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COMPARATIVE REPRODUCTIVE STRATEGIES OF THE GRASS SHRIMPS, *PALAEMONETES VULGARIS* AND *P. PUGIO* (DECAPODA, NATANTIA) IN GREAT SIPPEWISSETT SALT MARSH, MASSACHUSETTS, U.S.A.

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RESUMEN

Dos especies de camarones utilizados como alimento de otros animales (*Palaemonetes vulgaris* y *P. pugio*) coexisten en el canal estuárico del pantano salado de Great Sippewissett, Massachusetts. *P. pugio* es desplazado por *P. vulgaris* de las áreas profundas, con abundancia de *Codium*, hacia aguas con fondos de fango, donde el primero muestra una mayor mortalidad que el segundo. Se propone la hipótesis sobre la "diferente respuesta contra la depredación" para poder predecir que *P. pugio*, sometido a una mayor presión de predación que *P. vulgaris*, se reproduce mucho más para así compensar la mayor mortalidad causada por la depredación misma.

Ciento seis hembras adultas de *P. pugio* y doscientas setenta de *P. vulgaris* fueron capturadas con red los días 14,22 y 28 de julio de 1984 para intentar probar dicha hipótesis. *P. vulgaris* madura un aña antes que *P. pugio*, tal como muestran las diferencias de talla del caparazón. Para ambas especies, la fecundidad aumenta en proporción al tamaño del cuerpo. Sin embargo, la mayor (*P. pugio*) es más fecunda que *P. vulgaris*. El peso seco medio de los huevos de *P. pugio* es significativamente mayor que el de *P. vulgaris*. La comparación del índice gonosomático (G.S.I.), que constituye una medida relativa del esfuerzo reproductor, muestra que, entre estas especies, no hay diferencia en dicho esfuerzo.

Los resultados indican que las dos especies han alcanzado estrategias diferentes en cuanto a la reproducción. *P. pugio*, que llega a la madurez a una talla mayor que *P. vulgaris*, tiene la ventaja (en relación con esta mayor talla), de mostrar una mayor fecundidad, lo cual le compensaría la mayor pérdida de individuos causada por depredación. Todo esto nos habla en favor de la hipótesis propuesta anteriormente.

INTRODUCTION

The two species of grass shrimps, *Palaemonetes vulgaris* (Say, 1818) and *P. pugio* Holthuis, 1949, are sympatric in their distributions along the eastern coast of North America (Holthuis, 1952; Bousfield, 1956; Williams, 1984). Based on field and laboratory experiments, Thorp (1976) confirmed that *P. vulgaris* can competitively displace *P. pugio* from the preferred oyster shell substratum by interference competition. Occupancy of shell substratum is shown to be adaptive because shells provide greater protection from predators than does mud. Preliminary collection of these two species of shrimps made by the author on June 30, 1984 at the Great Sippewissett salt marsh reveals

that the distribution of *P. pugio* is confined to tidal creeks in waters of shallow and intermediate depths (0.1 m to 0.5 m). These habitats are bare muddy bottoms with scattered *Enteromorpha* beds. *P. vulgaris* not only coexists with *P. pugio*, but also extends along the tidal creeks well into the deep pools (down to about 3 m) vegetated by *Codium* where only a few *P. pugio* can be found. Following the protocol of Thorp (1976), from field and laboratory observations it is found that *P. vulgaris* can displace *P. pugio* from *Codium* substratum. *Codium* has been reported of benefit as a refuge for many small invertebrates (Meimer, unpubl.). Hence the spatial distribution pattern of these two species in Great Sippewissett salt marsh is similar to that described by Thorp (1976). A 'differential predation response' hypothesis is proposed to predict that *P. pugio* under higher predation pressure than that of *P. vulgaris* should reproduce more offsprings to compensate the higher predation mortality. The unique situation of these two sympatric species of shrimps provides the author a chance to test the proposed hypothesis and to see how these two shrimps have evolved different reproductive strategies in order to maximize their fitness.

