Continuous reproduction and episodic recruitment in nine shrimp species inhabiting a tropical seagrass meadow

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Abstract: Breeding and recruitment patterns were analysed and compared in a group of nine caridean shrimp species from seagrass meadows in a tropical locale, Puerto Rico. Embryo production took place throughout the year in populations of all species. No multispecies pattern in breeding intensity was detected. Most females sampled that carried embryos near hatching also had an ovary filled with vitellogenic oocytes ready for a new spawning. Laboratory observations on females incubating embryos confirm that they spawn again after incubated embryos hatch and the female undergoes a posthatching molt. Median period of embryo incubation ranged from 5–10 days in females of eight species maintained in the laboratory. Reproduction thus appears to be continuous in these tropical shrimps, with females producing successive broods at short intervals after they reach maturity. Increases and decreases in the smaller size classes of species size-frequency distributions suggest that recruitment intensity was variable throughout the year of sampling. Most importantly, the monthly highs and lows of recruitment strength were concordant among species with no apparent seasonal pattern. Given that larval production was continuous, the episodic recruitment pattern observed indicates that similar environmental (mortality) factors acted simultaneously on either the planktonic larvae or newly recruited juveniles of all species.

Key words: Caridean shrimp; Recruitment; Reproduction; Seagrass; Tropical

INTRODUCTION

Generalizations about latitudinal variation in annual breeding patterns of near-shore benthic marine invertebrates began with early workers such as Orton (1920). He hypothesized that tropical species should have continuous reproduction because the relatively stable elevated water temperatures of tropical habitats would allow year-round breeding. With increasing latitude, breeding seasons become more and more restricted to periods of higher water temperature. Since then, others (Thorson, 1950; Giese & Pearse, 1974; Sastry, 1983) have generally supported the idea that a majority of tropical species tend to breed continuously throughout the year or to have prolonged breeding seasons compared to intra- and interspecific relatives at higher latitudes. Thorson (1950) suggested that the important ultimate factor acting on the evolution of breeding patterns of marine benthic invertebrates was not temperature per se. In his view,

breeding and spawning were timed so that the planktonic larvae of benthic invertebrates would encounter adequate food supplies, e.g., during spring plankton blooms in temperate seas, during the brief periods of intense plankton production in polar seas. According to this hypothesis, larval food supplies for planktonic larvae occur throughout the year in coastal areas of the tropics, and, therefore, tropical marine invertebrates should be able to breed and produce larvae continuously throughout the year.

A corollary to this hypothesis of a latitudinal gradient in annual breeding and spawning periodicity of near-shore invertebrates is that recruitment periods should be related to breeding patterns, i.e., restricted when breeding is limited in time, continuous when larval production occurs throughout the year. However, there are certainly a variety of other ultimate factors that might influence patterns of larval production and recruitment, e.g., variation in currents that return larvae to adult habitats (Sastry, 1983; Scheltema, 1986; Roughgarden et al., 1988), variation in predation on planktonic larvae (Roughgarden et al., 1988), and competitive interactions among larvae of closely related species (Reese, 1968).

The review of crustacean breeding patterns by Sastry (1983) shows that there is certainly the tendency towards extended reproductive seasons and year-long reproduction with decreasing latitude in benthic shallow-water crustacean species. However, several exceptions were noted. One objective of this study was to test the hypothesis of continous reproduction in a group of nine shrimp species from the decapod crustacean taxon Caridea co-occurring in the same tropical seagrass meadow habitat. Another objective was to examine the generalization that recruitment occurs throughout the year in continuously breeding tropical crustacean species (Sastry, 1983). In this report, annual embryo production and recruitment in seagrass shrimp species are analysed and compared in order to test these hypotheses about breeding and recruitment patterns in tropical crustacean species.

