

Reproductive Differences among Delmarva Grass Shrimp (*Palaemonetes pugio* and *P. vulgaris*) Populations

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ABSTRACT

Populations of female grass shrimps (*Palaemonetes pugio* and *P. vulgaris*) were sampled from five coastal embayments in Delaware, Maryland, and Virginia (Delmarva) and compared with respect to reproductive and life history attributes. We observed interspecific differences in timing of reproduction, carapace length, ratio of carapace length to total body length, body weight, clutch weight, clutch size, and egg volume. Onset of reproduction in *P. vulgaris* lagged behind *P. pugio*. Although there was no difference in the relationship between clutch size and carapace length for the two species, carapace length/total body length in *P. pugio* was greater than that in *P. vulgaris*. A multivariate analysis of variance indicated significant differences in carapace length, clutch weight, body weight, clutch size, and egg volume attributable to effects of species, population, and interactions between them. At all sites, *P. pugio* produced larger eggs than *P. vulgaris*. Although the two species did not differ in reproductive effort, both species exhibited increases in reproductive effort with latitude. Clutch size also tended to increase with latitude for both species. In populations where both species were abundant, adult females of *P. pugio* were longer and heavier and produced heavier egg masses comprised of fewer, larger eggs.

INTRODUCTION

In a classic paper, Hutchinson (1961) raised the issue of how so many similar species are able to coexist in the plankton given the prediction, from the principle of competitive exclusion (Gause, 1934; Hardin, 1960), that one species should outcompete the others. Coexistence of similar species is exemplified by the "grass shrimps" *Palaemonetes pugio* Holthuis and *Palaemonetes vulgaris* (Say) that abound in marshes and bays of the Atlantic and Gulf coasts of North America. These two closely related species often co-occur in estuarine sites (Williams, 1984). Although both species exhibit similar distribution patterns across their geographic ranges, they exhibit differences in within-habitat usage. In previous studies, it has been shown that habitat partitioning in these species is a consequence of interspecific differences in physiological tolerances toward salinity (Thorpe and Hoss, 1975; Knowlton and Kirby, 1984;

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Knowlton and Schoen, 1984; Khan et al., 1995, 1997) and dissolved oxygen (Welsh, 1975), substrate and cover preferences (Arguin et al., 1989; Knowlton et al., 1994; Khan et al., 1995, 1997), and interference competition (Thorp, 1976). In the present study, we examine whether differences in reproductive strategies could also promote resource partitioning between *P. pugio* and *P. vulgaris* and how these differences are maintained across a range of environmental conditions.

There is some evidence to suggest that reproductive strategies differ between the two species. Chambers (1982) and Yan (1987) found that Massachusetts populations of *P. pugio* exhibit greater mean clutch size than *P. vulgaris* with the same reproductive effort (ratio of gonadal weight to body weight). Although seasonal breeding periods of *P. pugio* and *P. vulgaris* are thought to be similar (Knowlton, 1970), Hoffman (1980) observed that Delaware populations of *P. pugio* produced three or more clutches while *P. vulgaris* produced no more than two clutches within a single season.

Within a species, reproductive characteristics might be expected to vary according to season and geographic location due to differences in temperature, photoperiod, and salinity. Latitudinal clines in egg number have been observed in birds, fishes, and mammals such that clutch size increases with latitude (reviewed by Fleming and Gross, 1990). Such variation in clutch size may reflect differences in the growing season. Salinity may also influence clutch size in estuarine organisms. For example, Alon and Stancyk (1982) found that *P. pugio* fecundity increased with prolonged exposure to lower salinities.

The purposes of this study were to explore the extent to which *P. pugio* and differ reproductively and to examine these differences across a range of environmental conditions. Accordingly, we compared reproductive attributes of *P. pugio* and *P. vulgaris* from five marine and estuarine sites in Chesapeake and "outer" (Atlantic) bays of Virginia, Maryland, and Delaware, spanning a substantial salinity gradient and a wide range of latitude. We examined the effects of species and population level variation on reproductive characteristics. To determine broader geographical patterns in reproductive strategies, we compared results of this study of Delmarva populations with studies from populations in other regions.

