Competition in phenotypically variable and uniform populations of the tadpole shrimp *Triops longicaudatus* (Notostraca: Triopsidae)

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Summary. Life-history parameters (growth, reproduction, and survival) were measured from one genetically heterogeneous and three homogeneous populations of tadpole shrimp (*Triops longicaudatus*) raised under three competitive levels: 5, 10, and 16 shrimp per 38-l aquarium. Comparisons were made between the homogeneous populations (three monomorphic selfing lines) and a heterogeneous population (a mixture of the three lines) to test for increased productivity in genetically variable populations, a prediction of the tangled bank hypothesis for a short-term advantage to sexual reproduction. In most comparisons, the mixture of inbred lines performed better than expected from their individual performances in pure cultures but did not outperform the best performing line in any comparison. Decomposition of the mixed culture's performance into performances of the component inbred lines showed that not all lines experienced release from competition in the mixed culture. No genotype X environment interaction was found for any of the three fitness correlates, indicating that all three lines performed similarly under the three competitive conditions. These results provide little support for the tangled bank hypothesis and suggest that the levels of heterogeneity necessary for detectable resource partitioning in these shrimp may involve factors not considered in this study.

Key words: Evolution of sex – Tangled bank – Inbred lines – Competition, tadpole shrimp

The persistence of sexual reproduction is perplexing when one considers the cost of producing males relative to all-female reproduction (Williams 1975; Maynard Smith 1978). This "cost of sex" is two-fold when females invest equally in male and female offspring and when males contribute no more than a haploid pronucleus to their offspring. The original explanation for this paradox emphasized recombination and outcrossing as mechanisms for quickly incorporating advantageous mutations into a population (Fisher 1930; Muller 1932; Crow and Kimura 1965; Maynard Smith 1968). According to this hypothesis, the advantage of sexuality is maximal when populations are large, beneficial mutations occur frequently, and the selective advantage per mutation is small (Crow and Kimura 1965). Recently, this explanation has been rejected due to its invocation of group selection (Williams 1975; Maynard Smith 1978; Bell 1982) and has been superseded by explanations involving a short-term, individual advantage to sex (Williams 1975; Glesener 1979; Hamilton 1980; Bell 1982; Rice 1983; Case and Taper 1986).

Most short-term models of the maintenance of sexual reproduction invoke benefits of phenotypically variable progeny in a temporally or spatially varying environment (Bell 1982). The "tangled bank" model (Ghiselin 1974; Bell 1982, 1985) assumes spatially heterogeneous environments cause varying selective pressures that maintain sexuality and that habitats (patches) consist of an array of resource types which no individual phenotype is capable of exploiting completely. Phenotypically diverse offspring may utilize more of the available resources than phenotypically uniform progeny. Individuals experiencing the least resource competition are those with the rarest phenotypes, relative to their resource base, which results in selection for constant rearrangement of parental genotypes to enable production of these rare phenotypes. Implicit in this argument is the assumption that there are not enough clones to exploit all (or even many) resource types (Bell 1982).

Comparing performances of clonal or inbred lines grown in pure culture versus their combined performances in mixed culture has been proposed as an appropriate test of the tangled bank hypothesis (Bell 1985). Bell outlines two general predictions that would be consistent with the tangled bank hypothesis: 1) mixtures

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of clones should exhibit a higher yield than that expected from the average of the component lines grown in pure culture, and 2) clonal or inbred lines should perform differently in different environments; or in other words, there should be strong genotype X environment interactions.

In the present study, we have addressed these predictions by comparing performances of three inbred lines of the notostracan shrimp *Triops longicaudatus* (tadpole shrimp) in pure versus mixed culture to determine whether increased phenotypic variability leads to increased productivity, and, if so, whether the increased productivity is consistent with the tangled bank hypothesis. Several ecological fitness correlates (egg production, growth, and survivorship) were measured at three densities of the three lines grown in pure culture and in a mixture of all three lines to explore two questions: (1) does a phenotypically variable group of shrimp show higher productivity in these artificial patches than do monomorphic groups? and (2) do the individuals in phenotypically variable groups experience reduced competition as predicted by the tangled bank model?

