

Analysis of embryo production in a caridean shrimp guild from a tropical seagrass meadow

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ABSTRACT

Embryo production was compared among nine caridean shrimp species inhabiting seagrass meadows in a tropical location, the north coast of Puerto Rico. Reproduction occurred throughout the year in all species. During a short life span (less than one year), females reproduced continuously after reaching maturity, producing successive broods of embryos at short intervals. Analysis of allometry in brood size (number of embryos/brood) as a function of female size (carapace length) was done by calculating slopes of brood size/female size regressions with log transformed variables. Increase in brood size with female size was isometric in seven species and showed positive allometry in two others. However, the relationship of species mean log brood size on species mean log female size was negatively allometric, indicating that females of smaller species produced relatively larger broods for their size than did females of larger species. Analysis of covariance corroborated this conclusion. Log brood size means adjusted for differences in female size were significantly different among species, and adjusted species brood means were negatively correlated with species female size. The mechanism for enhanced reproductive output (in terms of brood size) in smaller species is unclear. In some crustacean groups, reduced embryo size has been selected for as a means of increasing brood size. Additionally, since embryo size and incubation period (duration of embryonic development) showed a significant positive correlation in this group of caridean species, smaller embryo size would also result in shorter incubation periods and thus larger numbers of broods per reproductive period. However, there was no relationship between species embryo size and species female size in this group, indicating that differential selection among species on embryo size as a means of increasing reproductive output has not occurred.

1 INTRODUCTION

In a study on the temporal pattern of reproduction and recruitment in nine caridean shrimp species inhabiting a tropical seagrass meadow (Bauer 1989), detailed observations on brood size, embryo size and female size were recorded on a large number of breeding females. These and supplemental observations on embryo incubation periods permitted the present analysis of the interrelationships of brood size, embryo size, female size and incubation period in these shrimps. Since the members of this suite of caridean species inhabit the same meadows and

were collected during the same time period, confounding variation in reproductive output due to latitudinal or habitat differences among species is reduced, i.e. breeding females of the guild were exposed to very similar environmental conditions. The goal of such an analysis is to propose and test hypotheses on the selective forces acting on reproductive output in these and, ultimately, other crustacean species.

2 NATURAL HISTORY AND REPRODUCTIVE PATTERNS

The nine most abundant carideans in *Thalassia testudinum*-*Syringodium filiforme* seagrass meadows at a site on the north coast of Puerto Rico (Dorado; 18°29'N, 66°15'W), sampled in 1981-82, were: *Thor manningi*, *Hippolyte curacaoensis*, *Latreutes fucorum*, *L. parvulus* (Hippolytidae); *Leander tenuicornis*, *Periclimenes americanus* (Palaemonidae); *Processa bermudensis*, *P. riveroi* (Processidae); and *Alpheus normanni* (Alpheidae) (Bauer 1985). *Hippolyte curacaoensis*, *Latreutes fucorum* and *L. parvulus* cling to seagrass blades, while *Thor manningi*, *Periclimenes americanus*, and *Leander tenuicornis* range over both the substrate and seagrass blades. *Alpheus normanni* constructs burrows in which adult male-female pairs occur, and the processid species burrow directly into the sediment by day. Laboratory observations show that burrowing species emerge at night and also that all other species appear most active in swimming and foraging at night. These laboratory observations confirmed the hypothesis, suggested by results of day-night sampling, that these species are primarily nocturnal. Densities estimated from night sampling were significantly higher than those based on day collecting in all species (Bauer 1985).

Reproduction (embryo production) was continuous throughout the year in all species at the population level (Bauer 1989). The percentage of mature females carrying embryos was never less than 20% in any species in any month and generally was much higher. The monthly variations in breeding intensity (% ovigerous females) were not concordant among the nine species, i.e. reproduction was continuous with no common seasonal pattern in the highs and lows of breeding intensity. Three environmental variables (temperature, salinity and qualitative observations on seagrass cover) were relatively constant throughout the year (Bauer 1985). The tropical seagrass meadows sampled were a classic example of a physically benign, stable tropical nearshore marine habitat (cf. Orton 1920). Breeding patterns observed for these seagrass shrimp populations generally fit predictions (Orton 1920, Thorson 1950, Sastry 1983 about continuous reproduction in littoral and neritic tropical marine invertebrates).