METHODS

Palaemonetes pugio and *P. vulgaris* populations were sampled during the breeding period (May, July, and September 1987) at five locations (Figure 1; see Knowlton et al., 1994 for details). Collecting locations were selected so that two pairs of Chesapeake and Atlantic sites occurred at similar latitudes and spanned a broad range of salinities. Values at Chesapeake sites ranged from about 12 ppt at Station 5 to about 25 ppt at Station 3 while those at both Atlantic sites (Stations 1 and 2) were about the same, averaging about 30 ppt (Figure 1, Appendix A). Collections at each site were timed to occur at roughly the same time of day and stage of tide (about two hours prior to low tide, Appendix A). Samples, obtained using long-handled D-frame dip nets, were preserved on site in 95% ethanol. At time of collection, salinity was measured with a hand-held refractometer, air and water temperatures with a pocket thermometer. Dissolved oxygen (mg/L) was determined using a modified Winkler method (Hach Chemical Co., 1977).

In the laboratory, we used a dissecting microscope to separate species per sample according to criteria in Holthuis (1952). Sex was determined by noting the form of the

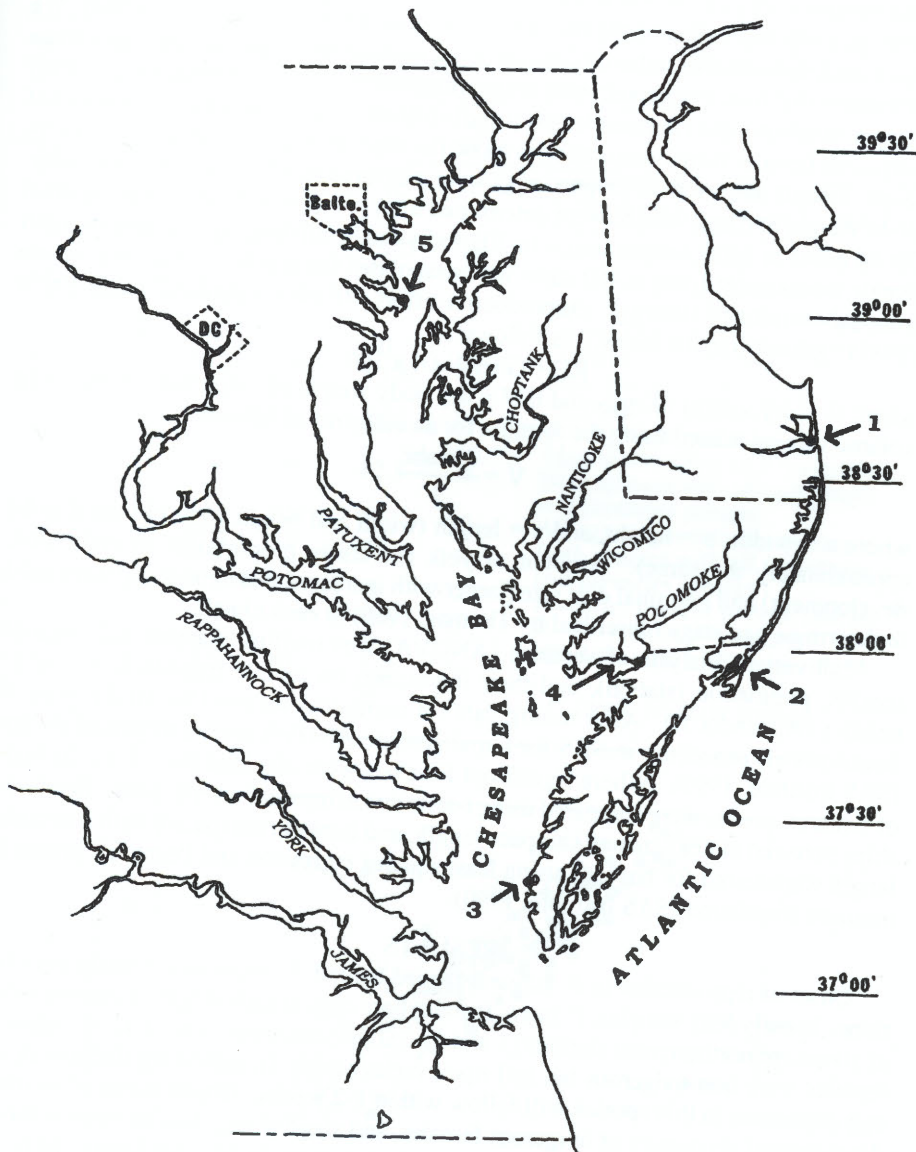


FIGURE 1. Locations of collection sites: 1 = Indian River Bay on Burton Island, DE; 2 = Chincoteague Bay, Chincoteague, VA; 3 = Kings Creek, Cape Charles, VA; 4 = Robin Hood Bay (of Pocomoke Sound), near Saxis, VA; and 5 = Mezik Pond, Sandy Point State Park, MD.