MATERIALS AND METHODS

Populations of shrimps inhabiting seagrass meadows (mixture of *Thalassia testudinum* Koenig and *Syringodium filiforme* Kuetzing) at Dorado, north coast of Puerto Rico (18°29'N, 66°15'W), were sampled monthly with 1-mm mesh nets for 1 yr (Bauer, 1985). Observations on breeding and recruitment are reported for nine species that accounted for 99.9% of the total caridean shrimp abundance (Bauer, 1985): the hippolytids *Latreutes fucorum* (Fabricius), *L. parvulus* (Stimpson), *Hippolyte curacaoensis* Schmitt, and *Thor manningi* Chace; the palaemonids *Periclimenes americanus* (Kingsley) and *Leander tenuicornis* (Say); the processids *Processa bermudensis* (Rankin) and *P. riveroi* Manning and Chace; and the alpheid *Alpheus normanni* Kingsley. Observations on breeding condition and size-frequency distribution were made on an approximate maximum of 300 ind · species^{-1} · month^{-1} from monthly night samples

($n = 20 \cdot \text{month}^{-1}$, March 1982 through February 1983) sorted to species. For each species, numbered samples were chosen at random until the total number of individuals arrived at or exceeded 300; all individuals of a species were used when that species' total monthly abundance was <300.

Breeding intensity of populations was measured as the percentage of *mature* females that carried embryos on the abdomen (% ovigerous). The size of breeding maturity in females was defined for each species as the size of the smallest female observed carrying embryos. Since females may not all reach maturity at the same size, a sample of females defined in this way may have included some smaller females that were nearly but not completely mature. The percentage of mature females breeding (= ovigerous) would be underestimated by this source of error. However, this method gives a conservative estimate of percent ovigerous when examining the question of continuous reproduction, includes all ovigerous females, and is standardized for the eight species in which female maturity could not be observed by other morphological characteristics. The one exception, *T. manningi*, has a sexual system in which females pass through a brief male phase. In this species, female maturity could be established exactly in each individual (Bauer, 1986).

In order to examine the question of multiple spawnings, concomitant measures of ovarian condition and developmental stage of incubated embryos were taken on all ovigerous females. The large vitellogenic oocytes of these small carideans can be easily observed through the thin carapace under a dissecting microscope. The degree of ovarian development was also estimated on a subjective scale from 1–4 (1–3 in *Latreutes* spp.), based on amount of space above the cardiac stomach occupied by the ovary, from Stage 1, no vitellogenic oocytes observed through the carapace to Stage 4, the space above the cardiac stomach filled with yolky oocytes. Degree of embryonic development was measured on a subjective scale modified from Allen (1966) (Bauer, 1986): Stage 1, embryo all yolk, no blastodisc visible; Stage 2, blastodisc visible, no eye or eye pigment developed; Stage 3, embryo with some degree of eye development but abdomen and cephalothorax fused; Stage 4, embryo near hatching, abdomen free from cephalothorax.

Incubation period (spawning to hatching) was estimated in freshly captured females with Stage 1 embryos (all yolk, no blastodisc visible). Such females were isolated in containers in laboratory aquaria (water temperature varied from 26 to 31 °C, salinity 34 to 36‰) and checked twice daily until hatching occurred.

Recruitment is defined (in the sense of Connell, 1985) as the entry of individuals into the juvenile and adult benthic population after settlement from a planktonic larval stage. In these shrimp populations, recruitment was seen as the entry of individuals into the smaller size classes of monthly size-frequency distributions. In each species, the maximum number of size classes observed in combined male and female monthly size-frequency distributions was determined (0.1 mm carapace length size intervals except for the larger *L. tenuicornis*, 0.25 mm size classes). Monthly recruitment was approximated in each species by calculating the proportion of the population in the lower 25% of all possible size classes observed in that species.

The Kendall concordance test (Tate & Clelland, 1957) was used to examine the null hypothesis of no joint variation among species in monthly values for (1) % breeding (ovigerous) and (2) recruitment estimates. In separate tests, monthly values for (1) % ovigerous and (2) recruitment were ranked within each species; the ranks of all species were summed for each month (observed monthly sum of ranks). The expected monthly sum of ranks and the coefficient of concordance W were calculated, and the null hypothesis $W = 0$ (no concordance among species in monthly values) was tested for significance using the procedures given in Tate & Clelland (1957).

