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LIFE-HISTORY VARIATION UNDER VARYING DEGREES OF INTRASPECIFIC COMPETITION IN THE TADPOLE SHRIMP *TRIOPS LONGICAUDATUS* (LECONTE)

Stephen C. Weeks

ABSTRACT

Four lines (3 selfing and 1 sexual) of the tadpole shrimp *Triops longicaudatus* (LeConte), reared in the laboratory, exhibited significant reductions in growth and egg production with increasing density (5, 10, and 16 shrimp per 40-l aquarium). Growth and fecundity were similar within the 2 morphologically distinguishable forms (long and short), whereas the long-form shrimp grew larger but produced fewer eggs than the short-form shrimp. Growth and age at death did not differ between the 2 reproductive classes. The sexual shrimp showed lower average egg production than the 3 selfing lines. Life-history trade-offs were not apparent between egg production, growth, and survivorship within any of the 4 lines examined. However, a nonsignificant negative correlation was found between mean egg production and growth among the 4 shrimp lines. These ecological results, combined with electrophoretic and morphological measures, reveal a consistent pattern of differences between the long and short forms of *T. longicaudatus.*

The study of crustacean life-history variation has primarily centered on higher crustaceans (Sutcliffe, 1953; Hamner *et al.*, 1969; Phillips *et al.*, 1977; Caldwell and Dingle, 1978; Kanciruk, 1980), with some notable exceptions (Hebert, 1974; Belk, 1977; Hebert and Crease, 1980; Browne, 1982; Lynch, 1980, 1985). Except for cladocerans and brine shrimp, life-history variation in the Class Branchiopoda has been largely overlooked. One such branchiopod is the tadpole shrimp *Triops longicaudatus* (LeConte). Most experimental work on this animal has focused on its effects in rice paddies, where its digging uproots and kills rice seedlings (Takahashi, 1977a, b; Scott and Grigarick, 1978, 1979). Except for these few studies, the ecology of *Triops* is relatively unknown.

Triops longicaudatus inhabits fresh-water ephemeral ponds ranging from 50° north latitude in western North America through Central America and into South America (Longhurst, 1955). Populations of *Triops* exhibit wide variation in sex ratio, usually showing a strong female bias (Linder, 1952). The sexual populations consist of a mixture of facultatively hermaphroditic females and sexual males, and all-female populations are comprised of only the former (Longhurst, 1955; Weeks, unpublished).

Tadpole shrimp are short-lived animals, completing their life cycle in a mere 30–40 days. They produce desiccation-resistant resting eggs which hatch within 24 h after hydration, given the appropriate levels of light, temperature, and oxygen concentration (Takahashi, 1977a; Scott and Grigarick, 1978, 1979). The initial nauplius quickly develops into a juvenile which then settles on the pond floor to take up the omnivorous habits characteristic of adult tadpole shrimp. *Triops* has a rapid growth rate, attaining a size of 15–20 mm total length in as little as 10 days and reproducing as early as nine days of age (Takahashi, 1977a; Weeks, unpublished). Tadpole shrimp produce up to 246 eggs/day which are subsequently buried or stuck to vegetation and pond detritus (Takahashi, 1977a).

In this study, life-history variation was examined in two reproductive and two morphological forms of *Triops longicaudatus* under various levels of intraspecific competition. Growth, survival, and reproduction of three selfing and one sexual line were compared at three densities in the laboratory to determine relative life-history responses to increased density in these four lines.

MATERIALS AND METHODS

The three selfing lines (hereafter referred to as clones 1–3) used in this experiment originated from 3 separate ponds near Portal, Arizona. Desiccated eggs of the sexual line (sexual 1) were purchased from Ward's Biological Supply Company, Rochester, New York, and are known to have been collected from ponds near Hurricane, Utah. Sexual 1 and clone 2 are morphologically distinct from clones 1 and 3. They are distinguished by the greater number of legless tail segments in the "long" form (sexual 1 and clone 2) relative to the "short" form (clones 1 and 3). Short-form shrimp typically have 5 legless segments (range 4–6), while long-form shrimp have an average of 8 legless segments (range 7–9). All lines are electrophoretically distinguishable and are monomorphic (except the sexual line) at 14 allozyme loci examined (Sassaman, unpublished). Electrophoretic differences within the 2 morphological forms are minimal, with only 1 fixed difference between the 2 lines within each form. Between-form difference is substantial with the 2 forms fixed for alternate alleles at 7 out of the 14 loci sampled. The sexual line is distinguished from the clonal lines on the basis of genetic polymorphism at 2 of the 14 loci sampled and by the presence of males in the population.