first pleopod endopod (shorter in female) or by the presence (male) or absence (female) of an *appendix masculina* on the endopod of the second pleopod (Williams, 1984). We also noted reproductive status of females (e. g., ovarian development) and percentage of females that were ovigerous. Body length (measured from tip of rostrum to posterior margin of telson) and carapace length (tip of rostrum to posterior end of carapace) of ovigerous females were measured with an ocular micrometer on the dissecting microscope. Length and width of stripped eggs were measured using the ocular micrometer. Body weight and egg weight were determined after shrimps and eggs were air dried for 48 hours at room temperature. In 203 individuals, all dried eggs found on each female were counted, but in 480 cases we extrapolated the number of eggs per female from subsamples of 100 eggs. Reproductive effort (RE) was calculated using Yan's (1987) "gonadosomatic index," as follows:

$$RE = G/(BW-G) \times 100$$

where G = dry weight of eggs and BW = dry body weight of ovigerous female. Egg volume was calculated using the formula for an ellipsoid as follows:

$$V = \frac{4 \pi abc}{3}$$

where a = width, b = height, and c = length (width and height were observed to be approximately the same). Amount of yolk (inversely proportional to embryonic development) and germinal disc size (larger with increased differentiation) were used to determine egg stage (described by Thomas, 1969) in each clutch.

Multivariate analysis of variance (ANOVA) was used to examine influence of species, population (station), and their interaction on female reproductive characteristics (Appendix B). After testing data for normality, we used the GLM (general linear model) procedure in SAS for a multivariate ANOVA with unbalanced design (SAS Institute, 1990). Where significant F-values were obtained from Type III Sum of Squares, means were compared using t-tests due to unequal sample sizes. Relationships between clutch size and carapace length, and between carapace length and body length were tested for linearity using least squares regression and Pearson's product-moment correlation (SAS Institute, 1990).

RESULTS

Onset of reproduction in *P. vulgaris* lagged behind *P. pugio* in our study populations. In early May samples, *P. pugio* females bore eggs in early stages of development at all except northernmost stations (1 and 5). At the same time, almost all *P. vulgaris* females were non-ovigerous but had ripe ovaries (Table 1), indicating that a peak of egg deposition in this species will follow within 1-2 weeks. Observations of ovarian development, frequency of ovigerous females, and stage of egg development in these populations indicate that the reproductive season starts in late April-early May in *P. pugio*, mid-May in *P. vulgaris*, and continuing into late September in both species (Table 1).

The two species differed in body form but not in the relationship between clutch size and carapace length. Slopes of the regression lines depicting the relationship between carapace length and body length differed significantly, with *P. pugio* exhibiting a steeper slope than *P. vulgaris* ($P < 0.05$, Fig. 2). Although clutch size values tended to be lower in *P. pugio* than in *P. vulgaris*, the slopes of the regression lines for clutch size and carapace length did not differ significantly (Fig. 3).

TABLE 1. Timing of reproduction as indicated by percentage of ovigerous females (% OF) in samples and stage of egg development, as measured by % of the area occupied by yolk. Description of ovarian development is also provided as an indication of reproductive state in pre-reproductive females because ovaries ripen before eggs are deposited and brooded on the pleopods.

Date	Station	<i>P. pugio</i>		<i>P. vulgaris</i>		Comments
		% OF	Egg stage	% OF	Egg stage	
May 6	1	0	-	0	-	Ovaries ripe in both species
May 6	2	27.8	83	0	-	Eggs in early stages in <i>P. pugio</i> Ovaries ripe in <i>P. vulgaris</i>
May 7	3	50	62	0.5	80	Mostly early stages in <i>P. pugio</i> Ovaries ripe in <i>P. vulgaris</i>
May 7	4	33.3	95	0	-	Eggs in early stages in <i>P. pugio</i> Ovaries ripe in <i>P. vulgaris</i>
May 7	5	0	-	0	-	Ovaries ripe in <i>P. pugio</i>
July 2	1	81.3	38	81.8	42	Both species with eggs in all stages of development
July 2	2	50	75	85.2	57	100-50% yolk in <i>P. pugio</i> Eggs in all stages in <i>P. vulgaris</i>
July 3	3	29.3	48	82.3	45	Both species with all egg stages and juveniles present
July 3	4	84.9	18	75	40	All egg stages in both species
July 3	5	81.5	16	0	-	Both species with all egg stages and juveniles present
Sept. 12	1	0	-	0	-	Juveniles present in both species
Sept. 12	2	1.1	0	13.6	29	80-0% yolk in <i>P. vulgaris</i>
Sept. 13	3	7.4	69	0	-	100-40% yolk in <i>P. pugio</i>
Sept. 13	4	5.6	30	1.2	5	
Sept. 13	5	0	-	0	-	1 <i>P. pugio</i> juvenile present