Embryo production was continuous at the individual as well as at the population level in these shrimp species. Laboratory observations revealed that females carrying embryos near to hatching also had ovaries filled with large vitellogenic oocytes. After embryos hatched, the female molted within a day or two. Spawning of a new brood of embryos then took place within a day if no male was present, sooner if a male was available for mating (similar to the carideans *Heptacarpus pictus* and *H. paludicola*, Bauer 1976, 1979). Statistical analyses on data for more than three thousand embryo-carrying females confirmed that females carrying embryos near hatching had ovaries ripe for a new spawning (Bauer 1989). Embryo incubation periods were short (5-10 days); once females reached maturity, they apparently produced uninterrupted successive spawns at short intervals until death. These small seagrass shrimp species probably have short life spans [less than one year; estimated from cohort analysis at 5 months in *Thor manningi* (Bauer 1986) corroborated by measurements on development and growth in laboratory-reared *Thor* spp. (Dobkin 1968); estimated at 2-5 months in *Latreutes* spp. from cohort

analysis (Salva 1984)]. Thus, females of these seagrass shrimp species appear to mature rapidly and to produce several successive spawns within a single short lifetime reproductive period.

3 DATA BASE

More than 3200 embryo-carrying females were examined from preserved collections taken in the year-long sampling program (Bauer 1985) in the Dorado, Puerto Rico, seagrass meadows. The number of embryos carried by females (= brood size) was counted only in females carrying embryos in early developmental stages. These stages (1 & 2) are modified (Bauer 1986) from a subjective scale of 1-4 for embryo development given in Allen (1966). Embryos observed at 6-25 \times under a stereomicroscope were staged as follows: Stage 1, embryo entirely of yolk, no tissue cap (blastodisc) visible; Stage 2, blastodisc present, but no eye or eye pigment developed; Stage 3, eye developed or developing, cephalothorax and abdomen of embryo not separated; Stage 4, embryo near hatching, with little yolk, cephalothorax and abdomen visibly separated. Broods containing Stage 1 & 2 embryos were rather tightly arranged under the female abdomen. However, broods with later-stage embryos were distended away from the abdomen and pleopods due to an increase in embryo size during development. Such advanced (Stage 3 & 4) embryos were easily dislodged from females during sampling and especially in handling after preservation; females carrying advanced embryos were not used in the analyses. The number of females examined with Stage 1 or 2 embryos was 661 (median number/species = 78, minimum = 24, maximum = 131).

Measurements of the greater and lesser diameters of Stage 1 and 2 embryos were taken using an ocular micrometer in a stereomicroscope at 25 or 50 \times magnifications. Five embryos were chosen haphazardly from a group of embryos separated from a given female, and the median greater and lesser diameters were used to represent embryo size from that female (median less affected by extremes than the mean in a small sample size). Embryo volume was calculated from the formula for an oblate spheroid (cf. Turner & Lawrence 1979):

$$v = \pi \times (d_1)^2 \times (d_2)/6$$

where v = volume (mm^3), d_1 = lesser embryo diameter and d_2 = greater diameter. Carapace length, a measure of female size, was the distance from the posterior edge of the eye orbit to the posterior mid-dorsal margin of the carapace.

4 BROOD SIZE AS A FUNCTION OF FEMALE SIZE

Table 1 gives mean brood size and mean breeding female size for the nine caridean species. The number of embryos incubated (brood size) by a female is a direct expression of its reproductive output. Intraspecific analyses and interspecific comparisons of the brood size/female size relationship often reveal possible selective forces or constraints acting on reproductive output in species from related taxa (e.g. Reaka 1979, Hines 1982). Allometric relationships can best be examined by linear regressions obtained from log transformation of the power curve $Y = aX^b$ (Gould 1966, Hartnoll 1982, Hines 1982) so that

$$\log Y = b(\log X) + \log a$$

Here, the allometry of brood size is examined within and among the nine caridean species. In

Table 1. Mean (\bar{X}) brood size (number of embryos/brood) and mean size (carapace length, mm) (\pm standard deviation) of breeding females in the nine species of tropical seagrass carideans. n: number of specimens.

