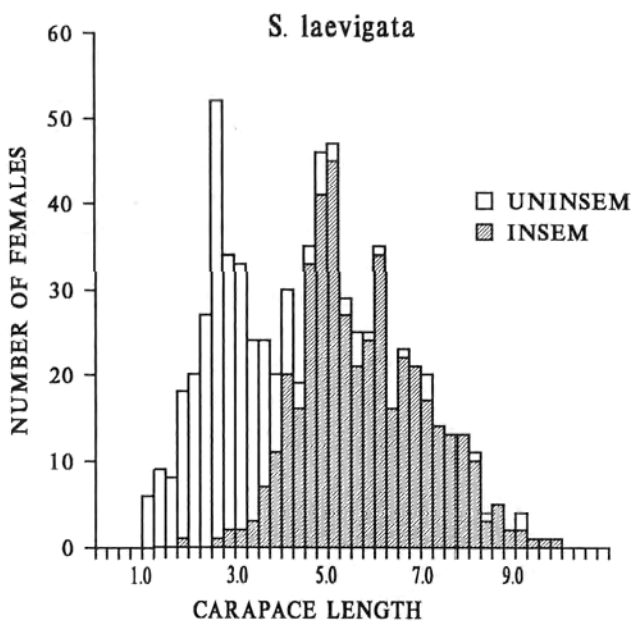
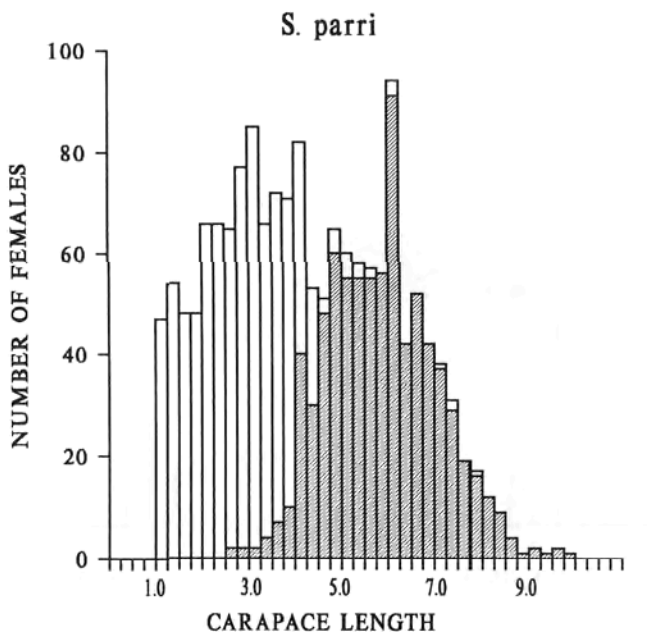


Fig. 2. Size distribution of females of *Sicyonia parri* ( $n = 1614$ ) and *S. laevigata* ( $n = 711$ ), showing the number of inseminated (hatched bars) and uninseminated females (unfilled bars) in each size class.