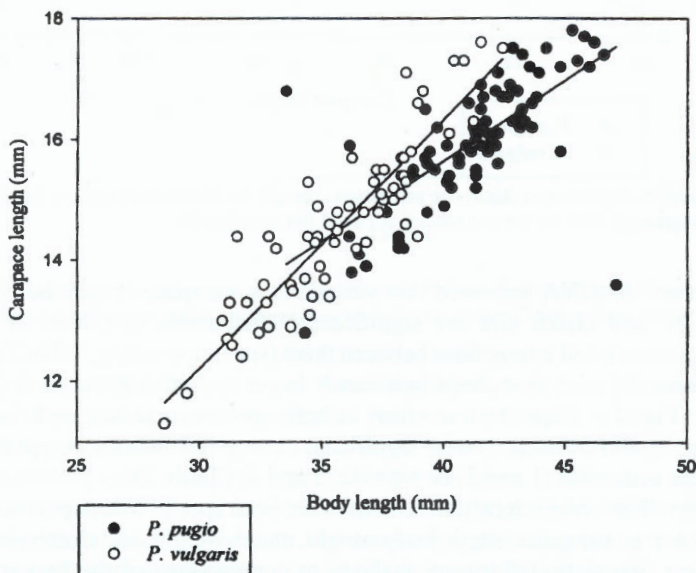


FIGURE 2. Morphological differentiation between female *Palaemonetes pugio* and *P. vulgaris*. Linear regression lines are included in graph; slopes of the regression lines for the two species differed significantly ($P < 0.05$).

TABLE 2. Results of a multivariate analysis of variance for effects of species, station, and their interaction on grass shrimp reproductive attributes. F-values calculated using Type III Sum of Squares are listed with levels of significance indicated in parentheses. For all measurements, Station, Species, and Station x Species had 1, 4, and 3 Degrees of Freedom, respectively. Complete ANOVA tables are provided in Appendix B.

Measurement	Species	Station	Species x Station
Carapace length	13.94 (0.0003)	18.56 (<0.0001)	12.60 (<0.0001)
Body weight	19.00 (<0.0001)	26.40 (<0.0001)	9.95 (<0.0001)
Clutch size	16.68 (<0.0001)	41.04 (<0.0001)	3.99 (0.0092)
Clutch weight	8.39 (0.0044)	60.91 (<0.0001)	4.32 (0.0060)
Egg volume	39.22 (<0.0001)	0.84 (0.4998)	1.25 (0.2944)
Reproductive effort	0.47 (0.4940)	17.61 (<0.0001)	0.55 (0.6480)

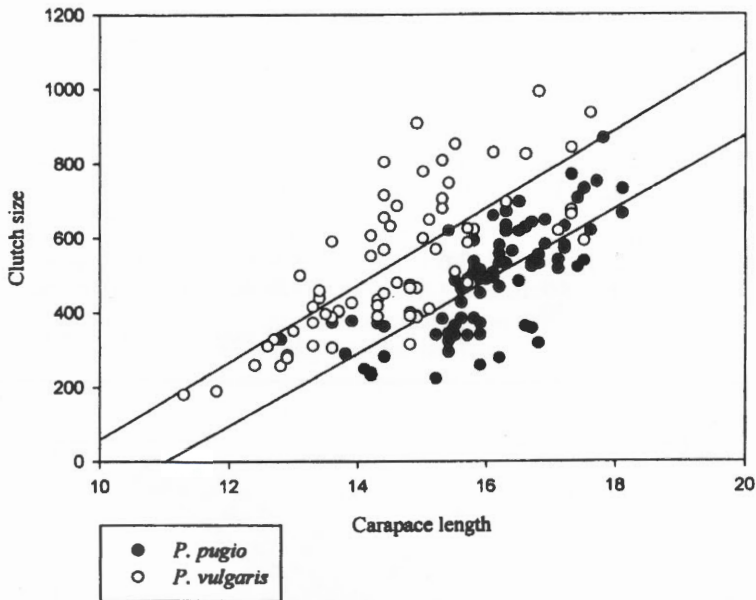


FIGURE 3. Relationship between clutch size and carapace length for *Palaemonetes pugio* and *P. vulgaris*. Slopes of the regression lines for the two species did not differ significantly.