Nauplii of *Triops* were reared in 40-l aquaria from field-collected soil. Shrimp were grown in these rearing tanks until they attained lengths of approximately 6–7-mm carapace length (reached in 7–11 days), upon which they were randomly assigned to the appropriate experimental tanks. Each experimental tank was filled with 27 l of deionized water to which 530 g (390 ml) of finely sieved soil (<250-μm diameter) was added. The tanks were under continuous light and aeration and were allowed to dry out naturally to simulate natural desert conditions. To prevent premature death due to desiccation, it was necessary to supplement 2 l of water to all tanks with shrimp surviving longer than 35–40 days. Temperature was allowed to fluctuate with that of the laboratory (an average of 25°C).

The experiment was run as a completely randomized 4 × 3 factorial design consisting of 4 line treatments [a, clone 1; b, clone 2; c, clone 3; and d, sexual 1] crossed with 3 density treatments [a, low (5 shrimp fed 0.20 g/day/shrimp); b, intermediate (10 shrimp fed 0.10 g/day/shrimp); and c, high (16 shrimp fed 0.0625 g/day/shrimp)]. The number of replicates per line × density combination ranged from 3–8.

A commercially prepared goldfish food (Item 136, Wardley's Product Company, Inc., Secaucus, New Jersey) was supplemented daily to all tanks. The initial food per tank was held constant at 1.0 g/day and was correspondingly reduced with mortality within each treatment (e.g., when 1 shrimp of a treatment of 5 died, the overall quantity of supplemented food per tank was decreased by 0.20 g/day). The above feeding regime was used to keep the food per shrimp constant within each treatment, so that a reduction in number of shrimp did not lead to increased food per individual for the surviving shrimp. The space per individual was under no experimental control except for initial conditions, and therefore increased with increasing mortality.

Growth and survivorship were measured daily by siphoning most of the water from each tank to remove molts and dead shrimp. The original water was readded after molts were removed. Size was determined by measuring carapace length of the daily molts with a dissecting microscope equipped with an ocular micrometer. Shrimp molted approximately every 2 days. Experiments continued and data were collected until the last shrimp in each tank died. At the end of each trial, egg production was assessed by sieving the eggs from the sediments and making a total count of intact and damaged eggs. Three measures of average productivity were calculated: (a) growth, measured as average increase in biomass per tank; (b) egg production, measured as total eggs produced per experimental tank; and (c) survivorship, measured as the average age at death in each tank.

All data were analyzed using the General Linear Models and Correlation Procedures of the SAS statistical package (SAS Institute Inc., 1985). A posteriori pairwise comparisons were made with the Student-Newman-Keuls multiple range test in all three univariate comparisons. All data were log-transformed and were subsequently found to be univariate normal with homoscedastic variances in all comparisons. Differences between lines were assessed with both univariate and multivariate analysis of variance tests using increase in biomass, egg production, and age at death averaged over all individuals within treatments as dependent variables. Multivariate F-ratios were calculated using Wilks' Lambda statistic. Correlation matrices were computed for all pairwise comparisons among the 3 dependent variables for each line: (1) within each density, (2) averaged across density, and (3) overall averages among lines.

RESULTS

Daily growth and survivorship are shown in Fig. 1. In all four lines, mortality appeared constant over the experimental period (Type II survivorship). Growth was indeterminate and approximately linear in all lines at all densities. The incomplete sampling for growth rate caused by nonsynchronous molting produced the apparent decreases in growth.

Table 1 gives the means and variances for the three average fitness measures in each experimental treatment. The four shrimp lines grew differently at these densities ($F_{3,53} = 3.10$, $P < 0.05$; Table 1A). The two morphological forms showed similar growth patterns with the long forms growing larger than the short forms. Density had a marginally significant negative effect on growth ($F_{2,53} = 3.12$, $P = 0.052$). All four shrimp lines were equally affected by increasing density ($F_{6,53} = 0.70$, $P > 0.65$).