RESULTS

BREEDING

Ovigerous females were found in all species in all months of the year (Table I). Although breeding was continuous in the sense that embryos were produced throughout the year in every species, there was intraspecific variation in monthly values for % breeding. The question was asked: do the monthly highs and lows of breeding intensity coincide among the nine caridean species in the year of sampling? Fig. 1 illustrates the variation of observed monthly sums of ranks for percent ovigerous from that expected using the Kendall concordance test. The deviation of observed from expected indicates the degree of concordance among species for a particular month (greater difference, higher concordance). Except for the March value, there was no major deviation of observed from expected sums of ranks. Results of a Kendall concordance test show that the monthly highs and lows of breeding intensity do not coincide in this group of species (coefficient of concordance, $W = 0.171$; $0.10 < P < 0.25$). A concordance test which
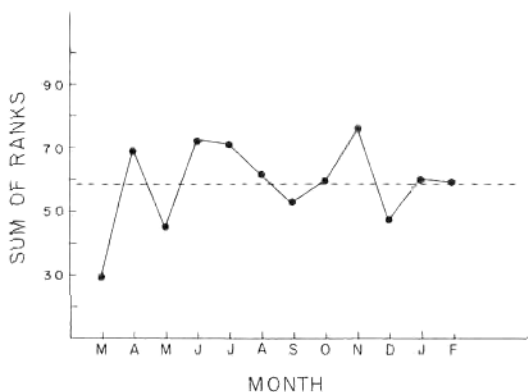

Fig. 1. Joint variation in breeding intensity (% ovigerous) estimates for mature females of nine seagrass-shrimp species. Values for monthly percent ovigerous (% mature females carrying embryos) were ranked within each species; the sum of ranks (solid circles) for all species for each month is plotted. The dotted line shows the value for the expected sum of ranks under the hypothesis of no concordance among species in estimates of percent ovigerous, which is accepted (Kendall concordance test; $0.10 < P < 0.25$).

TABLE I

Annual reproduction in nine shrimp species inhabiting a tropical seagrass meadow. Monthly values are the percentage of mature females carrying embryos (ovigerous) (defined size of female maturity given as carapace length, CL). Medians and 95% CI on percent ovigerous are given for each month for the group of nine species and for each species for the 12-month sampling period. The sample sizes of mature females are given in parentheses below each monthly value for percent ovigerous.

Species	Mar 82	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan 83	Feb	Species median (95% CI)
A. normanni	57.7	35.7	33.7	53.0	58.0	70.5	53.6	82.6	55.5	17.6	77.1	38.5	54.6 (35.7, 70.5)
2.7 mm CL	(26)	(14)	(86)	(83)	(131)	(95)	(56)	(23)	(9)	(17)	(35)	(13)	
H. curacavensis	70.6	85.2	60.0	76.9	76.6	70.4	81.8	60.0	87.9	54.7	71.6	75.3	73.4 (60.0, 81.8)
1.7 mm CL	(17)	(27)	(60)	(13)	(64)	(54)	(11)	(15)	(33)	(95)	(127)	(85)	
L. fucorum	39.9	68.0	70.7	80.7	75.0	46.1	69.7	66.7	84.3	78.2	81.2	75.0	72.8 (66.7, 80.7)
1.8 mm CL	(178)	(98)	(75)	(119)	(128)	(26)	(66)	(51)	(51)	(101)	(138)	(116)	
L. parvulus	42.4	100	59.4	100	98.1	86.7	80.6	95.6	94.4	80.0	79.8	67.9	83.6 (67.9, 98.1)
1.6 mm CL	(33)	(5)	(69)	(17)	(52)	(30)	(36)	(45)	(18)	(40)	(129)	(28)	
L. tenuicornis	28.6	100	70.6	51.9	67.4	75.9	50.0	82.3	100	75.0	44.4	77.8	72.8 (50.0, 82.3)
4.5 mm CL	(7)	(4)	(17)	(27)	(46)	(29)	(10)	(17)	(1)	(8)	(9)	(9)	
P. americanus	30.0	21.4	38.5	50.8	74.6	84.1	53.3	70.0	50.0	55.0	50.0	69.0	52.0 (38.5, 70.0)
1.6 mm CL	(10)	(14)	(52)	(61)	(118)	(44)	(30)	(10)	(4)	(40)	(74)	(29)	
P. bermudensis	40.3	81.8	38.6	80.8	73.2	71.0	88.2	76.9	71.7	78.0	77.4	33.3	75.0 (40.3, 80.8)
2.5 mm CL	(62)	(22)	(57)	(26)	(41)	(31)	(17)	(39)	(46)	(50)	(62)	(15)	
P. riveroi	45.8	42.9	80.0	50.0	43.3	54.5	30.0	33.3	40.0	21.7	52.2	80.0	44.6 (33.3, 54.5)
2.7 mm CL	(24)	(7)	(10)	(12)	(30)	(11)	(20)	(18)	(15)	(23)	(23)	(5)	
T. manningi	90.0	100	97.6	95.7	95.7	93.8	90.3	91.7	100	94.7	93.8	94.9	94.8 (91.7, 97.6)
1.2–1.8 mm CL	(30)	(23)	(41)	(23)	(69)	(48)	(72)	(60)	(10)	(19)	(32)	(39)	
Monthly median	42.4	81.8	60.0	76.9	74.6	71.0	69.7	76.9	84.3	75.0	77.1	75.0	
95% CI	30.0, 70.6	35.7, 100	38.5, 80.0	50.8, 95.7	58.0, 95.7	54.5, 86.7	50.0, 88.2	60.0, 91.7	50.0, 100	21.7, 80.0	50.0, 81.2	38.5, 80.0	