MATERIALS AND METHODS

Four stations (Stations A-D) in Great Sippewissett salt marsh were chosen for collection (fig. 1). Physical appearance and environmental characteristics of the stations are given in table I. Grass shrimps, *P. pugio* and *P. vulgaris* were collected by dipnet (3 mm mesh size) on July 14, 22, 28, 1984. Equal amount of fishing effort was spent on each station. Specimens were preserved with 10% seawater-formalin in situ.

In the laboratory, sex was determined on the basis of presence (males) and absence (female) of an appendix masculina on the endopod of the second pleopod (Williams, 1984). Carapace length (CL) and body length (BL) of all ovigerous shrimps were measured with a vernier caliper to the nearest 0.05 mm. Body weight (BW) was obtained by drying shrimps at 64°C for 24 h and then weighing with a Mettler H6 balance to the nearest 0.1 mg. For each female, the number of eggs (or embryos) carried was counted and defined as fecundity (F). Fecundity per mm of carapace length was also calculated. In addition, the average weight of each egg (or embryo) was obtained by dividing the dry weight of all eggs (or embryos) by the fecundity. Gonadosomatic index (G.S.I.), which is a relative measure of reproductive effort, was obtained with the following formula:

$$\text{G.S.I.} = \frac{G}{BW\text{-}G} \times 100$$

where G is the dry weight of eggs (or embryos).

Student's t-test was applied to test the significance of the difference between the reproductive characteristics of the two species.