Individual egg production was most severely affected by increased density, showing over an order of magnitude difference between low and high density ($F_{2,53} = 22.01$, $P < 0.0001$; Table 1B). Shrimp line was also significant ($F_{3,53} = 13.32$; $P < 0.0001$) with the two short-form shrimp producing the most eggs, clone 2 an intermediate quantity, and the sexual line producing the fewest eggs. As with growth, there was no significant line × density interaction in egg production ($F_{6,53} = 0.62$, $P > 0.70$).

Average age at death exhibited no trends

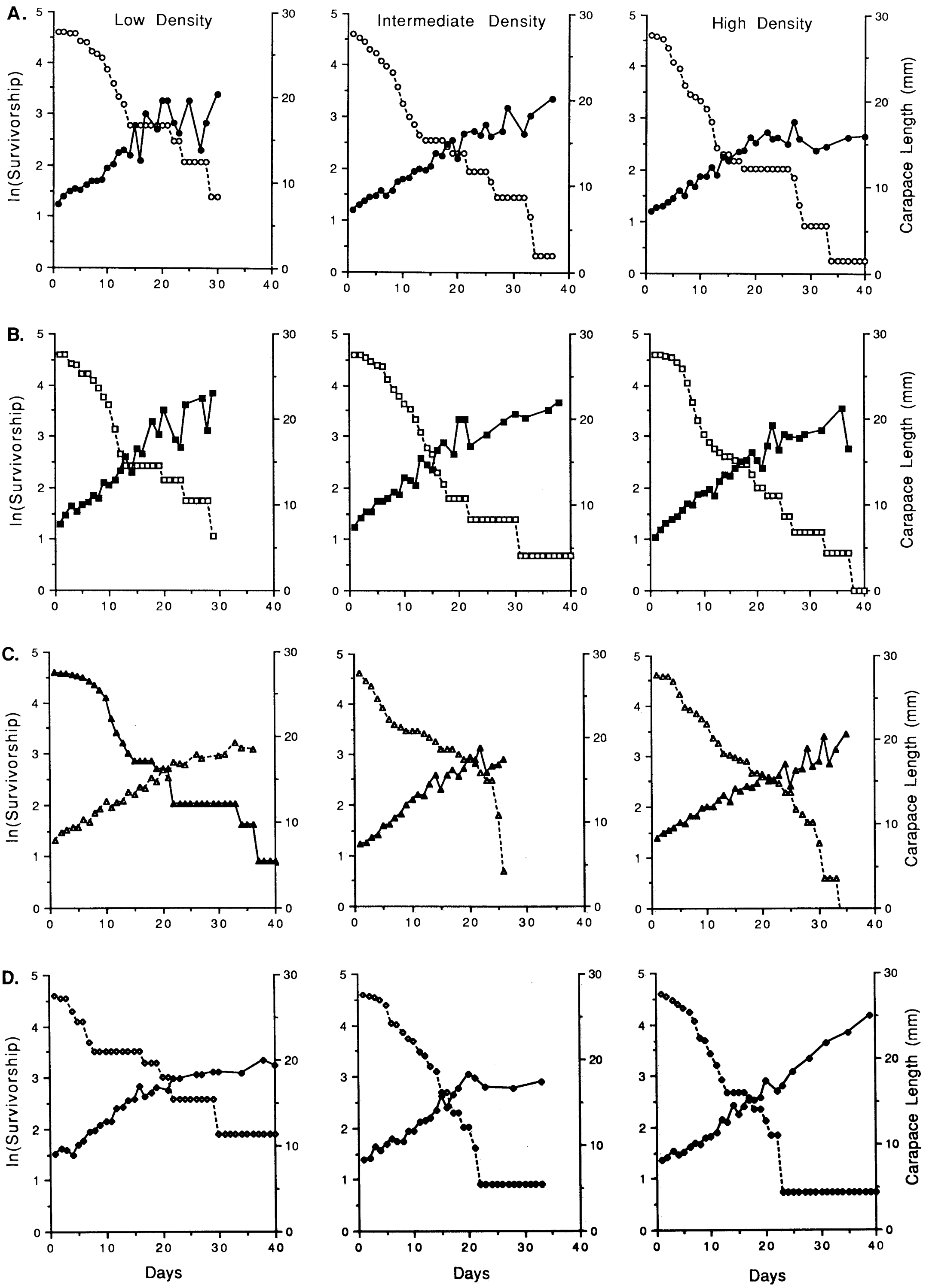

Fig. 1. Daily growth and survivorship for the four lines of *Triops longicaudatus* raised at three densities (5, 10, and 16 shrimp per 27-l aquarium). The four line designations are as follows: (A) clone 1 (short form), (B) clone 2 (long form), (C) clone 3 (short form), and (D) sexual 1 (long form). The open symbols represent the natural logarithm of average percentage of survivorship and the closed symbols represent average carapace length measured from daily molts. Both growth and survivorship are plotted against days in experiment.

Table 1. Average fitness measures for the four lines of *Triops longicaudatus* grown at three densities. Totals are weighted averages across either density or line. Standard deviations are in parentheses. Clones 1 and 3 are short-form while clone 2 and sexual 1 are long-form shrimp. Totals with the same letter superscript are not significantly different (Student-Newman-Keuls test; $P > 0.05$).

Density	Shrimp line				Total
	Clone 1	Clone 2	Clone 3	Sexual 1	
A. Individual biomass					
Low	0.33 (0.19)	0.35 (0.20)	0.30 (0.21)	0.40 (0.06)	0.33^a
Intermediate	0.19 (0.06)	0.33 (0.22)	0.27 (0.11)	0.28 (0.10)	0.26^a
High	0.13 (0.06)	0.26 (0.04)	0.23 (0.15)	0.29 (0.10)	0.22^a
Total	0.21^b	0.31^a	$0.27^{a,b}$	0.32^a	
B. Individual egg production					
Low	128.9 (115.4)	74.6 (94.0)	140.9 (63.0)	48.1 (43.9)	106.0^a
Intermediate	28.7 (16.4)	14.7 (8.8)	31.9 (14.3)	8.0 (5.0)	22.2^b
High	10.4 (13.2)	5.8 (5.8)	13.7 (5.1)	1.1 (0.8)	8.9^c