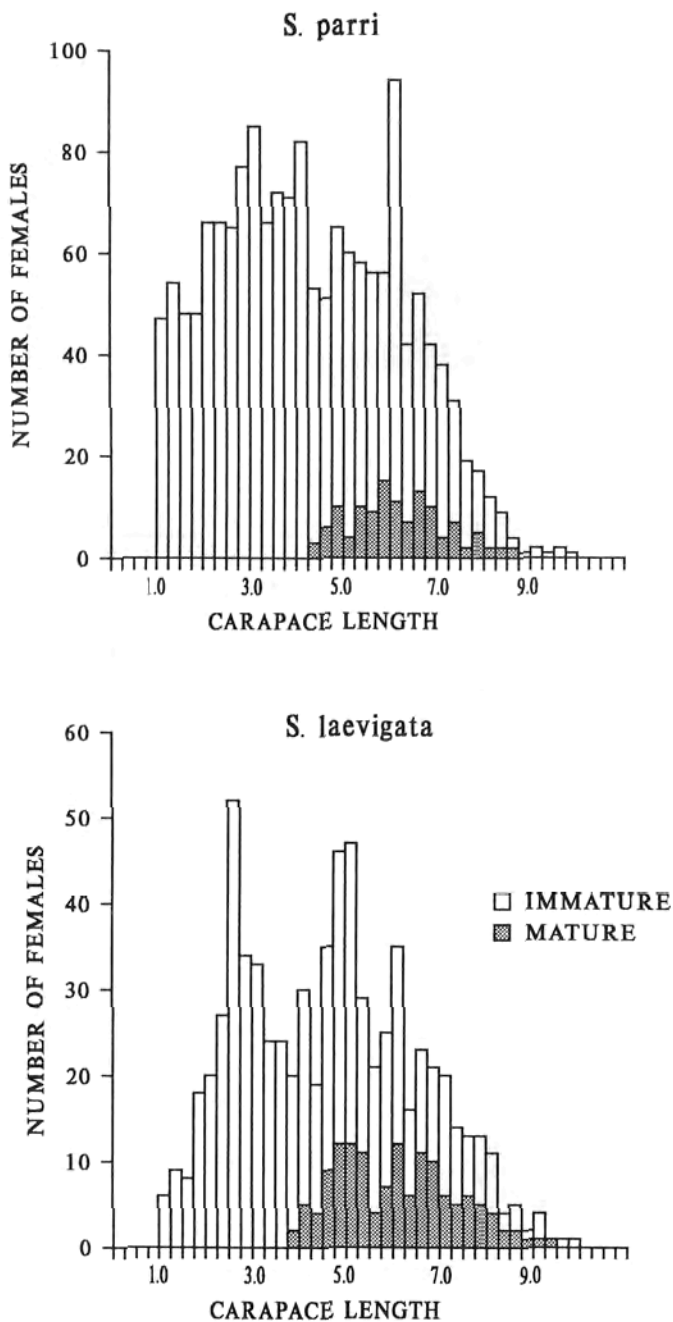


Fig. 3. Size distribution of females of *Sicyonia parri* and *S. laevigata*, showing the number of females with mature (cross-hatched bars) and immature (unfilled bars) ovaries in each size class.