Species	n	\bar{X} brood size	\bar{X} female size
<i>A. normanni</i>	55	95 \pm 72	4.5 \pm 0.7
<i>H. curacaoensis</i>	131	153 \pm 70	2.4 \pm 0.3
<i>L. fucorum</i>	98	57 \pm 24	2.3 \pm 0.3
<i>L. parvulus</i>	78	59 \pm 23	2.0 \pm 0.2
<i>L. tenuicornis</i>	40	593 \pm 311	6.7 \pm 1.0
<i>P. americanus</i>	99	56 \pm 27	2.1 \pm 0.2
<i>P. bermudensis</i>	84	129 \pm 82	3.5 \pm 0.5
<i>P. riveroi</i>	24	384 \pm 186	5.3 \pm 0.7
<i>T. manningi</i>	52	66 \pm 27	1.9 \pm 0.2

regression equations dealing with brood size and female size (Table 2), Y = number of embryos carried by a female (= brood size) and X is carapace length, a standard measure of body size in carideans (e.g. Bauer 1986, Kuris et al. 1987).

4.1 Intraspecific variation in brood size

Table 2 presents the regression equations of log brood size on log female size for all 9 caridean species. The slope indicating isometry in allometric analyses depends on the dimensions of the dependent and independent variables (Gould 1966). Thus, if Y and X have the same dimensions, e.g. are both linear measurements, then a slope of $b = 1$ indicates isometry. If, on the other hand, X is a linear measure (L) and Y is a volume (L^3), then a slope of 3 indicates isometry. The measure of brood size used here, i.e. number of embryos, has no dimension *per se*. However, it is proposed that a slope of 3 indicates isometry in the brood size on female size regressions because the number of embryos approximates a volume, i.e. the volume of the collective mass of embryos. The slopes (b) of regressions in Table 2 vary around a median of 3.05 from 2.38 to 3.90. The hypothesis that $b = 3$ can be accepted in those seven species in which the 95% confidence limits on b include $b = 3$ (all species except *Latreutes fucorum* and *Alpheus normanni*).

Negative allometry in brood size might indicate senescence of reproductive output in larger (older) females, while positive allometry could indicate selection for morphological or physiological changes in larger females increasing this measure of reproductive output. However, in 7 of 9 species, brood size increased isometrically with female size. The two species that showed a positive allometry in brood size, *Latreutes fucorum* and *Alpheus normanni*, differ greatly in general morphology, behavior and ecology. It is likely that the morphological and/or physiological adaptations accounting for the positive allometry are quite different in the two species. In *Alpheus normanni*, brood size in smaller females begins at a very low level (for their size) relative to other species. This is shown by the Y-intercept of the *A. normanni* (Table 2; significantly different from $Y = 0$, t-test, $p < 0.05$), lowest of any species. The differential increase in brood size ($b = 3.90$) in *A. normanni* may reflect some compensatory morphological or physiological adaptation lifting embryo production with increasing female size from a relatively low level in the smaller females.

4.2 Interspecific comparisons of brood size

It is obvious (Table 1, Fig. 1) that females from larger-sized species can carry greater absolute numbers of embryos than those from smaller species. The question that will be asked in this section is if females of smaller-sized species compensate for their smaller absolute body size by a relative increase in reproductive output, here measured by number of embryos in a brood.

Figure 1 shows a plot of log mean number of embryos (brood size) on log mean carapace length (female size) for all species. The linear regression for these data is:

$$\log (\bar{Y}) = 1.60 (\log \bar{X}) + 1.30$$

As discussed above, a slope of 3 indicates isometry in allometric equations of number of embryos on female carapace length. In this regression, $b = 1.60$ and the null hypothesis of $b = 3$ is rejected (95% confidence limits on b are 0.78, 2.42). Clearly, there is negative allometry in brood size when these species of different body size are compared. This analysis indicates that females of smaller species produced relatively more embryos for their size than did those of larger species.