Experimental organism

Triops longicaudatus inhabit freshwater ephemeral ponds ranging from 50° N latitude in western North America through Central America and into South America (Longhurst 1955). *Triops* populations exhibit wide variation in sex ratio, usually being strongly female-biased (Linder 1952). It appears that sexual populations consist of a mixture of facultatively hermaphroditic females and sexual males and that clonal populations contain only the former (Weeks unpubl.). Longhurst (1955) found that individuals from clonal populations had testicular tissue intermixed with ovarian tissue and proposed that asexual reproduction was accomplished by self-fertilization.

Tadpole shrimp complete their life cycle in 30–40 days. They produce desiccation-resistant resting eggs which hatch within 24 h after hydration, given appropriate levels of light, temperature, and oxygen (Takahashi 1977; Scott and Grigarick 1978, 1979). Nauplii quickly develop into juveniles, which then settle on the pond floor to take up the omnivorous habits characteristic of adult tadpole shrimp. Individuals attain sizes of 15–20 mm in as few as 10 days and reach sexual maturity as soon as 9 days after hatching (Takahashi 1977; Weeks unpubl.). Tadpole shrimp produce up to 246 eggs per day which are buried or stuck to vegetation and pond detritus (Takahashi 1977). Given its reproductive polymorphism, as well as its relatively short generation time, *Triops* is a suitable experimental animal for testing the predictions of the tangled bank model.

Materials and methods

All three clonal lines used in this experiment are patchily distributed in several ponds near Portal, Arizona. Most ponds contain

Table 1. Experimental design (see text for further details). Number of replicates per line by density treatment are shown in parentheses

Line	Density		
	Low	Intermediate	High
Clone 1	5 clone 1 (n = 5)	10 clone 1 (n = 7)	16 clone 1 (n = 5)
Clone 2	5 clone 2 (n = 7)	10 clone 2 (n = 5)	16 clone 2 (n = 6)
Clone 3	5 clone 3 (n = 7)	10 clone 3 (n = 5)	16 clone 3 (n = 8)
Mixed	2 clone 1, 1 clone 2, 2 clone 3 (n = 6)	4 clone 1, 3 clone 2, 3 clone 3 (n = 6)	6 clone 1, 5 clone 2, 5 clone 3 (n = 5)

only a single clone, but clones 2 and 3 co-occur in a single known location. All three lines used in this study were collected from monoclonal ponds. Clone 2 has more legless tail segments ("long" form) than clones 1 and 3 ("short" form). The short-form lines differ at one of 13 electrophoretically sampled loci, whereas both short-form lines differ from the long-form line at 7 of the 13 sampled loci (Sassaman unpubl.).

The experiment was run as a completely randomized 4 x 3 factorial design. There were four "line" treatments: (1) pure clone 1; (b) pure clone 2; (c) pure clone 3; and (d) a mixture of the three clonal lines (Table 1). Each line was reared under three density treatments: (a) low (five shrimp fed 0.20 g/day/shrimp); (b) intermediate (ten shrimp fed 0.10 g/day/shrimp); and (c) high (sixteen shrimp fed 0.0625 g/day/shrimp). The mixed treatments were set up as follows: (a) low density = two clone 1, one clone 2, and two clone 3; (b) intermediate density = four clone 1, three clone 2, and three clone 3; and (c) high density = six clone 1, five clone 2, and five clone 3 (see Table 1). The number of replicates per culture X density combination ranged from five to eight (Table 1).

Shrimp were reared in 38-l glass aquaria, which were allowed to dry out naturally to simulate desert conditions. No treatment was allowed to dry out completely; in the longest-lived replicates, 5–10 l of water were added to prevent desiccation-related mortality. Initial food (Wardley goldfish food) per tank was held constant at 1.0 g/day and was proportionately reduced with mortality within each treatment (i.e., when one shrimp in a treatment of five died, the overall quantity of food per tank was decreased by 0.20 g/day). The above feeding regime was used to keep 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. Therefore, constant competitive pressure for food was maintained throughout the experiment on all surviving shrimp. Space per individual was under no experimental control except for initial conditions, and therefore increased with increasing mortality.