Total	52.8^a	35.0^b	69.1^a	18.0^c	
C. Age at death					
Low	9.16 (2.37)	7.04 (2.31)	10.74 (4.98)	7.87 (3.91)	8.90^a
Intermediate	6.19 (1.41)	7.88 (2.28)	5.64 (2.43)	7.69 (2.70)	6.75^a
High	6.57 (3.40)	7.30 (0.91)	7.93 (3.05)	6.92 (2.45)	7.28^a
Total	7.18^a	7.36^a	8.48^a	7.51^a	

across either shrimp line or density ($P > 0.15$ in all comparisons; Table 1C).

The multivariate comparison across all three dependent variables revealed highly significant density ($F_{6,102} = 6.88, P < 0.0001$) and shrimp-line effects ($F_{9,124} = 6.26$, $P < 0.0001$). The multivariate shrimp line × density interaction was not significant ($F_{18,145} = 1.18$, $P > 0.25$).

Correlation coefficients calculated between growth, reproduction, and survivorship are reported in Table 2. All significant correlations within density were positive (Table 2A). There was a trend of increased negative correlation between growth and reproduction and growth and age at death at the highest density, though no negative correlation was significant. All correlations averaged across density were positive within each line (Table 2B). A single average measure of each of the three variables among the four lines revealed a nonsignificant negative correlation between growth and reproduction and positive correlations between age at death and both growth and egg production (Table 2C).

DISCUSSION

The three density levels used in this study produced significant levels of intraspecific competition within each of the four lines of *Triops* examined, as indicated by both decreases in egg production and growth with increasing density (Table 1, Fig. 1). All four lines showed similar relative decreases in growth and reproduction with increasing density, revealed by nonsignificant interaction effects among all comparisons. The densities used in this experiment were similar to those measured in the Arizona ponds, where the clonal lines were collected (Weeks, unpublished), Therefore, increased densities of *T. longicaudatus* in these natural communities should be associated with decreased levels of growth and reproduction.