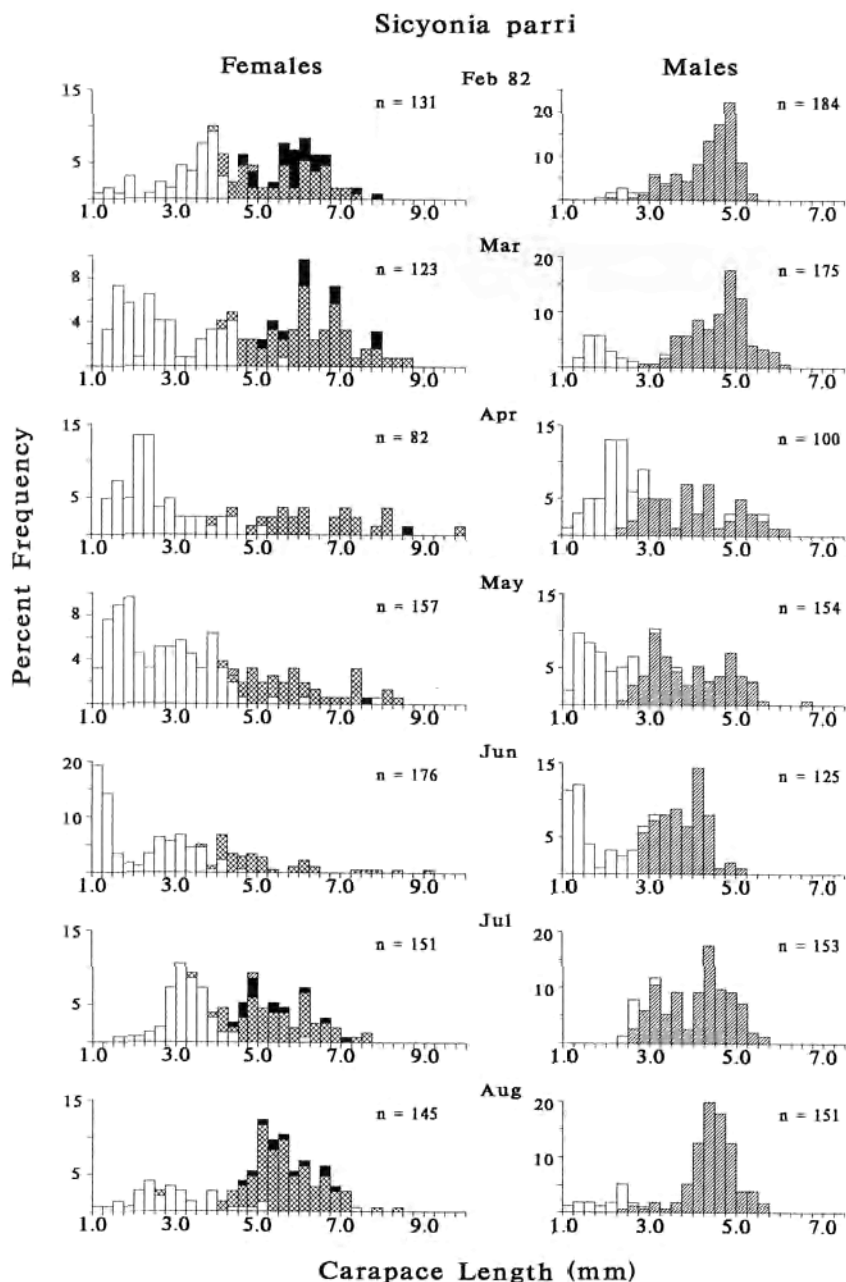


Fig. 4. Monthly size-frequency distributions of females and males of *Sicyonia parri* (February–August, 1982) showing their reproductive condition. For histogram bars of females, unfilled = uniseminated with immature ovary; cross-hatched = inseminated with immature ovary; filled = inseminated with mature ovary. For males, unfilled = petasma not fused; hatched = petasma fused.



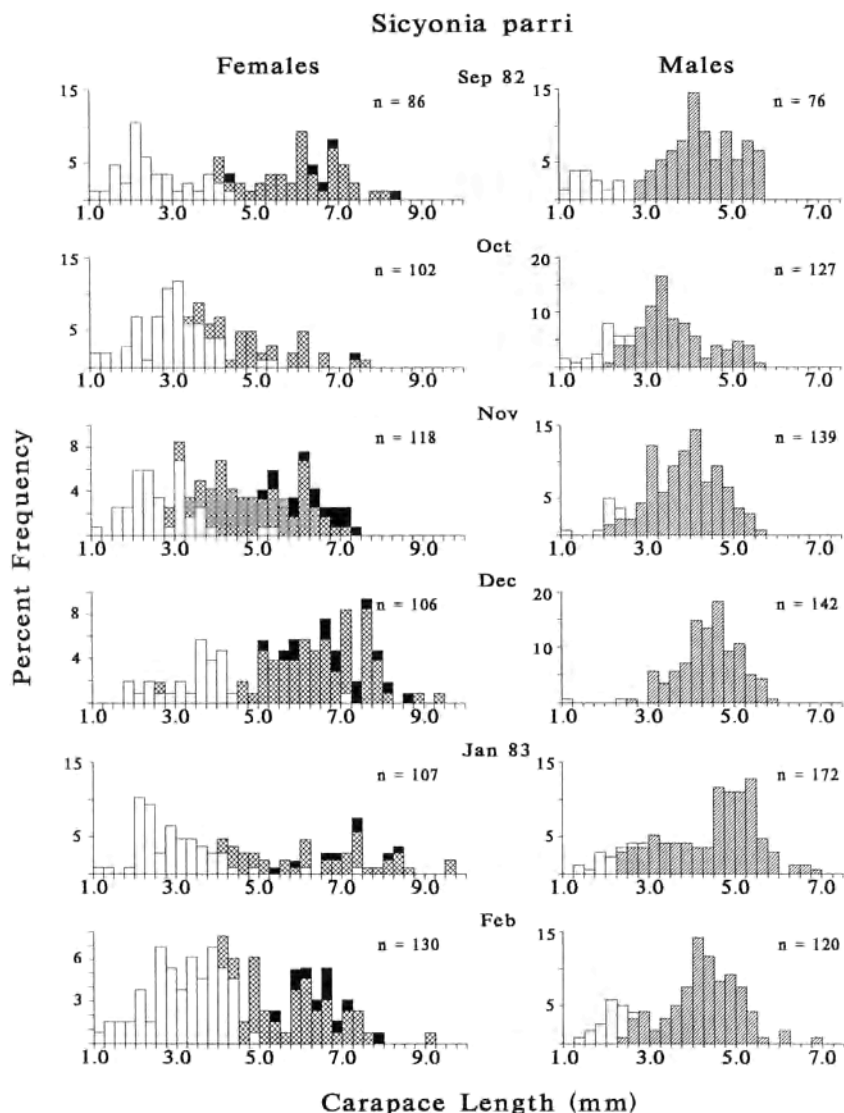


Fig. 5. Monthly size-frequency distributions of females and males of *Sicyonia parri* (September, 1982–February, 1983) showing their reproductive condition. For histogram bars of females, unfilled = unseminated with immature ovary; cross-hatched = inseminated with immature ovary; filled = inseminated with mature ovary. For males, unfilled = petasma not fused; hatched = petasma fused.