Three measures of productivity were recorded in each treatment: (a) growth, measured as increase in individual biomass; (b) egg production, measured as total eggs produced per experimental tank; and (c) survivorship, measured as survivors per day. Experimental tanks were siphoned daily to remove dead shrimp and to record the number of survivors per day. The original water was then reintroduced into the tanks and the appropriate quantity of food was added. This procedure allowed measurement of survivorship with the least possible disturbance. Experiments continued and data were collected until the last shrimp in each tank died.

Egg production was measured at the end of each experiment by screening out eggs from the soil in each tank with a 300 micron screen (egg sizes ranged between 325 and 375 microns in diameter). Two categories of eggs were recorded: (a) intact eggs (any egg with no apparent physical damage), and (b) eggshells (eggs with obvious physical defects). Only eggshells that were greater than

50% the diameter of a nomal egg were counted to avoid overcounting damaged eggs. Most eggshells were almost entirely intact with a single large tear. *Triops longicaudatus* have a tendency to cannibalize their own eggs, leaving only empty eggshells (Weeks pers. observ.). Therefore, eggshells are not necessarily a direct result of inferior eggs.

Statistical procedures

All data were analyzed using the General Linear Models and Lifetest procedures of the SAS statistical package (SAS Institute 1982). All parametric univariate comparisons were tested for normality of data (SAS Proc Univariate) and homogeneity of variance (Bartlett's test).

Average increase in individual biomass per tank was calculated by measuring the biomass of each shrimp at time of death and subtracting the average biomass of the shrimp at the start of the treatment. Total biomass was computed for the tank, and this value was subsequently corrected for density by dividing by the number of shrimp initially added to the tank. Average number of eggs per individual was calculated by dividing the total number of eggs produced in a tank (intact eggs + eggshells) by the number of female shrimp in each tank.

A two-way multivariate analysis of covariance was used to compare mean egg production and biomass. The number of "shrimp-days" (surviving shrimp per day summed over days) was used as a covariate to standardize for the possible confounding effect of differing survivorship between density and line treatments. The covariate, shrimp-days, affected all line X density treatments homogeneously ($P > 0.05$) within each comparison. Growth and egg production in mixed culture were compared against monoclonal growth and reproduction using an orthogonal contrast of the mixed treatments versus a weighted combination (weighted by the numbers of each clone initially added in the mixed treatment) of the three clonal lines.

Survivorship was analyzed by comparing survivorship curves for the four cultures (3 clones and mixed) averaged across replicate tanks. Heterogeneous survivorship among cultures was compared separately within each density treatment with the Logrank chi-square test (Mantel 1966; Peto and Peto 1972) in the Lifetest procedure (SAS Institute 1982). In this distribution-free test, two or more survival curves are compared through the use of a chi-square analysis. The calculation of observed failures is simply the summation of all deaths over the time period of study, resulting in an observed value for each group. The expected number of failures is calculated by estimating the "extent of exposure to risk of death" for each group being compared (Peto et al. 1977). A chi-square value is then calculated for each group and these values are summed for all groups. The total chi-square value is compared to a standard chi-square table. The benefit of the Logrank chi-square test is its use of the entire survivorship distribution relative to a portion of that distribution for single measures of survival (such as "lethal dose-50" or median survival) which can lead to unreliable results (Peto et al. 1977).

A comparison of performance of the clonal lines in mixed relative to pure culture (see below) was accomplished by partitioning the growth and survivorship of clonal forms (short versus long) in the mixed cultures and comparing this to each form's growth and survivorship in pure culture. In the growth analysis, a direct statistical comparison was available for the long-form line (clone 2), whereas clones 1 and 3 were indistinguishable and therefore were combined into a short-form category.

Growth and egg data were log-transformed. The transformed data were subsequently found to be normally distributed except for the comparison of increase in individual biomass between shrimp grown in pure and mixed cultures ($P < 0.01$) (see below). All comparisons had homogeneous variances ($P > 0.05$) except the comparison mentioned above ($P < 0.005$) and eggs produced per female reproductive day ($0.025 < P < 0.01$).