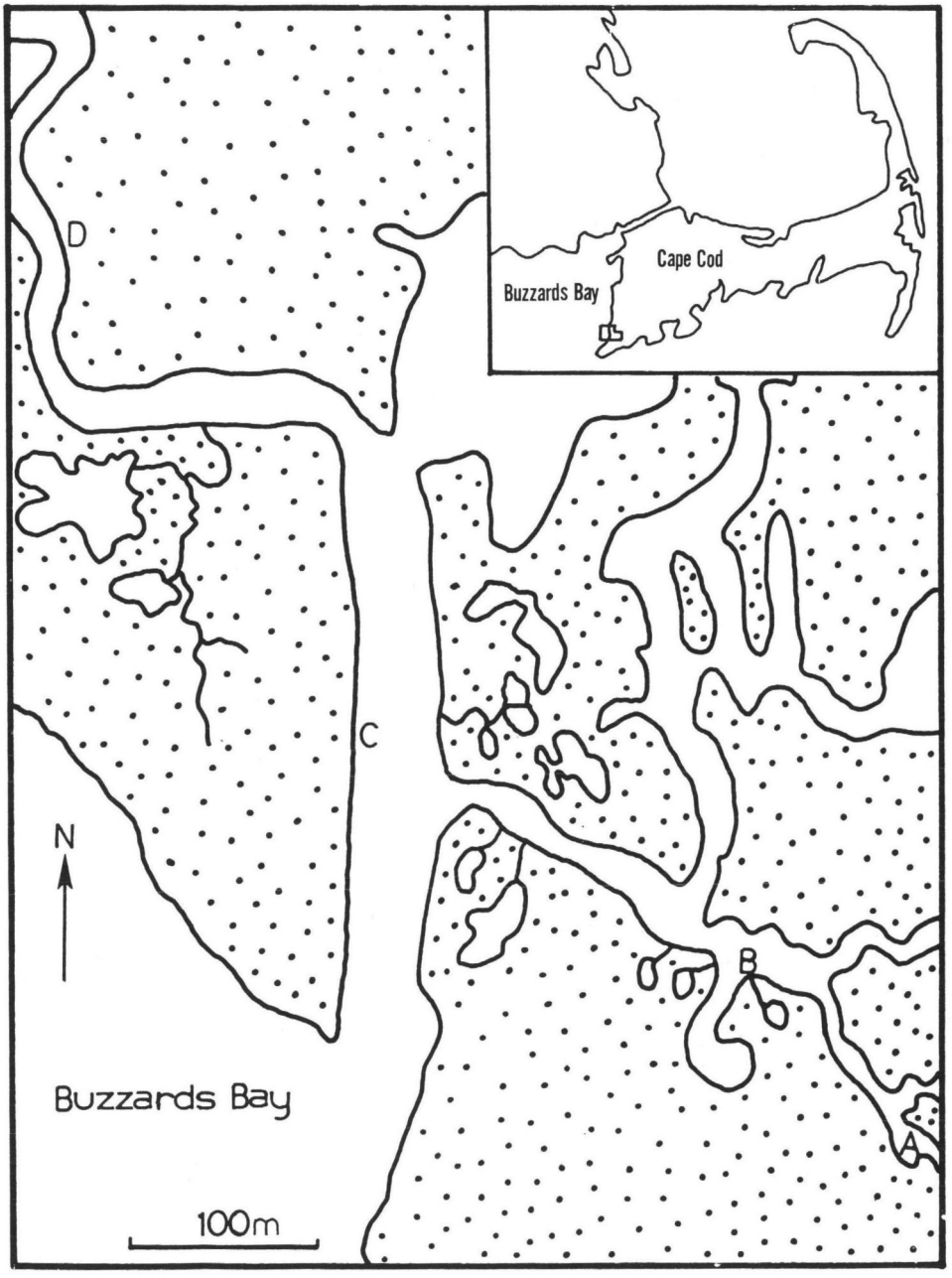

Fig. 1. The study area and collection stations (A, B, C, D) in Great Sippewissett salt marsh.

TABLE I

Environmental characteristics of Stations A-D (collections and measurements made on July 14, 22, 28, 1984)

	Salinity (‰)	Water temp. (°C)	Physical appearance
Station A	14.0-17.0	29.0-31.5	Shallow bare muddy bottom with *Enteromorpha*; depth: 0.1-1.1 m
Station B	17.0-22.0	29.0-31.5	Muddy bottom with *Enteromorpha* and few *Codium*; depth: 0.5-2.0 m
Station C	29.0-30.0	30.0-31.5	Deep pool with dense *Codium*; depth: 1.0-2.0 m
Station D	29.0-30.0	30.0-31.5	Deep pool with dense *Codium*; depth: 1.0-2.0 m

RESULTS

A total of 960 shrimps were collected. Most of the 268 *P. pugio* came from the shallowest Station A, although some were from Station B, and very few were from Stations C and D. In contrast, most of the 692 *P. vulgaris* were collected from Stations C and D (fig. 2).

Carapace lengths of ovigerous *P. vulgaris* females (N = 270) ranged from 5.60 mm to 9.20 mm with a mean value of 7.10 mm; 65% of the catch was between 6.50 mm and 7.50 mm CL. For ovigerous *P. pugio* females (N = 106), the carapace lengths ranged from 6.70 mm to 10.00 mm with a mean value of 8.70 mm, and approximately 89% of the catch was between 8.00 mm and 9.50 mm (fig. 3). Difference in mean carapace length between the two species was statistically significant ($P<0.001$).

The linear relationships between carapace length and body length of ovigerous females of these two species are:

P. vulgaris $BL = 3.31 + 3.11\ CL\ (r^2 = 0.86)$
P. pugio $BL = 11.46 + 2.42\ CL\ (r^2 = 0.52)$

The slopes of the regressions for the two species were significantly different ($P<0.001$). The significant difference in carapace length, along with the difference in body length, indicates that *P. vulgaris* matures at a smaller size than *P. pugio*.

The regression relationships between carapace length and fecundity of the two species are:

P. vulgaris $F = 3.08\ CL^{2.37}\ (r^2 = 0.44)$
P. pugio $F = 1.92\ CL^{2.62}\ (r^2 = 0.43)$

The slopes of the regressions are significantly different ($P<0.001$). The regression relationships indicate that, for both species, fecundity increases in proportion to body size. Thus, *P. pugio*, with the larger body size is more fecund than *P. vulgaris*.