#### BREEDING PATTERNS

Breeding adults were collected in both species throughout the year (Figs. 4–7). Sexual maturity of males was indicated by fusion of the petasmata (gonopods). Males

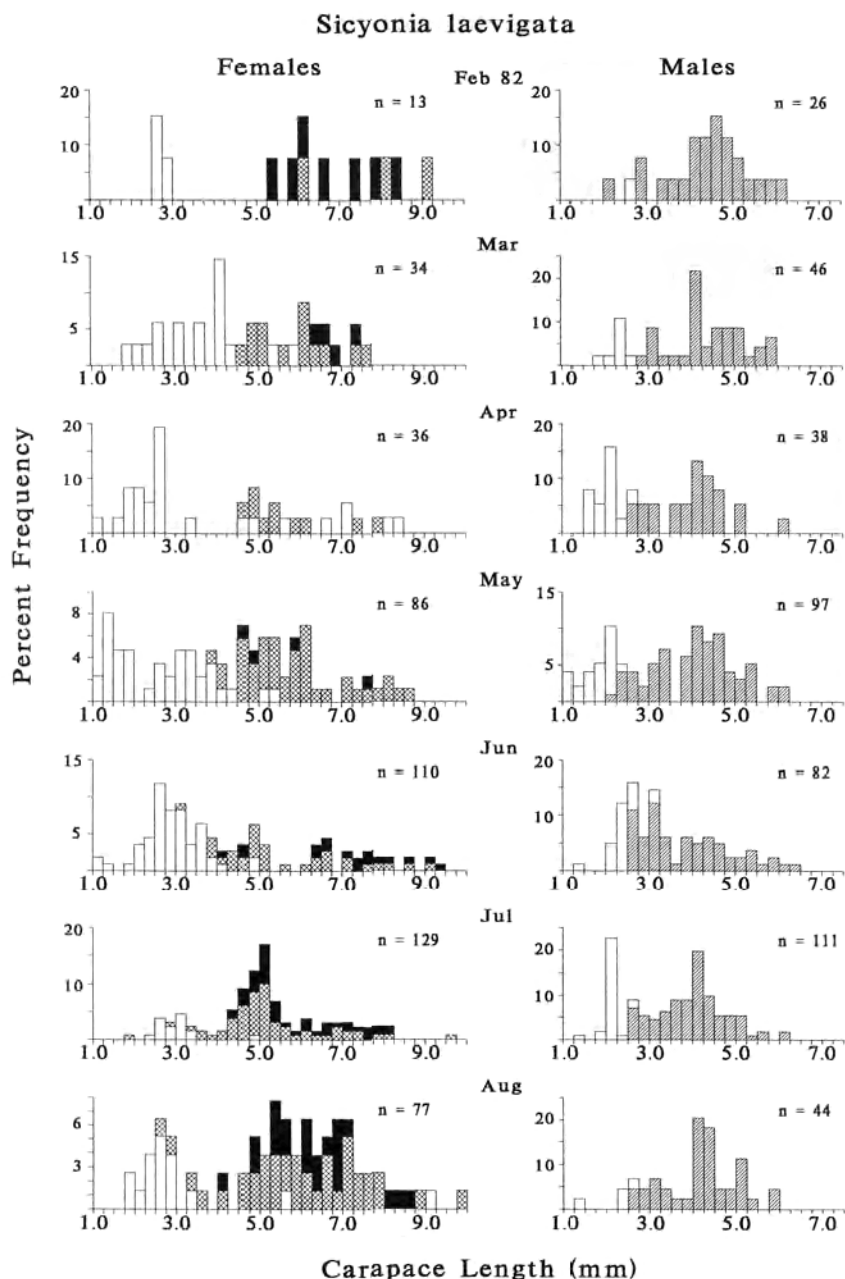


Fig. 6. Monthly size-frequency distributions of females and males of *Sicyonia laevigata* (February–August, 1982) showing their reproductive condition. For histogram bars of females, unfilled = uninseminated with immature ovary; cross-hatched = inseminated with immature ovary; filled = inseminated with mature ovary.

For males, unfilled = petasma not fused; hatched = petasma fused.