The hypothesis that smaller species have a relatively higher reproductive output (in terms of brood size) than larger species was examined with analysis of covariance (ANCOVA) of log number of embryos (brood size) on the covariate log female carapace length (female size). The assumption of homogeneity of slopes could not be met for all nine species ($p = 0.01$). *Alpheus normanni* and *Latreutes fucorum* were eliminated from the analysis since the slopes of the brood size/female size regressions (Table 2) were significantly different from 3 while those of the other 7 species were not. The hypothesis of homogeneity of slopes in these seven species was accepted ($p = 0.53$). In the seven species, the hypothesis that log brood size means (adjusted for female body size) are not different (equivalent to testing for homogeneity of the Y-intercepts, Sokal & Rohlf 1981: 521) is rejected ($p < 0.001$). The ANCOVA involved extrapolation of

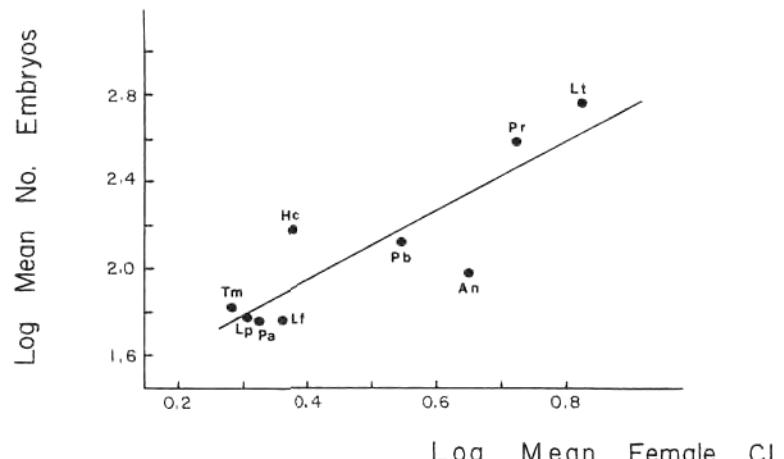


Figure 1. Interspecific comparisons of brood size as a function of female size in the nine seagrass shrimp species. Log mean number of embryos (brood size) is plotted against log mean breeding female carapace length (CL, in mm). The regression equation is: $\log (\bar{Y}) = 1.60 (\log \bar{X}) + 1.30$. Species symbols are: An – *Alpheus normanni*; Hc – *Hippolyte curacaoensis*; Lf – *Latreutes fucorum*; Lp – *L. parvulus*; Lt – *Leander tenuicornis*; Pa – *Periclimenes americanus*; Pb – *Processa bermudensis*; Pr – *P. riveroi*; Tm – *Thor manningi*.

Table 2. Regression equations of log number of embryos (brood size) on log CL (carapace length in mm, the measure of female size). Y: number of embryos, X: female carapace length, a: Y-intercept, b: slope, n: number of specimens, r^2 : coefficient of determination (squared Pearson correlation coefficient). In all regressions, $p(H_0: b = 0) < 0.001$. 95% confidence limits on b are given.

Species	n	$\log(\text{number of embryos}) = b(\log \text{CL}) + \log a$	r^2	95% limits
<i>A. normanni</i>	55	$\log(Y) = 3.90(\log X) - 0.65$	0.78	3.32, 4.48
<i>H. curacaoensis</i>	131	$\log(Y) = 2.94(\log X) + 1.03$	0.75	2.64, 3.23
<i>L. fucorum</i>	98	$\log(Y) = 3.66(\log X) + 0.38$	0.59	3.04, 4.27
<i>L. parvulus</i>	78	$\log(Y) = 2.67(\log X) + 0.96$	0.52	2.07, 3.26
<i>L. tenuicornis</i>	40	$\log(Y) = 3.17(\log X) + 0.12$	0.86	2.74, 3.60
<i>P. americanus</i>	99	$\log(Y) = 3.28(\log X) + 0.62$	0.64	2.78, 3.77
<i>P. bermudensis</i>	84	$\log(Y) = 2.88(\log X) + 0.50$	0.54	2.30, 3.46
<i>P. riveroi</i>	24	$\log(Y) = 3.05(\log X) + 0.34$	0.66	2.08, 4.02
<i>T. manningi</i>	52	$\log(Y) = 2.38(\log X) + 1.10$	0.31	1.37, 3.39