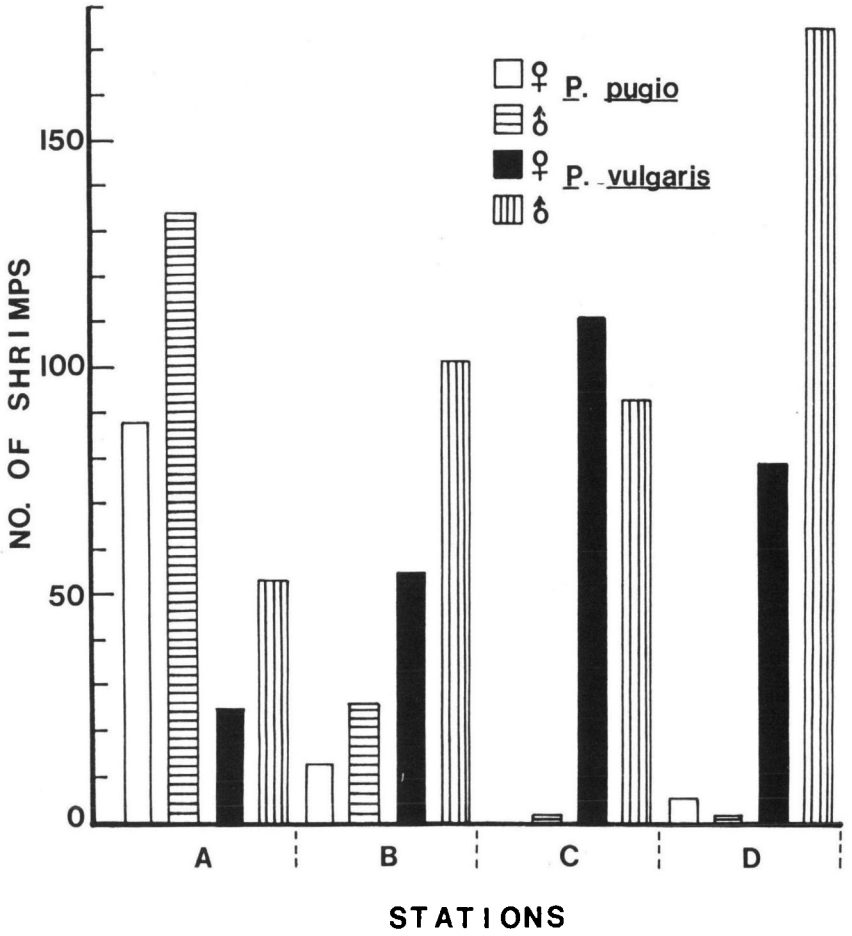

Fig. 2. Number of male and female shrimps of *Palaemonetes pugio* Holthuis and *P. vulgaris* (Say) collected from Stations A-D.

Fecundity (eggs or embryos per female) for *P. pugio* ranged from 351 to 819 with an average of 590, and for *P. vulgaris* it ranged from 171 to 545 with an average of 330. A significant difference in mean fecundity per shrimp between species was observed ($P<0.001$, fig. 4).

A significant difference also exists between the mean fecundity per unit length (mm CL) of the two species ($P<0.001$). For *P. pugio* the range is 39.7 to 86.9 with mean 66.4; for *P. vulgaris* the corresponding value is 23.0 to 74.7 and the mean is 46.5 (fig. 4). *P. pugio* has higher fecundity per shrimp and per unit carapace length than *P. vulgaris*.

The mean dry weight of eggs (or embryos) of *P. pugio* was significantly higher than that of *P. vulgaris* (ranges: 62.9 μg-88.9 μg vs. 43.0 μg-85.0 μg; mean 71.5 μg vs. 56.1 μg) ($P<0.001$, fig. 4).