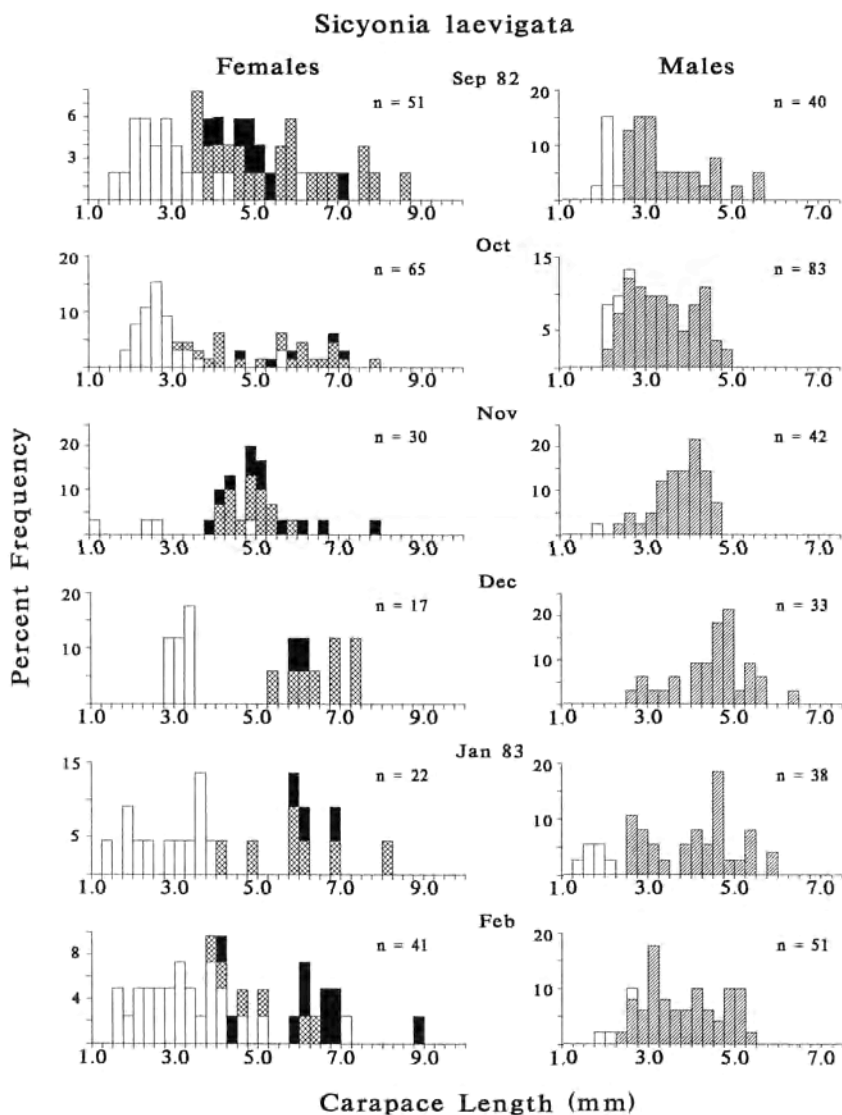


Fig. 7. Monthly size-frequency distributions of females and males of *Sicyonia laevigata* (September, 1982–February, 1983) showing their reproductive condition. For histogram bars of females, unfilled = uninseminated with immature ovary; cross-hatched = inseminated with immature ovary; filled = inseminated with mature ovary. For males, unfilled = petasma not fused; hatched = petasma fused.

with fused petasmata dominated male size frequency distributions except in the smallest size classes (Figs. 4–7), indicating that males reached reproductive condition very soon after arrival onto the seagrass meadows from the plankton. Females with stored

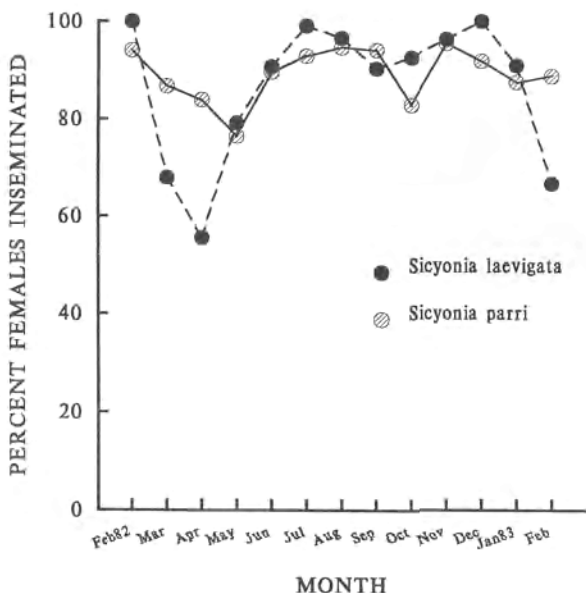


Fig. 8. Temporal pattern of insemination in *Sicyonia parri* and *S. laevigata*. Figured for each month is the percentage of adult females with sperm masses in the seminal receptacles.

sperm in the seminal receptacles were collected during all months of the year in both species (Figs. 4–7). The percentage of adult females that were inseminated was high throughout the year, with lowest values of 76.5% and 55.6% in *S. parri* and *S. laevigata*, respectively (Fig. 8).