Multivariate ANOVA indicated that variations in carapace length, body weight, clutch weight, and clutch size are significantly attributable to effects of species, population (station), and interactions between them (species x station; Table 2). Across all populations, *P. pugio* produced significantly larger eggs than *P. vulgaris* ($t = 9.47$, $P < 0.0001$, Fig. 4). Reproductive effort in both species increased with increasing latitude (Fig. 5), and differences were significant between all stations except those that were adjacent oceanside (1 and 2) or bayside (3 and 4) (Table 3).

Significant first-order interactions occurred between species and population for the following features: carapace length, body weight, clutch weight, and clutch size (Table 2). Therefore, we restricted means analyses to comparisons of the two species to populations where we obtained sufficient sample sizes of ovigerous females of both species (Station 1: *P. pugio*, $n = 21$, *P. vulgaris*, $n = 23$; Station 3: *P. pugio*, $n = 16$,

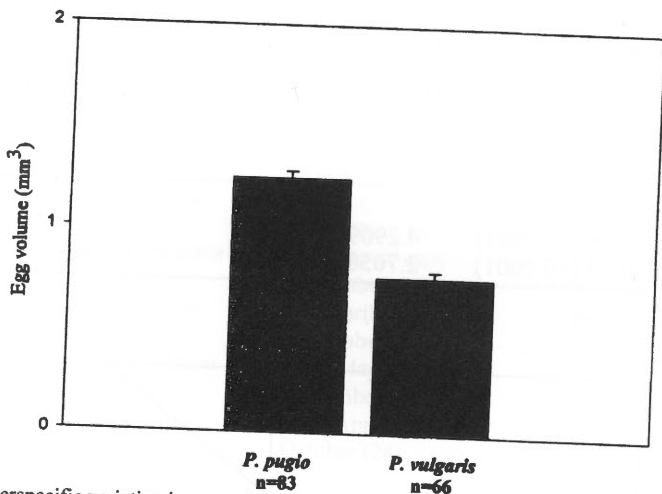


FIGURE 4. Interspecific variation in egg volume. Volume of *Palaemonetes pugio* eggs was 162% greater (mean \pm standard error; $1.2461 \pm 0.0369 \text{ mm}^3$) than that of *P. vulgaris* eggs ($0.7678 \pm 0.0323 \text{ mm}^3$).

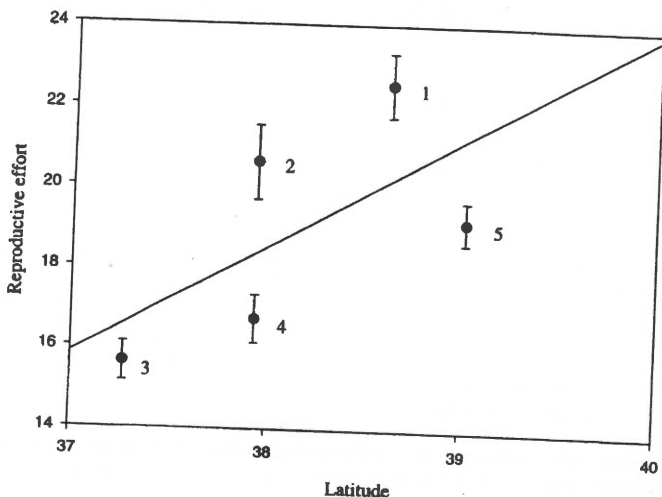


FIGURE 5. Latitudinal variation in reproductive effort for *Palaemonetes pugio* and *P. vulgaris* combined, with regression line fitted to means (adjacent number indicates station); each vertical bar indicates standard error.

P. vulgaris, $n = 20$). Station 2 was dominated by *P. vulgaris*, Stations 4 and 5 by *P. pugio*; these differences in distribution patterns are thought to arise from different salinity tolerances exhibited by the two species (Knowlton et al., 1994). *Palaemonetes pugio* exhibited mean carapace lengths 1.12-1.16 times greater than in *P. vulgaris* (Station 1: $t = 6.0937$, $P < 0.0001$; Station 3: $t = 6.7855$, $P < 0.0001$). We observed similar trends in dry body weight measurements, *P. pugio* being 1.43-1.58 times heavier than *P. vulgaris* (Station 1: $t = 7.6324$, $P < 0.0001$; Station 3: $t = 5.9727$, $P < 0.0001$). Mean clutch weights were 1.31-1.40 times greater in *P. pugio* than in *P. vulgaris* (Station 1: $t = 5.5982$, $P < 0.0001$; Station 3: $t = 3.0025$, $P < 0.004$). At

TABLE 3. Results of t-tests comparing reproductive effort among populations occurring at Stations 1-4, expressed as t values, with levels of significance indicated in parentheses. Station 5 was not included in the means analyses because only one species (*P. pugio*) was found there.