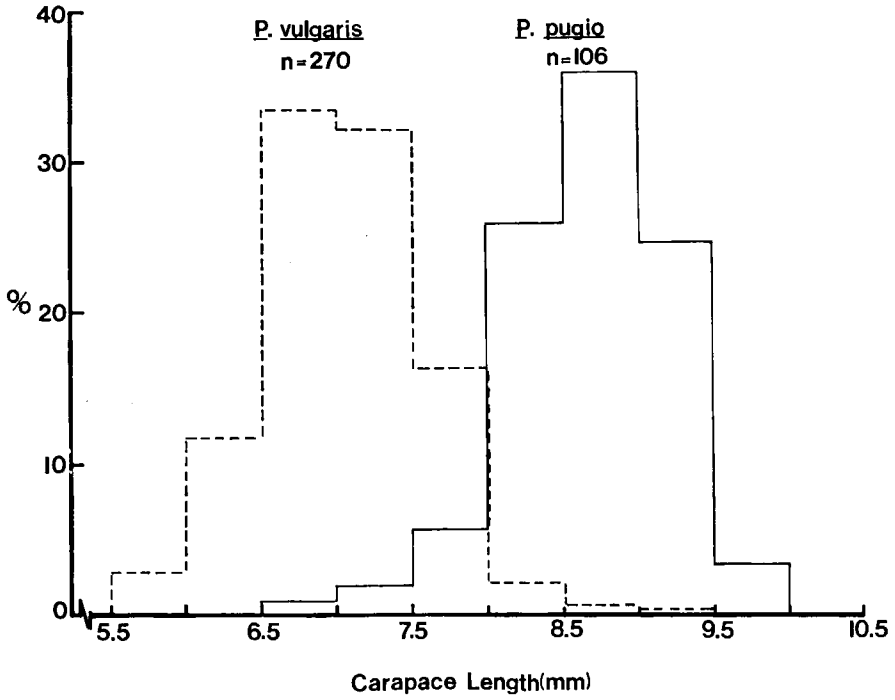

Fig. 3. Percentage frequency distribution of ovigerous shrimps of *Palaemonetes pugio* Holthuis and *P. vulgaris* (Say).

The G.S.I. values, however, the range for *P. pugio* was 15.6-29.2 with a mean of 22.8; and for *P. vulgaris* the range was 11.4-35.0 with a mean of 22.9. Statistical analysis of G.S.I. values failed to show any significant difference between these two species ($P>0.05$, fig. 4). Evidently both species devote approximately equal amount of reproductive effort per clutch.

DISCUSSION

Comparisons of carapace length, body length, fecundity, weight per egg (or embryo) between *P. pugio* and *P. vulgaris* all indicate that there are significant differences in these reproductive characteristics. However, they are all size-dependent, i.e. the larger *P. pugio* certainly has higher values than the smaller *P. vulgaris*. Nevertheless, G.S.I., a size-independent ratio, indicates no significant differences between the reproductive effort per clutch of the two species.

Hoffman (unpubl.) demonstrated that in Delaware, *P. pugio* can produce three or more clutches over the breeding season, but that *P. vulgaris* produces no more than two clutches per season. If the same patterns occur for these species in the Great Sippewissett salt marsh, the annual production of offspring by *P. pugio* would be significantly higher than that of *P. vulgaris*.