considers all nine species at once might hide joint variation within subgroups of species. Spearman's rank correlation coefficients were calculated on values of monthly percent ovigerous for all possible pairs of species. Only two of 36 pairs of species showed positive correlation coefficients that were statistically significant (*T. manningi* and *L. tenuicornis*, $0.025 < P < 0.05$; *P. bermudensis* and *L. parvulus*, $0.01 < P < 0.025$). In summary, there is no evidence for joint variation in breeding pattern among all nine species nor among major subgroups of species.

Embryo production was continuous not only on the population level but also on the individual level. Evidence from concomitant observations on developmental stage of incubated embryos and ovarian maturity in females taken in field samples shows that most females produced successive broods after reaching maturity, i.e., after spawning the first time. Females incubating embryos in early stages of development showed no or little ovarian development while those carrying embryos near hatching had ovaries in advanced (near to spawning) condition. Table II lists Spearman's rank correlation coefficients calculated for the variables *degree of embryonic development* (nearness to hatching) and *degree of ovarian development* (nearness to spawning). In all species, correlations between estimates of these parameters are highly positive and statistically significant (Table II).

TABLE II

Tests of correlation between degree of ovarian and embryo development in incubating females and their broods. Spearman's rank correlation coefficient (r_s) was calculated to test the null hypothesis of no positive correlation between the variables (1) degree of ovarian development in females and (2) degree of development in their incubated embryos. Degree of ovarian development was classified in four stages except for *Latreutes* spp., in which only three ovarian stages were recognized; degree of embryo development ranged from 1–4 on a subjective scale for all species. Values of r_s are listed for each species. Values of the variate z ($= r_s \sqrt{n-1}) \geqq 1.65$ correspond to $P (H_o) \leqq 0.05$. n = number of females with embryos on which observations were made.

Species	r_s	z	n
A. normanni	0.737	13.2	322
H. curacaoensis	0.885	18.1	418
L. fucorum	0.850	24.3	816
L. parvulus	0.832	16.5	393
L. tenuicornis	0.721	8.0	124
P. americanus	0.832	14.0	283
P. bermudensis	0.821	14.3	305
P. riveroi	0.832	8.0	93
T. manningi	0.795	15.0	406

Laboratory observations made on these seagrass carideans confirmed that females that carried a brood of embryos near to hatching and that also had an ovary filled with vitellogenic oocytes soon spawned a new brood. After a female's embryos hatched, it underwent a posthatching molt within several hours to two days. Within a few hours to 2 days after the posthatching molt, spawning of embryos took place in the absence

of males, indicating that, in nature, mating and subsequent spawning must take place within this time period, as in several other small caridean species (Bauer, 1976, 1979). Thus, both laboratory observations on captive females and statistical analysis of breeding condition from field samples indicate that females of these seagrass species produced successive broods continuously once they began to breed.

Females not only spawned one brood after another, but they also did so rather quickly. Estimates of incubation periods for embryos ranged from 5–10 days among the eight species on which observations were taken (Table III). The period from one spawning to the next would be the incubation period plus the variable amount of time ($\approx$ 1–4 days, as discussed above) that it takes the female to undergo the posthatching molt and subsequent mating.

TABLE III

Estimates of embryo incubation period (Stage 1 to hatching) in days. Md, median; Min, minimum; Max, maximum; n, number of incubating females observed.