Adult females with mature ovaries were collected in all months of the year except for April (*S. laevigata*) and June (*S. parri*) (Figs. 4–7). All females of *S. laevigata* with mature ovaries ( $n = 138$ ) were also inseminated, as were nearly all (118 of 122) in *S. parri*. Although the absolute values for “percentage adult females with mature ovaries” were generally higher in *S. laevigata* than in *S. parri*, the temporal pattern of highs and lows was similar (Fig. 9). The ranked monthly values for this measure of breeding activity of *S. parri* and *S. laevigata* are positively correlated (Spearman rank coefficient,  $r_s = 0.694$ ,  $0.005 < p < 0.01$ , one-sided test).

#### RECRUITMENT

Juvenile, sexually immature individuals were present in samples of both species throughout the year (Figs. 4–7). Recruitment, estimated by the percentage of the population sample in juvenile size classes, was quite variable (Fig. 10). There were decided highs and lows in recruitment, with peak values in April–June, September and October, and in January and February (1983) for both species (Fig. 10). The ranked monthly

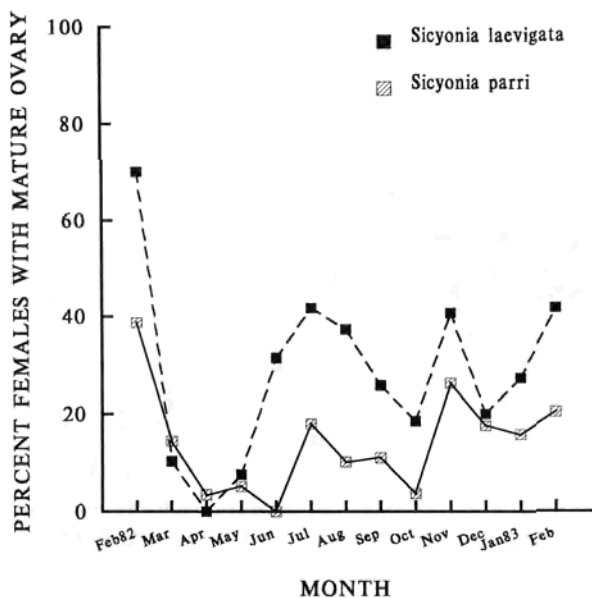


Fig. 9. Temporal pattern of ovarian maturity in *Sicyonia parri* and *S. laevigata*. Figured for each month is the percentage of adult females with an ovary staged as "mature".

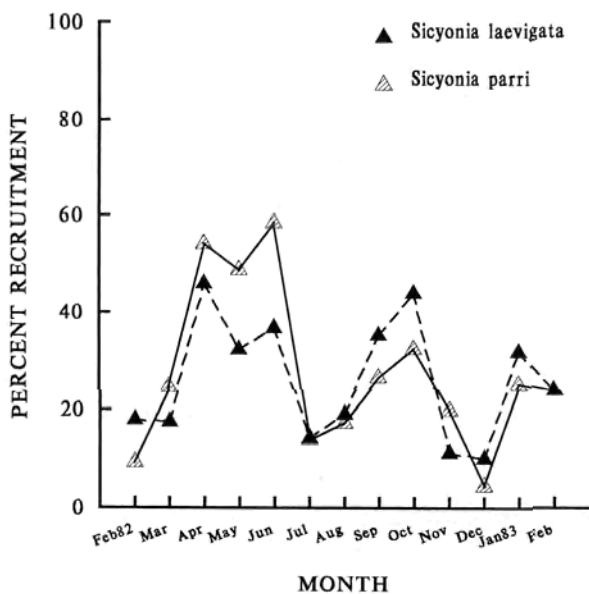


Fig. 10. Temporal pattern of recruitment in *Sicyonia parri* and *S. laevigata*. Figured for each month is the percentage of the population sample in the juvenile size classes.

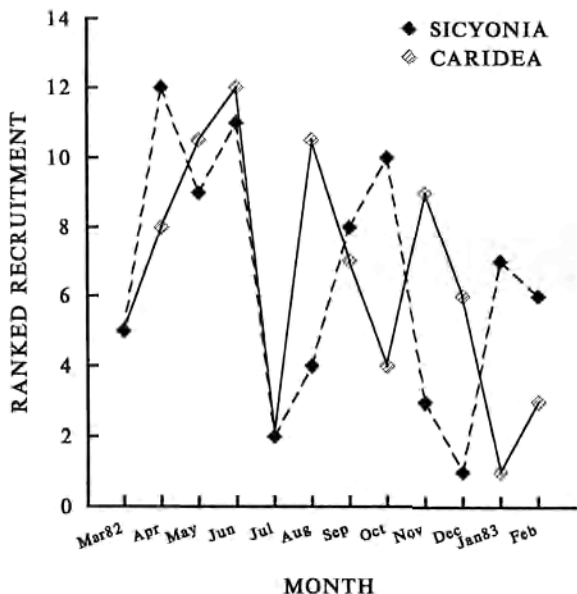


Fig. 11. Comparison of monthly ranks of combined caridean (from Bauer, 1989) and combined *Sicyonia* spp. recruitment values.

values for "percent recruitment" of *S. parri* and *S. laevigata* are highly and positively correlated ( $r_s = 0.874$ ,  $p < < 0.001$ , one-sided test).