Results

Comparisons of overall performance

At the low and intermediate densities, survivorship was higher in the mixed than the pure cultures (Fig. 1), though this difference was not statistically significant (logrank chi-square, $0.05 < P < 0.10$). Survivorship was equivalent among all lines at the highest density (logrank chi-square, $P > 0.40$). A comparison of mixed survival to that expected from a weighted average of survivorship in the three pure lines, revealed significantly higher survivorship at the intermediate density only (logrank chi-
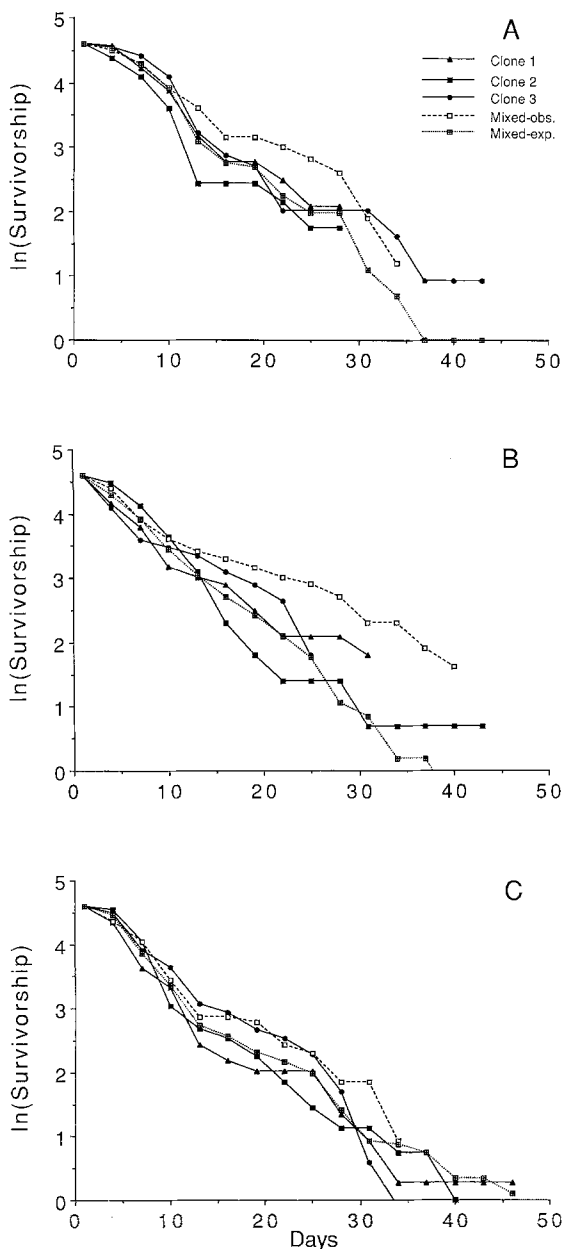
Fig. 1 A–C. Tadpole shrimp survivorship in mixed and pure culture. Predicted (mixed-exp.) and observed (mixed-obs.) survivorship are displayed. Density treatments are: *A* five (low), *B* ten (intermediate), and *C* sixteen (high) shrimp per tank
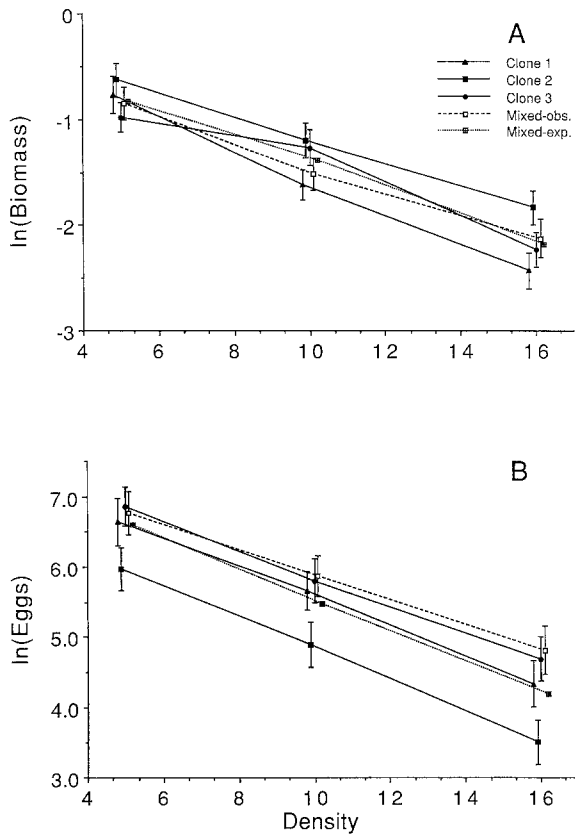
Fig. 2A and B. Measures of growth rate and egg production of *Triops* lines at each density: **A** Average individual biomass for tadpole shrimp in all lines at all densities and **B** Average individual egg production per female (see text for calculations of these variables). Adjusted means and standard errors are plotted for each line at each density. Observed and predicted performance is shown for the mixed cultures