Species	Md	Min	Max	n
A. normanni	10	9	12	17
H. curacaoensis	4.5	4	6	10
L. fucorum	6	5	7	8
L. parvulus	7	5	8	5
P. americanus	8	6	9	7
P. bermudensis	5	4	6	4
P. riveroi	9	8	9	6
T. manningi	8	6	10	20

RECRUITMENT

Variations in recruitment throughout the year of sampling are indicated by variations in the proportion of the population in the smaller size classes (new recruits). There was high intraspecific variation in monthly recruitment, as defined above, for all species (Table IV). In order to test the hypothesis that there was a common periodicity or concordance in the highs and lows of recruitment among the nine species, a Kendall concordance test was conducted on ranked monthly recruitment values. The summed monthly ranks for all species (Fig. 2) show that there was definite congruence in the highs and lows of recruitment. The temporal concordance in recruitment values is statistically significant ($W = 0.524$, $P < 0.005$). Fig. 2 shows that there were major episodes of recruitment in May, June, and August as well as in April and November. The lowest recruitment values occurred in July and January. Recruitment in these species thus appears to have been episodic rather than truly continuous or seasonal.

TABLE IV

Estimates of recruitment intensity, approximated in each species by the percentage of the species population sample within the lower 25% of the maximum range of size classes observed in the 12-month sampling period. Medians and 95% CI on recruitment intensity are given for each month for the group of nine species and for each species for the 12-month sampling period. Sample sizes for monthly size-frequency distributions are given in parentheses below recruitment intensity estimates.

| Species	Mar 82	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan 83	Feb	Species median (95% CI)
A. normanni	19.3 (89)	50.0 (80)	36.6 (303)	39.9 (306)	6.5 (294)	27.5 (295)	48.7 (308)	24.1 (87)	44.1 (59)	30.9 (68)	21.2 (99)	25.0 (36)	29.2 (21.2, 44.1)
H. curacaoensis	47.8 (69)	49.4 (83)	60.0 (255)	84.8 (145)	67.0 (312)	76.3 (299)	75.8 (62)	56.0 (41)	37.3 (75)	46.9 (294)	33.7 (312)	30.9 (207)	52.7 (37.3, 75.8)
L. fucorum	0.3 (346)	4.2 (285)	25.8 (318)	15.0 (301)	8.3 (289)	32.4 (296)	13.4 (291)	13.3 (113)	39.1 (294)	13.7 (284)	5.9 (304)	13.4 (336)	13.4 (5.9, 25.8)
L. parvulus	18.8 (112)	38.5 (26)	21.0 (210)	34.5 (58)	9.2 (119)	66.5 (257)	31.1 (164)	12.1 (132)	22.8 (92)	34.4 (209)	8.7 (333)	10.4 (77)	21.9 (10.4, 34.5)
L. tenuicornis	34.1 (41)	26.3 (19)	42.2 (83)	34.5 (165)	7.1 (210)	41.0 (156)	25.0 (72)	26.0 (50)	25.0 (12)	33.0 (36)	2.0 (49)	2.6 (38)	26.2 (7.1, 34.5)
P. americanus	32.5 (77)	20.0 (75)	39.4 (360)	28.5 (375)	4.6 (306)	64.7 (329)	14.7 (95)	16.3 (43)	53.6 (28)	23.0 (187)	17.6 (210)	26.7 (134)	24.8 (16.3, 39.4)
P. bermudensis	25.4 (209)	27.4 (62)	37.2 (218)	25.4 (59)	7.2 (69)	17.1 (76)	31.9 (47)	22.3 (112)	40.0 (175)	4.3 (141)	5.0 (121)	4.8 (42)	23.8 (5.0, 31.9)
P. riveroi	43.4 (83)	55.2 (29)	79.6 (167)	57.1 (42)	11.9 (59)	51.9 (54)	27.0 (63)	30.4 (56)	45.5 (66)	45.5 (110)	12.9 (62)	52.4 (21)	45.5 (27.0, 55.2)
T. manningi	28.9 (128)	33.0 (88)	47.3 (226)	57.7 (201)	22.8 (342)	50.5 (317)	23.8 (294)	22.0 (254)	31.0 (42)	23.5 (81)	9.1 (176)	20.0 (135)	26.4 (22.0, 47.3)
Monthly median	28.9	33.0	39.4	37.2	8.3	50.5	27.0	22.3	39.1	30.9	9.1	20.0	
(95% CI)	18.8, 43.4	20.0, 50.0	25.8, 60.0	25.4, 57.7	6.5, 22.8	27.5, 66.5	14.7, 48.7	13.3, 30.4	25.0, 45.5	13.7, 45.5	5.0, 21.2	4.8, 30.9	
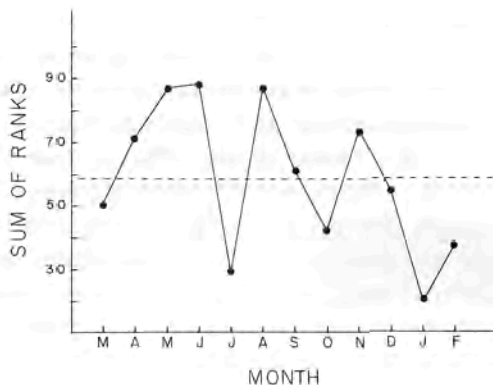
Fig. 2. Joint variation in estimates of recruitment intensity (% population in the smallest 25% of all possible size classes in each species) in the nine seagrass shrimp species. The deviation of the sum of observed recruitment ranks (solid circles) for each month and all species about the expected sum of ranks (dotted line) is shown. The null hypothesis of no concordance in the highs and lows of ranked recruitment values among species is rejected (Kendall concordance test; $P < 0.005$).