The pattern of combined, ranked recruitment estimates of the two *Sicyonia* species is compared (Fig. 11) with similarly calculated recruitment estimates for nine caridean shrimp species, inhabiting the same seagrass meadows, among which monthly recruitment was concordant (Bauer, 1989). Monthly recruitment values for the caridean and *Sicyonia* spp. were not significantly correlated ( $r_s = 0.284$ ,  $p > > 0.10$ , one-sided test).

## DISCUSSION

In this tropical zone ( $18^\circ\text{N}$  latitude) *Sicyonia* spp., adult females with mature ovaries indicative of imminent spawning were found in all but one (non-coincident) month of the 13-month sampling period. The pattern of ovarian maturity and insemination shown by these species suggests continuous, year-round reproduction at the level of the population, without evidence for a strong seasonal component or peak. The question of whether individual females, upon reaching sexual maturity, display continuous, successive cycles of ovarian development and spawning throughout the year cannot be clearly answered from results of this study. In females of nine caridean shrimp species from the same location (Bauer, 1989), a previous spawning was shown

by the presence of embryos attached to the female abdomen. Most females carrying embryos ready to hatch also had a mature ovary with yolk-filled oocytes, and laboratory evidence showed that a new spawning took place soon after hatching of the previous brood. This and other evidence suggested that individual caridean females from this location produced successive broods continuously from attainment of sexual maturity until death. In contrast, *Sicyonia* spp., like all penaeoid shrimp, do not incubate embryos, but broadcast fertilized eggs directly into the water. Sperm receptacles are lined with cuticle and thus stored sperm is cast off when the female molts. Mating and insemination must take place after a molt in order to replenish the store of sperm (Bauer, 1991). The lack of insemination in some adult females might be explained, in part, by their collection in the short period between a molt, when sperm masses are cast off, and mating, when re-insemination occurs.

Anderson et al. (1985) showed that females of *S. ingentis* had multiple spawns between the spring reproductive molt, when insemination took place, and the fall molt in which sperm packets were lost. A high percentage of adult females of *S. parri* and *S. laevigata* were inseminated during all months in this study. If the successive cycles of ovarian development and spawning by inseminated females in *S. ingentis* is a general phenomenon in the genus, then the year-round insemination of most adult females in these tropical species suggest that individual females may continue spawning cycles from the onset of sexual maturity to death. (The life span of females on the seagrass meadows, based on analysis of population cohorts, has been estimated at 4–8 months by Rivera Vega, 1985.) However, the relatively low monthly values in the percentage of adult females with mature ovaries suggests a relatively long refractory period in individual females between one spawning and subsequent rematuration of the ovary prior to the next spawning.

Breeding patterns of *S. parri* and *S. laevigata* can be compared to those of other *Sicyonia* species from higher latitudes. As in this study, all studies on sicyoniid reproduction (Brusher et al., 1972; Cobb et al., 1973; Kennedy et al., 1977; Anderson et al., 1985) have used the characteristic of an ovary dominated by postvitellogenic, yolk-filled oocytes as the indicator of female breeding activity, i.e., imminent spawning. Anderson et al. (1985) showed that this characteristic gave the same results in describing reproductive pattern as did a gonadosomatic index in *Sicyonia ingentis*. Like *S. parri* and *S. laevigata*, the subtropical species *S. brevisrostris* exhibits a pattern in which some reproductive females are found throughout the year, but, unlike these tropical species, there is a strong seasonal peak in the percentage of females with "ripe" or "mature" ovaries. In populations from the west coast (26–28°N, Cobb et al., 1973) and east coast of Florida (28°N, Kennedy et al., 1977), peak reproductive periods were from late fall through winter. Combined samples of *Sicyonia* spp. from many locations (26–29°N) off Louisiana and Texas in the northwestern Gulf of Mexico contained females with ripe ovaries throughout the year (Brusher et al., 1972). However, peaks in "percentage of ripe ovaries" were apparent from January to April in *S. brevisrostris* and May to September in *S. dorsalis*. Highly seasonal spawning, restricted to 4 months

(June through September) was found in *S. ingentis* (Anderson et al., 1985), sampled just off the California coast at 34° N, an area under the influence of the cold, south-flowing California current. For this genus of penaeoid shrimp, the classical paradigm of continuous reproduction at lower latitudes, with increased seasonality of breeding period at higher latitudes (Thorsen, 1950; Sastry, 1983), seems to apply. However, the intensity of reproduction during the year in the tropical species, as measured by the percentage of females with mature ovaries (Fig. 9), is considerably less than that (30–80%) of the subtropical *S. brevirostris* (Cobb et al., 1973; Kennedy et al., 1977) and especially that (75–90%) of the temperate zone *S. ingentis* (Anderson et al., 1985) during the seasonal peak reproductive periods of the latter two species.