Table 3. Means (\bar{X}) of Stage 1 and 2 embryo volumes (mm^3) for the nine caridean species. The greater (d_2) and lesser (d_1) diameters (mm) corresponding to those of a measured embryo with a volume closest to the mean volume are given for Stage 1 embryos for each species. A single asterisk by the species name indicates those species in which the mean volume of Stage 2 embryos was significantly different from that of Stage 1 embryos (t -test, $p < 0.05$). n: number of female broods examined, **no observations.

Species	\bar{X} volume	Stage 1 embryos (n)	d_2	d_1	\bar{X} volume	Stage 2 embryos (n)
<i>A. normanni*</i>	0.030	35	0.44	0.36	0.033	20
<i>H. curacaoensis*</i>	0.005	66	0.24	0.20	0.007	65
<i>L. fucorum</i>	0.012	46	0.40	0.24	0.012	50
<i>L. parvulus</i>	0.012	30	0.36	0.24	0.013	48
<i>L. tenuicornis*</i>	0.028	22	0.42	0.36	0.033	18
<i>P. americanus*</i>	0.013	59	0.36	0.26	0.016	37
<i>P. bermudensis*</i>	0.008	45	0.32	0.22	0.012	39
<i>P. riveroi*</i>	0.010	10	0.30	0.26	0.015	14
<i>T. manningi*</i>	0.026	39	0.42	0.34	**	**

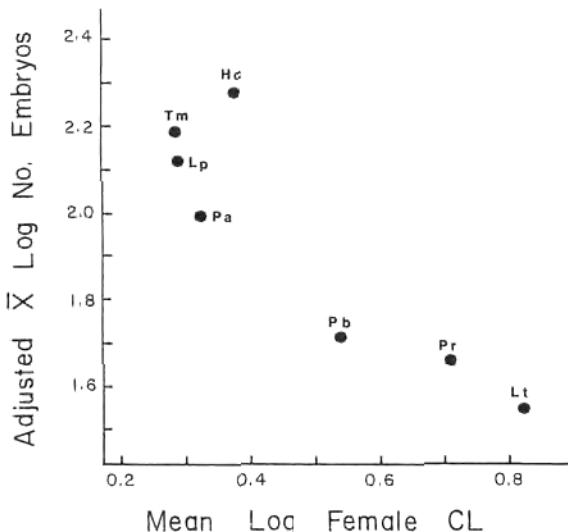


Figure 2. Mean log brood size (number of embryos/brood) for seven species adjusted by ANCOVA for body size plotted against mean log female carapace length (CL). $r = -0.90$. Species symbols as in Figure 1.

brood size/female size regressions in order to compare species in which female sizes did not overlap. This biased the analysis in favor of accepting the hypothesis of no difference in adjusted log brood size means (Snedecor & Cochran 1967: 430). In spite of this possible bias, adjusted log brood size means were significantly different among the seven species. *Latreutes fucorum* and *A. normanni* were similarly analysed, and for these two species, adjusted log brood size means were also significantly different ($p < 0.001$).