DISCUSSION

Various authors (Giese & Pearse, 1974; Rokop, 1974; Sastry, 1983) have distinguished between truly continuous and year-round, asynchronous breeding in marine invertebrates. In truly continuous breeding, all mature individuals in the population are reproductively active throughout the year. In asynchronous, year-round breeding, there is breeding during only part of the year on an individual basis, but breeding periods are out-of-phase among individuals so that some proportion of the population is breeding all year long.

Breeding took place throughout the year of sampling in these nine species of seagrass carideans, and there was no evidence for concordance among species in monthly variations in breeding intensity. The pattern of reproduction observed seems to fit that of reproduction continuous both on the population and individual levels. In all species, most females that were carrying embryos near hatching were also close to spawning another brood (ovary filled with vitellogenic oocytes). Statistical tests of correlation between degree of ovarian development and degree of embryonic development, done on a cumulative annual sample of incubating females in each species, were highly significant. Laboratory observations confirmed a pattern of successive female spawns.

If females were producing successive broods without interruption, one might expect that values for percent ovigerous (Table I) would be consistently high. However, laboratory observations have shown that 1–4 days can pass between hatching of one brood and spawning of the next. Females collected during this period would not be carrying embryos and would have been scored nonbreeding. Perhaps more importantly, the method for setting the size of female maturity (size of smallest ovigerous female

observed) probably caused percent breeding (ovigerous) to be underestimated in all species except *Thor manningi*. These two factors may explain the lower values observed and intraspecific variation in percent ovigerous females for the other eight species of this group of continuously breeding shrimps. In *T. manningi*, maturity can be determined by morphological features in each female (Bauer, 1986) so that % ovigerous was not underestimated, and monthly values observed were consistently high (90–100%). In all species, stage of ovarian development was recorded in ovigerous females to investigate the question of multiple spawnings, but it was not recorded in nonovigerous females. Observations on ovarian condition in nonovigerous females nearing or past reproductive size (which in future studies might be tentatively established by preliminary inspection of samples) could be useful in distinguishing small females not yet really mature from nonovigerous females near to spawning, i.e., reproductive.

Comparison of breeding patterns of these tropical caridean shrimp species with other shallow water caridean assemblages from warm (Kikuchi, 1962; Bauer, 1976; Oya & Oka, 1985) and cold (Allen, 1966) temperate latitude habitats does support a generalization for *this* group of invertebrates that breeding is continuous in the tropics but seasonal at higher latitudes. General environmental features of the seagrass habitat investigated fit a classical "Ortonian" view of a stable, physically benign, tropical marine shallow-water habitat. Water temperature and salinity measurements were relatively stable (Bauer, 1985) throughout the year. Qualitative observations on seagrass occurrence and density indicated little change during the sampling period. Habitat conditions apparently allow (physiologically) year-round reproduction on the population level in these tropical shrimp species.