	Station		
	1	2	3
2	1.5763 (0.1172)		
3	7.8075 (<0.0001)	4.2909 (<0.0001)	
4	4.4620 (<0.0001)	2.7050 (<0.0100)	0.5952 (0.5526)

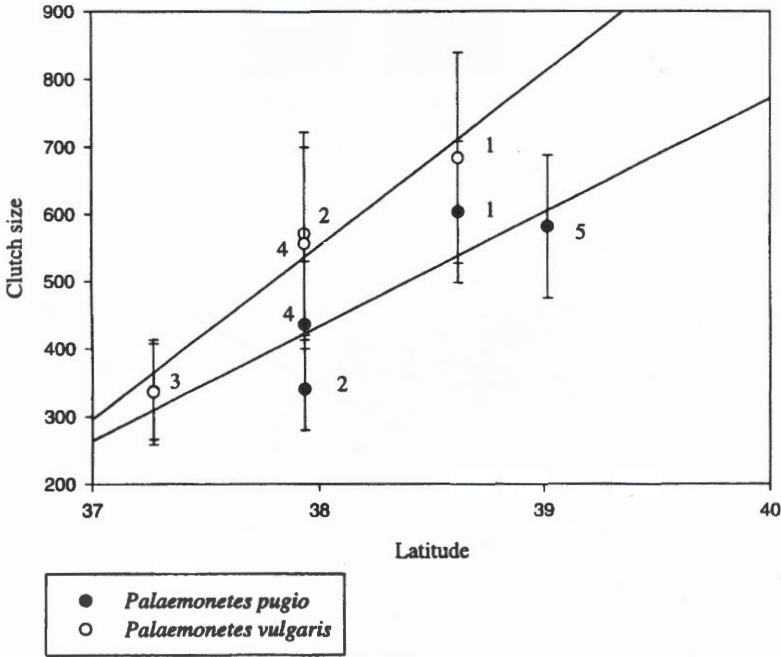


FIGURE 6. Latitudinal variation in clutch size for *Palaemonetes pugio* and *P. vulgaris*, with regression line fitted to means (adjacent number indicates station); each vertical bar indicates standard error.

Station 1, *P. vulgaris* mean clutch size was 1.13 times larger than that of *P. pugio* ($t = 2.3165, P < 0.025$). No significant difference in clutch size was detected between the two species at Station 3 ($t = 0.0325, P = 0.9741$). Both species exhibited a trend of increasing clutch size with latitude (Fig. 6).

DISCUSSION

Populations of *P. pugio* and *P. vulgaris* occurring in Delmarva bays differed significantly in a number of reproductive attributes that may correspond to differences in reproductive strategies. Between populations where both species were abundant, *P. pugio* was determined to be larger and heavier, producing clutches that were heavier but sometimes smaller in egg number, compared with *P. vulgaris*. The breeding season in *P. pugio* lasted approximately two weeks longer than in *P. vulgaris* in the populations

TABLE 4. Length of breeding seasons of *Palaemonetes pugio* and *P. vulgaris* at different coastal locations.

Location	Species	Breeding season (weeks)	Authority
Woods Hole, MA	both	June to late August (10)	Faxon, 1879; Jenner, 1955
Narragansett Bay, RI	<i>P. pugio</i>	May to late July (10)	Welsh, 1975
Canary Creek, DE	<i>P. pugio</i>	mid-May to early September (16)	Hoffman, 1980
	<i>P. vulgaris</i>	late-May to early September (15)	
Cape Charles, VA	<i>P. pugio</i>	late April to late September (22)	this study
	<i>P. vulgaris</i>	early May to late September (20)	
Bogue Sound, NC	both	early April to mid- October (28)	Broad, 1957; Knowlton and Williams, 1970
North Inlet, SC	<i>P. pugio</i>	late March to mid- October (29)	Alon and Stancyk, 1982
Galveston Bay, TX	<i>P. pugio</i>	March to October (31)	Wood, 1967

we studied (Table 4). Differences in onset of reproduction between these species may allow *P. pugio* to produce more broods per season than *P. vulgaris*. In Delaware, Hoffman (1980) observed that *P. pugio* began spawning in mid-May and produced three or more broods per season while *P. vulgaris* began spawning in late May and produced only two broods. Our study indicates that differences in breeding season between these species may occur across populations in the Delmarva region. Such differences may also serve to reduce competition among planktonic zoea larvae, which are morphologically very similar (Broad, 1957).