In Figure 2, adjusted log brood size means are plotted as a function of mean log female carapace length (size) for the group of seven species. There is a significant negative correlation between adjusted log brood size means and log female size means ($r = -0.90$; $p < 0.05$), i.e. in this group, females of smaller-sized species produced relatively more embryos (for their size) than did females of larger species. Similarly, the adjusted log brood size mean of *Latreutes fucorum* (2 102) is significantly larger ($p < 0.001$) than that of *Alpheus normanni* (1 182), the species with larger female size (Table 1). Females of smaller species are limited by absolute size in the number of embryos they can carry, and there has apparently been selection for a relatively higher reproductive output (in terms of numbers of embryos produced and carried by females) to compensate for this.

5 EMBRYO SIZE

The size of the newly fertilized egg (embryo) may reflect the action of various, sometimes opposing, selective pressures acting on reproductive output and larval development. Small embryo size permits a larger brood size for a given energetic allocation to reproduction, thus increasing the number of larvae hatched (Steele & Steele 1975). On the other hand, large embryo size may allow the larva to hatch and later settle at a larger size, with increased probability of survival (Strathmann 1977, Hines 1986). In comparisons of embryo size among species within a taxon, larger embryo size may indicate hatching at an advanced stage of development. Such an advanced larva is exposed for a shorter time to the intense mortality

presumed characteristic of the planktonic environment (Thorson 1950, Grahame & Branch 1985), although this advantage is counterbalanced by the disadvantage of reduced larval dispersal.

Duration of embryonic development is positively correlated with embryo size in some crustacean groups (Wear 1974, Steele & Steele 1975), but not in others (reviewed in Hines 1986). In the seagrass caridean species under consideration, the time that embryos are incubated (= developmental time from spawning and fertilization to hatching) could be an important factor in the number of broods produced per reproductive period, since females of these species produce broods successively throughout their short lifetimes (Bauer 1989). If incubation period varies positively with embryo size, reproductive output could be increased by a reduction in embryo size, with the concomitant shortening of incubation period and the resultant increase in the number of broods per reproductive period.

Wear (1974), both with his own data and that reviewed in the literature, showed that embryo size increased during development in several decapod species. In the seagrass caridean species, the mean volume of Stage 2 embryos was significantly different (larger than that of Stage 1 to 6 of 8 species) (Table 3). Only observations on broods composed of Stage 1 embryos were used in the subsequent analyses to avoid confounding variation due to differences in embryo developmental stage and for consistency among species.

5.1 Interspecific comparisons in embryo size

It was shown earlier that the smaller species produced, for their size, relatively higher numbers of embryos per brood than did larger species. Increased brood size could be accomplished by a reduction in embryo size, here measured as embryo volume. The question was asked: do smaller species tend to have smaller embryo sizes than larger species? The answer is negative: there was no correlation between species mean log embryo volume and species mean log female carapace length in this group of shrimps ($r=0.30$, $p>0.05$).

5.2 Duration of embryonic development and embryo size

The duration of embryonic development (period incubated by females) is positively correlated with embryo size (volume) ($r=0.75$; $p<0.05$) (Fig. 3) in the eight of these nine species for which incubation periods have been estimated (Bauer 1989). Species could conceivably increase

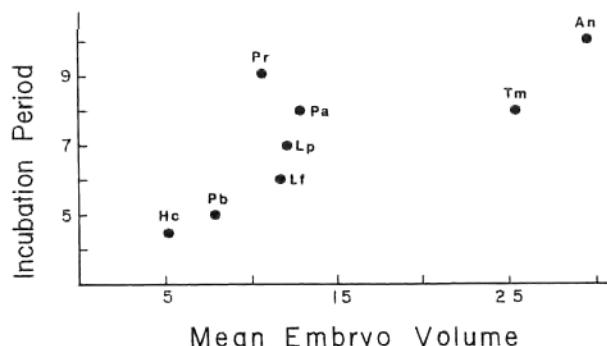


Figure 3. Embryo incubation period (days) of 8 seagrass species plotted against their mean embryo volumes ($\text{mm}^3 \times 10^3$). $r=0.75$. Species symbols as in Figure 1.

reproductive output by increasing the number of broods per unit time through a decrease in embryo developmental time by means of smaller embryo size as discussed above. The question was asked: do smaller species also have greater reproductive output in terms of increased number of broods per unit time as a result of shortened incubation periods? There is no significant correlation between species measures of incubation period and mean breeding female body size (carapace length) ($r = 0.48$, $p > 0.05$). It appears that there is no tendency towards shortened incubation periods in smaller species in this group of seagrass shrimps.