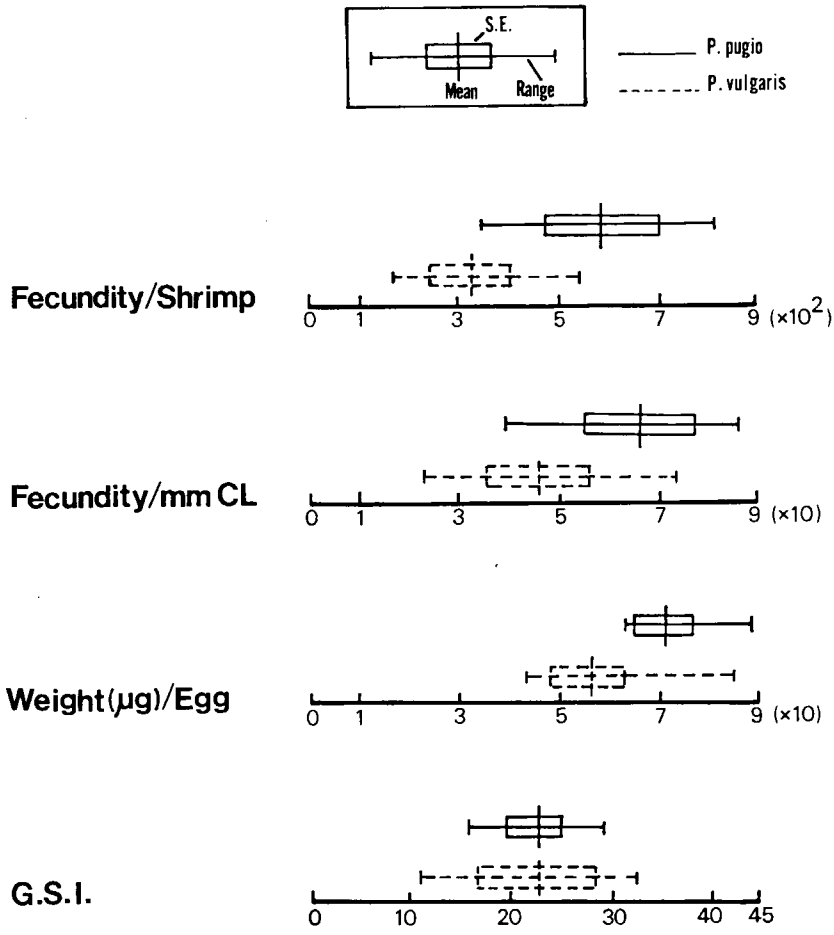

Fig. 4. Comparisons of size-dependent (fecundity/shrimp, fecundity/mm CL, weight/egg) and size-independent (G.S.I.) reproductive characteristics of *Palaemonetes pugio* Holthuis and *P. vulgaris* (Say).

Since both species expend equal reproductive effort in each clutch, why then does *P. pugio* reproduce at a larger size and produce more offspring than *P. vulgaris*? The answer to this question may be that habitat differences between the two species can lead to differences in mortality. The situation of these two species in Great Sippewissett salt marsh is analogous to that described by Thorp (1976): *P. pugio* is displaced from *Codium* shelter to open muddy bottom where it suffers higher predation pressure than *P. vulgaris*. For *P. pugio*, the inevitably higher loss to predators before and after maturity may be compensated for by delaying reproduction until it reaches a larger body size. This strategy offers the size-dependent benefit of higher fecundity. The results indicate that the proposed 'differential predation response' hypothesis is accep-

table. It seems reasonable to assume that reproductive strategies of *P. pugio* and *P. vulgaris* are the responses to differential predation pressure which can maximize an individual's life time reproductive success in its particular environment.

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REFERENCES

BOUSFIELD, E. L., 1956. Studies on the shore Crustacea collected in eastern Nova Scotia and Newfoundland, 1954. Bull. Nat. Mus. Canada, **142**: 127-152.

HOFFMAN, C. P., Jr., unpublished. Growth and reproduction of Palaemonetes pugio and P. vulgaris populations in Canary Creek, Delaware. Master's thesis, 1980, University of Delaware, 125 pp.

HOLTHUIS, L. B., 1952. A general revision of the Palaemonidae (Crustacea Decapoda Natantia) of the Americas. II. The subfamily Palaemoninae. Occ. Paper. Allan Hancock Found, **12**: 1-196.

MEIMER, J. P., unpublished. Morphology and development of Codium fragile in Great South Bay, New York. Master's thesis, 1972, Adelphi University, New York, 48 pp.

THORP, J. H., 1976. Interference competition as a mechanism of coexistence between two sympatric species of the grass shrimp Palaemonetes (Decapoda: Palaemonidae). Journ. exp. mar. Biol. Ecol., **25**: 19-35.

WILLIAMS, A. B., 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida: 1-550. (Smithsonian Inst. Press, Washington, D.C.).

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