Recruitment in *Sicyonia parri* and *S. laevigata* at this tropical site in Puerto Rico can be described as continuous in that there were juveniles in the populations in all months of sampling. However, recruitment values were highly variable throughout the year, and a strictly seasonal pattern is not apparent. The highs and lows of recruitment were significantly and positively correlated in the two species, indicating that similar factors controlled recruitment of these sicyoniids. In the only studies on annual recruitment in another sicyoniid species, both Cobb et al. (1973) and Kennedy et al. (1977) found a strong seasonal pulse of recruitment in the months following the peak spawning season in the subtropical species, *S. brevirostris*.

Bauer (1989) found that the timing of recruitment was highly concordant among nine species of carideans sampled together with *Sicyonia parri* and *S. laevigata*. However, in the present study, recruitment highs and lows of caridean species and *Sicyonia* spp. were not significantly correlated, indicating that different processes affected the relative abundance of juveniles arriving at the seagrass meadows from the plankton in the two groups. Caridean embryos are incubated by the female and hatch as advanced zoeal larvae, while the fertilized eggs of sicyoniids, like all penaeoids, develop completely in the plankton and hatch as less advanced nauplius larvae. We suspect that processes affecting larval survival in the plankton, such as food supply and predators, may differ in carideans and sicyoniids, perhaps accounting for differences in survival and recruitment pattern and success at this tropical location.

Bauer (1989) hypothesized that the episodic but concordant caridean recruitment in these seagrass meadows was not due to variations in embryo output of females, since monthly measures of breeding intensity were not concordant among the nine species. Rather, variation in processes acting simultaneously on the larvae of the carideans in the plankton was hypothesized as the explanation for agreement in recruitment. If processes in the planktonic larval environment were the major factors explaining the observed sicyoniid recruitment, they are different from those that acted on the carideans. It is possible that, unlike that of the carideans, *Sicyonia* spp. recruitment is directly related to the intensity of spawning. The percentage of adult females with mature ovaries was positively correlated in *S. parri* and *S. laevigata*, indicating similar spawning highs and lows in their breeding populations. When the graphs of ovarian maturity and recruitment are compared (Figs. 9 and 10), it can be seen that recruitment



peaks fall between the highs in breeding intensity, suggestive of a return of juveniles 2–3 months after peaks in indicators of female spawning. The time it takes for a spawned, fertilized egg to develop in the plankton to the pre-settlement stage, the postlarva, is 1 month in the Gulf of Mexico *S. brevis* (Cook & Murphy, 1965). Assuming that duration of larval life of *S. parri* and *S. laevigata* is similar to that of *S. brevis* and given that in this study up to a month could have passed after the arrival of a set of postlarvae before sampling, then a lag period of 2–3 months between peaks of female spawning and pulses of recruitment is not unreasonable.

The view that relatively benign physical conditions in many tropical habitats are conducive to year-round reproduction in nearshore, benthic marine invertebrates is supported by this study on sicyoniid shrimp, as well as that by Bauer (1989) on carideans. The seagrass cover of the meadows sampled was qualitatively constant throughout the study, and the basic environmental parameters of temperature and salinity varied little throughout the sampling period (Bauer, 1985). Although reproduction and recruitment did take place throughout the year in both caridean and sicyoniid populations, a comparison of their recruitment patterns shows that the factors controlling recruitment may be quite different in the two groups.

#### ACKNOWLEDGEMENTS

This study is based on samples taken when the senior author (R.T. Bauer) was a faculty member of the Department of Biology, University of Puerto Rico, Rio Piedras (UPR). The financial support of UPR OCEGI and FIPI grants to R.T. Bauer and the many hours of help by student assistants in collecting and sorting samples is gratefully acknowledged by the authors. Measurements for reproductive condition and size frequency distributions of *Sicyonia* spp. were done by the junior author (L.R. Vega) as part of a master's thesis at UPR. Final data compilation and analysis was conducted by R.T. Bauer with the support of grants from the Louisiana Sea Grant Program (NOAA No. NA89AA-SG226) and Louisiana Enhancement Quality Support Fund (LEQSF 1989-92-RD-A-20). Our thanks to the anonymous reviewers of the manuscript for their helpful suggestions and comments.

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