In all populations, eggs of *P. pugio* were larger than those of *P. vulgaris*. Increasing offspring size is a reproductive strategy that may increase offspring fitness. In plants, large seeds can be expected to have selective advantage, and increases in egg size in animals are positively correlated with hatching success, survival, tolerance of starvation, size at hatching, and growth (Roff, 1992). Within the Palaemoninae, there is evidence that egg size increases starvation tolerance. For example, Mashiko (1985) determined that larvae (of the freshwater shrimp, *Palaemon paucidens*) hatched from larger eggs were significantly more tolerant of starvation than those hatched from smaller eggs.

Latitudinal trends in clutch size and reproductive effort were apparent in the mid-Atlantic populations we studied. Both species exhibited increases in clutch size with latitude (Fig. 6). Fleming and Gross (1990) found that latitudinal patterns in clutch size in Pacific salmon arose from a negative relationship between latitude and egg size. We did not observe any latitudinal trend in egg size in our study populations. Instead, we found that reproductive effort increased with latitude for both *P. pugio* and *P. vulgaris* (Fig. 5).

Reproductive characteristics may vary with latitude in response to differences in the length of the breeding season. Breeding in *Palaemonetes* spp. is dependent on photoperiod and temperature (Little, 1968). A pattern of shorter breeding season with

TABLE 5. Comparison of reproductive characteristics between Delmarva and Massachusetts populations of *Palaemonetes pugio* and *P. vulgaris*. Mean \pm standard deviation for Delmarva populations sampled July 1987 (present study); means for Massachusetts populations sampled July 1984 (Yan 1987).

Characteristic	<i>Palaemonetes pugio</i>		<i>Palaemonetes vulgaris</i>	
	Delmarva	Massachusetts	Delmarva	Massachusetts
Carapace length (mm)	16.0 \pm 1.1	8.7	14.6 \pm 1.4	7.1
Clutch size	487 \pm 143	590	542 \pm 194	330
Clutch weight (μ g)	53.3 \pm 7.9	62.9	38.6 \pm 4.2	56.1
Reproductive effort (%)	18.4 \pm 4.3	22.8	21 \pm 5.3	22.9

increasing latitude in *P. pugio* and *P. vulgaris* is clear when our results are combined with data in the literature (Table 4). The observed increases in reproductive effort with latitude in *P. pugio* and *P. vulgaris* may be a consequence of more northern populations compensating for shorter breeding seasons. Other abiotic factors may also influence expression of life history traits. Alon and Stancyk (1982) attributed differences in life history traits of two different South Carolina populations of *P. pugio* to effects of salinity and other environmental variables. Although we did not sample enough populations to differentiate between effects of salinity and latitude, we found that outer bay (Atlantic) populations exhibited greater reproductive effort at similar latitudes than inner bay (Chesapeake) populations (Fig. 5). Both species exhibited a significantly greater reproductive effort at Station 2 (Atlantic) than Station 4 (Chesapeake) despite close latitudinal proximity (Table 3).

In Massachusetts populations of *P. pugio* and *P. vulgaris*, Yan (1987) found that the former species had a longer carapace length and produced a heavier clutch with no greater reproductive effort (Table 5). In contrast to our results on Delmarva populations, Yan (1987) determined that the Massachusetts population of *P. pugio* produced larger clutches than *P. vulgaris*. This difference apparently arises from higher fecundity of *P. pugio* and lower fecundity of *P. vulgaris* in the Massachusetts population than in Delmarva populations. For both species, reproductive effort was slightly higher and carapace length was shorter in the Massachusetts population (Table 5). Although Yan (1987) did not measure egg size directly, the sample population of *P. vulgaris* from Massachusetts produced a heavier clutch comprised of fewer eggs, which suggests that the eggs were heavier and may be larger than in Delmarva populations. No such trend in *P. pugio* egg size was seen between the two populations.

Yan (1987) concluded that *P. pugio* produces more offspring than *P. vulgaris* in order to compensate for greater exposure to predation pressure. Thorp (1976) suggested that there might be differences in relative predation pressure between *P. pugio* and *P. vulgaris* when he determined that *P. vulgaris* displaces *P. pugio* from preferred and more protected strata (e.g., shell) to mud. Increased predation pressure is expected to select for earlier onset of reproductive maturity (Gadgil and Bossert, 1970) if there are no indirect effects of predation on prey food supply (Abrams and Rowe, 1996). If there are such indirect effects, increased predation pressure will have the opposite effect and predation can select for delayed maturity and increased body size (Kawecki, 1993; Abrams and Rowe, 1996). However, investigation of possible predator or prey effects on life history traits requires an experimental approach.