Wear (1974) suggested that developmental time of incubated embryos varied with the quantity of yolk (embryo volume) in the newly spawned embryo, i.e. more yolk to metabolize, longer developmental times at the same temperature. Steele & Steele (1975) and Steele (1977) proposed that faster developmental times of smaller embryos simply reflects the well-known inverse relationship between size and metabolic rate in biological systems. The embryo incubation periods of these tropical seagrass species were quite short compared to temperate or boreal species (cf. Wear 1974, Allen 1966). Wear (1974) found, as one might suspect, that incubation periods decreased with increasing temperature in the British species studied. Incubation periods were extrapolated to temperatures (27–30°C) similar to those (26–28°C) at which the tropical seagrass species in this study were maintained. Although the embryos of British species did not survive at these temperatures, it is interesting to note that the predicted incubation periods were similar (6–11 days) to those observed in the tropical carideans. Short embryo incubation periods in these tropical species may be a life history adaptation for increasing the number of broods spawned per unit time. However, the Wear (1974) study suggests the alternative hypothesis that short developmental periods in tropical carideans may be a simple metabolic response to elevated water temperatures in the tropical habitat.

6 LIFE HISTORY CONSIDERATIONS

Reproductive characteristics of these nine tropical caridean species do not clearly fit into contrasting predictions of life history models (Pianka 1970, Stearns 1976, Grahame & Branch 1985). They do approach the r end of the r - K continuum of deterministic models. Life spans of these shrimps are probably short (a few to several months), and growth to reproductive maturity appears rapid (Bauer 1986, Salva 1984). Once maturity is reached, embryos are produced in successive spawns at short intervals (1–2 weeks) between spawns (Bauer 1989). Although the term iteroparous is usually associated with multiple spawnings, these species might be considered semelparous in the sense that there is a brief but continuous burst of reproduction during a single reproductive period in a relatively short lifetime (cf. Sastry 1983), an r life history characteristic of fluctuating, unstable environments. The adult habitat (tropical seagrass meadows on the north coast of Puerto Rico) appears relatively stable in terms of basic environmental parameters such as temperature, salinity, and substrate (seagrass cover) (Bauer 1985, 1989). The stability of these species' larval planktonic habitat is unknown. Although tropical planktonic environments are often considered to be predictable relative to temperate and boreal ones, the episodic recruitment, concordant among all species, observed for this group of shrimps (Bauer 1989) may indicate otherwise. Thus the reproductive and other life history traits observed for these species may better fit stochastic ('bet-hedging') models for species, in which adults live in stable environments but in which juvenile (= larval) mortality is variable (Stearns 1976). In the physically stable tropical seagrass meadows in which these species live, predation pressure by fish appears intense (Randall 1967, Heck 1979, Weinstein & Heck 1979, Heck &

Orth 1980, Roblee & Zieman 1984). This source of mortality (stable throughout the year?) is probably responsible for the short (less than one year) life spans of these shrimps and may be the major selective force favoring their rapid maturity and high reproductive effort (Bauer 1989).

These species are relatively small for caridean shrimp, and body size clearly limits absolute embryo production in these as in most other crustaceans. In terms of embryo production as a life history trait, the negative allometry in brood size exhibited by these species suggest that there has been selection such that small species put more resources into reproduction than do large species. Smaller species might increase the number of progeny produced per brood by decreasing embryo size (as in brachyuran crabs, Hines 1982) which would also have the effect of decreasing embryo incubation period and thus increasing the number of broods produced per reproductive life span. However, there was no trend toward smaller embryo size in the smaller species of this group. The mechanism that allows smaller species to produce larger broods (relative to their size) remains unknown, but it might be a morphological feature such as a relatively high allocation of cephalothoracic space for ovarian development and egg accumulation.

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