The nonstop production of successive broods after maturity observed in this study in most females, i.e., continuous reproduction on the individual level, may be a life history adaptation. Cohort analysis of three species (Bauer, 1986; Salva, 1984) has indicated short (2–5 months) life spans in these small-sized species, with cohorts entering, passing through, and leaving the population during the year. Females from any one cohort cannot afford to wait for some "best" time of the year to produce larvae. They must mature and reproduce rapidly (and continuously) before suffering mortality, e.g., fish predation which is thought to be intense in these habitats (Randall, 1967; Heck & Orth, 1980; Ogden, 1980). Cameron (1986) found both seasonal and continuous reproduction in four sea urchin species in seagrass meadows off the south coast of Puerto Rico. In these species, life span may be on the order of years, and adults of some species apparently are adapted to spawn during a season which may be optimal for larval survival and subsequent settlement. In terms of life history models (Stearns, 1976; Grahame & Branch, 1985), the seagrass shrimp species studied, with their apparent pattern of rapid growth to maturity and nonstop larval output during a short (in three species analysed) life span, appear to be on the "r" end of a "r–K" spectrum of life history traits when compared to the sea urchins studied by Cameron (1986). This comparison underscores the danger of extending generalizations about reproduction from one group to others with different phylogenetic histories. Differences in basic

reproductive biology (morphology, physiology) and life history traits may explain why there are so many exceptions (e.g., ophiuroids, Hendler, 1979; crustaceans, Sastry, 1983; corals, Harrison et al., 1984; Schlesinger & Loya, 1985) to the classically held view of continuous reproduction in tropical marine invertebrates.

Although breeding (embryo and larval production) was continuous, recruitment of these shrimp populations onto the seagrass meadows was definitely episodic. The smaller size classes of these species sometimes showed dramatic increases and decreases in relative abundance. If recruitment had been truly continuous (similar in strength throughout the year), one would expect to see relatively stable size-frequency distributions. Static size-frequency distributions of these species were not observed; new cohorts were identified and followed through time in three species that have been analysed (Bauer, 1986; Salva, 1984). More importantly, recruitment was not only episodic but concordant among species, occurring at similar time periods during the year. This suggests that recruitment was being influenced by the same factor or factors in all nine species.

Possible conditions which might produce discontinuous or highly variable continuous recruitment are (1) high temporal variation in embryo production by parent populations and (2) significant temporal variation in mortality on (a) planktonic larvae or (b) newly recruited juveniles before sampling. It has been shown that females living in the sampled seagrass meadows produced larvae all year. However, there is no data to indicate that larvae that settled on the grass beds were produced by females living there. If the parent shrimp populations that produced the larvae lived at some other geographic area(s), reproduction in all such populations would have to be episodic but synchronous (given stable larval and new-recruit mortality) in order to explain the pattern of recruitment observed. A more likely explanation for episodic recruitment that was concordant among species is that mortality on planktonic larvae was temporally variable. An ultimate factor or selective pressure that may have caused development of seasonal breeding patterns at higher latitudes is seasonality of the larval food supply (phyto- and other zooplankton) (Thorson, 1950; Giese & Pearse, 1974; Sastry, 1983). Seasonality of tropical oceanic phytoplankton and zooplankton abundance is typically considered slight relative to that of higher latitudes (Rhyther, 1963; Longhurst, 1981; Parsons et al., 1984). However, Yoshioka et al. (1985) have observed significantly higher Chl a values and zooplankton abundances during the summer in oceanic areas off the south coast of Puerto Rico which were correlated with changes in hydrographic conditions. Thus, temporal variation in larval food supply with subsequent variation in larval mortality and recruitment is a possibility in this tropical area. Alternatively, although the insular shelf is quite narrow (1–2 km) off the north coast of Puerto Rico, where this study was conducted, the larval populations that stocked the seagrass meadows may have developed in nearby shallow neritic waters where seasonal or other variation in plankton production would be more likely in a tropical latitude. Other factors, such as variations in currents that return planktonic larvae to seagrass meadows, might be responsible for the patterns observed. Finally, episodic variation in recruitment could have resulted if

intensity of larval settlement from the plankton was more or less continual but mortality on newly settled juveniles in the seagrass meadows before monthly sampling was quite variable.

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