In our study, we observed substantial differences in life history traits within and between two closely related species, *P. pugio* and *P. vulgaris*. Both species exhibited geographical variations that may reflect plasticity in life history traits or adaptation to local conditions. Future experiments, in which animals from widely separated sites are maintained under controlled environmental conditions, will elucidate whether these differences reflect plasticity or fixed differences among populations. We also observed interspecific differences in life history traits, summarized as follows: adults of *P. pugio* began reproducing earlier in the season and were longer and heavier, producing an egg mass with fewer, larger eggs than those of *P. vulgaris*. Physiological and behavioral differences have been regarded as important factors promoting resource partitioning between two closely related species that are frequently sympatric. Our study provides evidence that interspecific variation in timing of reproduction and other elements of reproductive strategy are also important.

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APPENDIX A. Abiotic parameters measured at collecting stations. Each station included two study sites: A = a marina consisting of wooden pilings, buttresses, docks, etc. B = nearby sand, mud, or oyster shell flats typically bordered by marsh vegetation (*Spartina alterniflora* at Stations 1-4, *Phragmites australis* at Station 5).

Month	Station	Time	Salinity (ppt)	Air temp. (°C)	Water temp. (°C)	Dissolved O ₂ (mg/l)
May	1A	1550	24	21	17	9.9
	1B	1610	27	20	13	9.5
	2A	1830	28	19	14	8.8
	2B	1855	22	18	15	8.7
	3A	0850	20.5	14	16	4.7
	3B	0910	21	16	16	9.0
	4A	1115	15.5	19.5	16	6.6
	4B	1130	16	19	16	7.8
	5A	1530	9	20	18	9.5
	5B	1555	9	22.5	19	10.7
July	1A	1405	33.5	29	23.5	7.2
	1B	1450	33	32	22	7.2
	2A	1720	33.5	26	23.5	10.1
	2B	1745	33	24	25	11.4
	3A	0620	25.5	24.5	26	4.0
	3B	0645	24.5	24	25.5	3.3
	4A	1030	17	29.5	26	4.7
	4B	1105	16.5	28	26	7.3
	5A	1520	11	31	29	7.3
	5B	1555	11.5	33	29.5	7.4
September	1A	1350	32	26	25	6.7
	1B	1435	32	24	24	7.0
	2A	1700	33	25	24.5	6.8
	2B	1740	32.5	24	24	5.1
	3A	0605	27.5	22	24	4.3
	3B	0625	27.5	22	24	4.5
	4A	1030	17	22	23	2.5
	4B	1050	17.5	21.5	23	5.7
	5A	1515	12.5	24	25	8.5
	5B	1535	12	23.5	23.5	5.5

APPENDIX B. More detailed tabulation of results (summarized in Table 2) of multivariate ANOVA pertaining to effects of station, species (*Palaemonetes pugio* and *P. vulgaris*), and their interaction (Station*Species) on reproductive attributes.

Carapace length

Source	DF	Type III SS	Mean Square	F Value	P > F
Station	4	65.82136235	16.45534059	18.56	<0.0001
Species	1	12.35722881	12.35722881	13.94	0.0003
Station*Species	3	33.50236478	11.16745493	12.60	<0.0001

Body weight

Source	DF	Type III SS	Mean Square	F Value	P > F
Station	4	0.05466830	0.01366708	26.40	<0.0001
Species	1	0.00983553	0.00983553	19.00	<0.0001
Station*Species	3	0.01545745	0.00515248	9.95	<0.0001

Clutch size

Source	DF	Type III SS	Mean Square	F Value	P > F
Station	4	2131635.441	532908.860	41.04	<0.0001
Species	1	216630.862	216630.862	16.68	<0.0001
Station*Species	3	155335.574	51778.525	3.99	0.0092

Clutch weight

Source	DF	Type III SS	Mean Square	F Value	P > F
Station	4	0.00635852	0.00158963	60.91	<0.0001
Species	1	0.00021906	0.00021906	8.39	0.0044
Station*Species	3	0.00033843	0.00011281	4.32	0.0060

Egg volume

Source	DF	Type III SS	Mean Square	F Value	P > F
Station	4	0.31408827	0.07852207	0.84	0.4998
Species	1	3.65023949	3.65023949	39.22	<0.0001
Station*Species	3	0.34877494	0.11625831	1.25	0.2944

Reproductive effort

Source	DF	Type III SS	Mean Square	F Value	P > F
Station	4	1110.816493	277.704123	17.61	<0.0001
Species	1	7.417646	7.417646	0.47	0.4940
Station*Species	3	26.095286	8.698429	0.55	0.6480