Table 2. Univariate and multivariate two-way analysis of covariance results. Average individual biomass and average egg production per female are the dependent variables compared in a 4×3 factorial design of four lines crossed with three densities. Shrimp-days was used as a covariate to adjust for the possibly confounding effect of differential survival between treatments

Source	Num (df)	Den (df)	Mean square[a]	F	Pr > F
Shrimp-days					
a) Biomass	1	59	8.8969	66.34	0.0001
b) Eggs	1	59	7.8776	15.60	0.0002
Density					
a) Biomass	2	59	4.8199	35.94	0.0001
b) Eggs	2	59	13.2776	26.29	0.0001
c) MANOVA	4	116	0.3855	17.71	0.0001
Line					
a) Biomass	3	59	0.4636	3.46	0.0220
b) Eggs	3	59	3.9507	7.82	0.0002
c) MANOVA	6	116	0.5453	6.83	0.0001
Density × line					
a) Biomass	6	59	0.1174	0.88	0.5186
b) Eggs	6	59	0.0743	0.15	0.9889
c) MANOVA	12	116	0.8918	0.57	0.8625
Orthogonal contrast-mixed vs. pure					
a) Biomass	1	59	0.0223	0.17	0.6849
b) Eggs	1	59	2.0514	4.06	0.0484
c) MANOVA	2	58	0.9167	2.64	0.0802
Error					
a) Biomass	–	59	0.1341	–	–
b) Eggs	–	59	0.5051	–	–

[a] Value reported for MANOVA is the Wilks' Lambda statistic

square, $P < 0.05$; Fig. 1). Survivorship was never significantly higher than that of the best surviving line at any density. Survivorship was significantly reduced with increasing density (logrank chi-square, $P < 0.01$).

Individual biomass and number of eggs per female showed a denisty effect, indicating increased levels of competition, as well as a clonal line effect, indicating heterogeneous line performance in both the univariate and multivariate comparisons (Table 2, Fig. 2). Average growth in the mixed treatment was higher than that of pure cultures of clone 1, and average egg production was higher in mixed than in pure cultures of clone 2 (Tukey's HSD, $P < 0.05$). Neither growth nor egg production was highest overall in the mixed treatment. Shrimp in the mixed treatment did produce more eggs but did not grow faster than expected from a weighted average of the clonal lines grown in pure culture (Table 2). There was no significant difference between mixed and average pure performance ($P > 0.05$), when both egg production and growth were considered simultaneously (Table 2).

Neither fitness correlate showed a significant density X line interaction at either the univariate or multivariate level; the F-ratio being less than one in all measures

(Table 2). The nonsignificant interactions indicated that all lines ranked similarly under increasing density and that the mixed treatment had a similar decrease in productivity with increasing density as did the phenotypically uniform lines (Fig. 2).

Clonal performance in mixed and pure culture

Clonal performance was separated into short-form (clones 1 and 3) versus long-form (clone 2) performance in mixed relative to pure culture, to assess whether all clonal lines were experiencing "incomplete" competition in the mixed treatments. The two morphological forms showed differential survival at the two lowest densities (logrank chi-square, $P < 0.05$). Plots of survivorship versus days in treatment (Fig. 3) showed that the short-form shrimp survived better in the mixed treatments at the intermediate density (logrank chi-square, $P < 0.01$) whereas clone 2 shrimp survived equally well in both mixed and pure culture at all densities ($P > 0.25$).