The shapes of the survivorship and growth curves (Fig. 1), as well as the responses to increased density, are similar to those found in *Triops cancriformis* (see Takahashi and Gohda, 1981) and *Artemia sâlina* (see Browne, 1982). In a laboratory experiment, Takahashi and Gohda (1981) reported reductions in growth with increasing density but no effect of density on early survivorship. Maximum egg production of *T. cancriformis* was found at an intermediate density, with a steep decline in productivity at higher densities. Browne (1982) reported Type II survivorship in laboratory-reared brine shrimp. These published results concur well with those described in this study.

No evidence was found to indicate resource allocation trade-offs between any two of the three fitness correlates measured

Table 2. Pairwise correlations between the three fitness measures in each of the four lines of *Triops longicaudatus*. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Line	*N*	Biomass/eggs	Biomass/age at death	Eggs/ age at death
A. Within density				
Low				
Clone 1	5	0.621	0.591	0.502
Clone 2	7	0.770*	−0.190	0.356
Clone 3	8	0.853**	0.870**	0.795*
Sexual 1	3	0.835	0.987	0.735
Intermediate				
Clone 1	7	0.159	−0.210	−0.686
Clone 2	5	0.930*	0.532	0.248
Clone 3	5	0.625	0.896*	0.881*
Sexual 1	4	0.484	0.899	0.775
High				
Clone 1	5	0.614	0.936*	0.740
Clone 2	6	−0.247	−0.113	0.488
Clone 3	7	−0.091	0.968***	0.065
Sexual 1	3	−0.371	−0.772	0.877
B. Averages across density				
Clone 1	17	0.666**	0.613**	0.518*
Clone 2	18	0.486*	0.018	0.179
Clone 3	20	0.391	0.729***	0.587**
Sexual 1	10	0.433	0.256	0.497
C. Among lines	4	−0.659	0.116	0.560

within lines. The data averaged across individuals within a treatment and across densities indicated that survivorship, reproduction, and growth were positively associated within all four shrimp lines (Table 2A, B). Consequently, it appears that individuals within a shrimp line performed either well or poorly, rather than trading poor performance in one life-history measure for increased performance in another.

There was a trend for increased negative correlation between growth and both egg production and survivorship at the highest density. Browne (1982) reported a negative correlation between age at death and length of life-span in *Artemia salina* raised under a low food diet, but no correlation in these parameters in shrimp raised under a high food diet. Similarly, he reported a negative correlation between fecundity and survivorship at the low diet, but a positive correlation at the high diet. These results parallel those of this study and indicate an increased likelihood of resource allocation trade-offs in branchiopods reared under increased levels of resource stress. Under favorable conditions, fitness parameters may be positively correlated, with some individuals performing well and some poorly. Under increased levels of resource depletion, allocation decisions may make fitness tradeoffs more apparent (Horn and Rubenstein, 1984).

The only likely life-history trade-off was found between growth and egg production in the two morphological forms (Table 2C). Though the correlation proved nonsignificant, the limited data indicate genetically fixed differences in resource allocation strategies between the long- and short-form shrimp.

Reproductive form contributed only slightly to the measured differences among these four shrimp lines. Only in egg production did the sexual shrimp differ from the three clonal lines (Table 1B). The nonsignificant density × line interactions demonstrated that the sexual and clonal lines responded similarly to increasing density. This result, as well as the similar levels of variability in these three fitness measures (Table 2), is not expected in comparisons between sexual and unisexual organisms (Bell, 1982), and thus provides no insight into the persistence of the sexual lines in natural habitats.

The long- and short-form shrimp showed similar patterns of growth and reproduction within lines but converse patterns between lines. The long-form shrimp tended to grow larger but produced fewer eggs than the short-form shrimp (Table 1). Thus, the long- and short-form shrimp not only differ electrophoretically and morphologically, but also exhibit different patterns of resource allocation to growth and egg production.

The ecological results of this study combined with genetic and morphological data (Sassaman, unpublished) indicate that the long- and short-form shrimp are quite different, and may actually be different races or subspecies that cooccur in a number of desert habitats. Further genetic and morphological studies on these shrimp should shed light on this possibility.

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