Analysis of covariance for increase in biomass in pure relative to mixed treatments for the two shrimp forms showed a significant line effect (Table 3). In this analysis, the mixed treatment was divided into short-form (clones 1 and 3) and long-from (clone 2) performance. Thus, there are five culture treatments (clone 1,
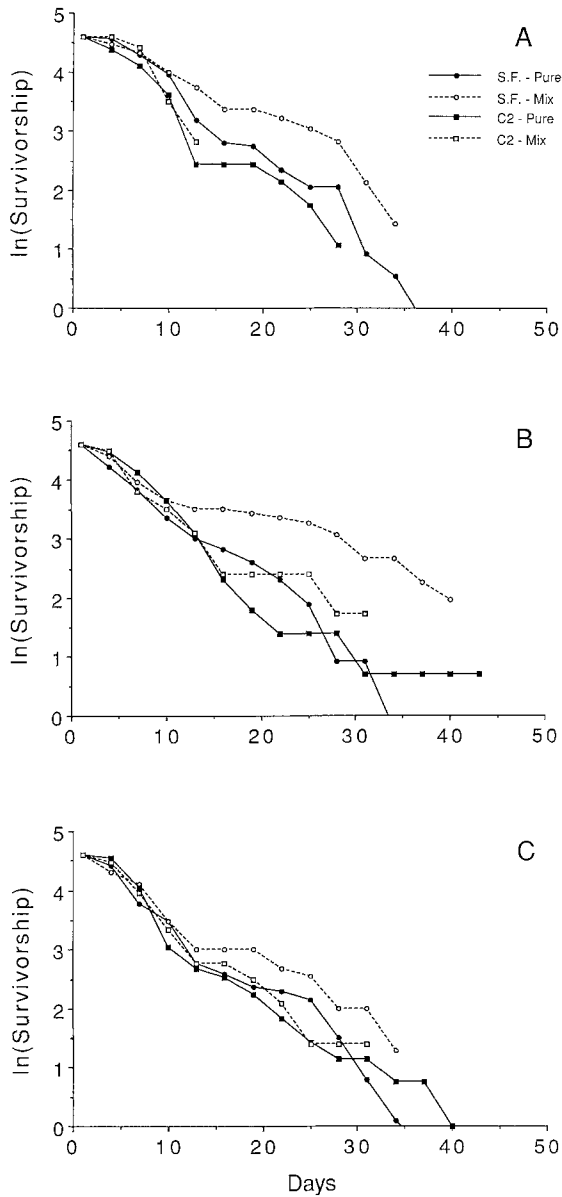
Fig. 3 A–C. Survivorship of short-form (S.F.) and long-form (C2) shrimp in mixed and pure culture. Densities are: **A** Low=five shrimp per tank; **B** Intermediate=ten shrimp per tank; and **C** High=16 shrimp per tank. Survivorship in pure tanks (-Pure) is shown as *filled symbols* and *solid lines* whereas that in mixed tanks (-Mix) is shown as *open symbols* and *dashed lines*. Heterogeneous survivorship was found in the low and intermediate densities (lo-grank chi-square; $P<0.05$) but not at the high density ($P>0.10$)

Table 3. ANCOVA for the effects of density, line, and density X line interaction on growth rate of tadpole shrimp grown in pure and mixed cultures. The five line treatments in this comparison are: (a) Clone 1 pure, (2) Clone 2 pure, (3) Clone 3 pure, (4) Short-form (Clones 1 and 3) mixed, and (5) Long-form (Clone 2) mixed. Shrimp-days was used as the covariate as described above

Source	Biomass/Indv.			
	df	MS	F	P
Shrimp-days	1	5.621	7.28	<0.01
Density	2	2.085	2.70	n.s.
Line	4	3.546	4.59	<0.005
Density × line	8	0.708	0.92	n.s.
Error	75	0.772		
Total	90			
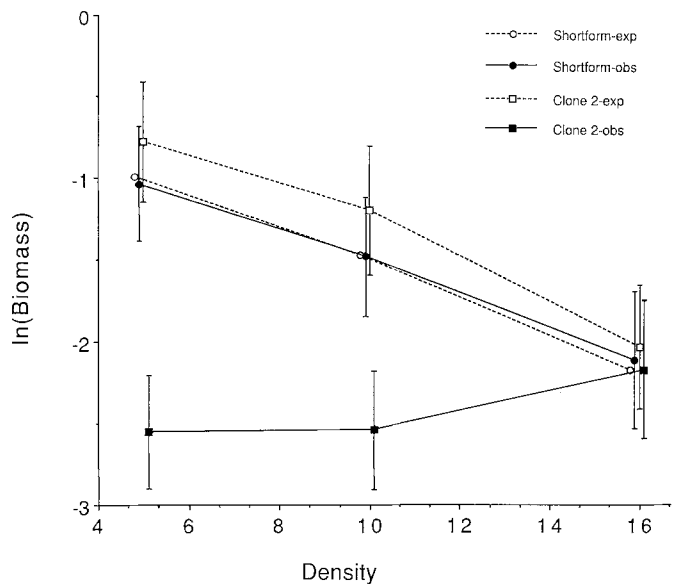
Fig. 4. Adjusted mean individual biomass of short-form (Clone 1 + Clone 3) and long-form (Clone 2) shrimp in pure and mixed culture. Clone 2 performance is illustrated by *squares* whereas short-form performances are represented by *circles*. Performances of the clonal lines in pure culture (−exp) are shown as *open symbols* and *dashes lines* whereas mixed performances (-obs) are represented by *filled symbols* and *solid lines*

2, and 3 in pure culture, short-form shrimp in mixed culture, and long-form shrimp in mixed culture) crossed with three density treatments. Growth was significantly lower in clone 2 when in the presence of the short-from shrimp than when grown in pure culture (Tukey's HSD, $P<0.05$). Clone 2's performance was poorest at the low and intermediate densities with the difference unapparent at the highest density (fig. 4). The short-form's performance in this comparison indicates that growth was not significantly different ($P>0.05$) in mixed and pure culture.

Discussion

The experimental design used in this study allowed us to test two predictions of the tangled bank hypothesis as outlined by Bell (1985): (1) the mixture of inbred shrimp lines should exhibit a higher yield than that expected from the average of the component lines grown in pure culture, and (2) the three inbred lines should perform differentially in different environments. There are two possible mechanisms by which a mixed treatment could outyield pure treatments of the component members: (a) an absolute difference in yield at all densities; and (b) increased relative yield of the mixture under increased resource competition.

The first prediction appears to be borne out in these experimental treatments. Survivorship and egg production in the mixed treatment clearly showed higher than expected performance based on average responses in the pure cultures, though growth was nearly the same as expected. This result supports the tangled bank hypothesis, and is in agreement with many similar experimnents which have found increased yield in mixtures relative to the expected yields of component lines grown in pure culture (e.g., Gustafsson 1953; Sakai 1955; Allard 1961; Lewontin and Matsuo 1963; Bhalla and Sokal 1964; England 1968; Allard and Adams 1969; Moav and Wohlfarth 1974).

A more stringent test of the tangled bank hypothesis is to compare the performance of the mixed treatments to that of the best performing component line (Bell 1985). An example of such a relationship is that of AR and CH inversion lines of *Drosophila pseudoobscura* grown separately and in mixtures (Beardmore et al. 1960; Battaglia and Smith 1961; Dobzhansky and Pavlovsky 1961; Beardmore 1963; Dobzhansky et al. 1964). Mixed AR and CH populations sustain more individuals than either the AR or CH lines grown in pure culture under condtions of adult crowding (Dobzhansky and Pavlovsky 1961) and larval crowding (Beardmore et al. 1960) at 25° C. Under "optimal" conditions (e.g., no competition at any stage of the life cycle), the mixed AR and CH populations perform as expected by performance in pure culture (Ohba 1967). The above experiments provide strong support for the tangled bank hypothesis by showing that mixed populations perform better than expected as well as better than the best performing component line in competitive environments. In our study, none of the three fitness correlate were significantly higher in the mixed treatment relative to that exhibited by the best performing line in pure culture.

Although many experiments do show increased performance of a mixture relative to that expected from the component lines, the mechanism of the increased productivity is not entirely clear. The tangled bank hypothesis relies on facilitation or incomplete competition between lines grown in mixture. Replacing a number of competing individuals of like phenotype with individuals of an alternate phenotype should decrease competition, and therefore increase productivity for all individuals involved. The greater the difference in phenotype, the lower the likelihood of resource overlap, and the greater the likelihood of release from resource competition. In this experiment, we expected that individuals of all three clones in the mixed culture would show increased productivity relative to individuals reared in pure culture. Decomposition of the mixed performance into short-form (clones 1 and 3) and long-form (clone 2) performance is an appropriate test of this prediction. The short-form shrimp clearly survived better in mixed relative to pure culture. Short-form growth was similar in both treatments. On the other hand, long-form survivorship was nearly the same under the two treatments, and growth was significantly reduced in mixed relative to pure culture. This is an unexpected result when one considers that long-form shrimp are electrophoretically

and morphologically very different from either of the short-form clones, which are themselves morphologically indistinguishable.

Kearsey (1965) has shown that a nonlinear relationship between productivity and resources in two lines of *Drosophila melanogaster* can lead to a competitive interaction between lines that yields better than expected productivity in mixed relative to pure cultures. Clearly, an improved performance in mixed culture can be the result of competitive interactions of component lines (Kearsey 1965; Nunney 1983). Thus, while increased productivity of mixed populations is a necessary component of the tangled bank hypothesis, it is not sufficient to conclude that incomplete competition produces the superior performance without showing that the increased productivity is a result of equal or greater performance of all component lines.

Increased relative yield of the mixture under increased resource competition is a second mechanism by which a mixed treatment could outyield pure treatments of the component members. No fitness correlate showed a significant density X clonal line interaction, and increasing density seemed to obscure rather than enhance the differences between observed and expected survivorship. This finding contradicts most theoretical works that assume phenotypically variable populations will be increasingly superior in patches with increasing numbers of propagules (Williams and Mitton 1973; Williams 1975; Maynard Smith 1976; Taylor 1979; Bulmer 1980; Bell 1985). Our finding is consistent with a study by Ellstrand and Antonovics (1985) on *Anthoxanthum odoratum* in which sexual progeny were found to have higher productivity than asexually propagated tillers of equivalent size, but only at lower densities. Decreased mixed advantage with increased density indicates that sexually produced (variable) individuals may indeed have an adaptive advantage over their asexually produced (uniform) counterparts, but that high densities may mitigate this advantage. Above a certain density, phenotypically variable individuals may be equivalent to phenotypically uniform individuals. This is counterintuitive when one assumes that variable offspring partition their resources and, therefore, should be less adversely affected by increased levels of competition than uniform offspring that are unable to accomplish such partitioning.

Finally, the second assumption of the tangled bank hypothesis, that the three inbred lines should perform differentially under the three density treatments, was not supported by this experiment. It is clear from Figs. 1–3 that all three clonal lines ranked similarly under all three density treatments. Neither egg production nor growth exhibited a significant density X clonal line interaction, indicating similar reductions in both parameters under increasing density. In fact, very little of the total variation in these two factors was explained by the density X clonal line interaction at either the univariate or multivariate level. Thus, these three inbred lines maintained their relative positions under all three competitive environments; a result not predicted by the tangled bank hypothesis.

It appears that some level of resource partitioning

has been attained in the mixed cultures, but a significant amount of overlap must still exist which causes a competitive interaction between the long- and short-form shrimp. This result is incompatible with an explanation relying on resource partitioning for maintenance of phenotypic variability in a spatially heterogeneous environment. The two forms of shrimp have fixed differences at over half of the loci examined, a situation similar to that found between two facultatively self-fertilizing strains of the land snail *Rumina decollata* (Selander and Kaufman 1973; Selander and Hudson 1976). This genetic difference is much greater than one would ever expect among progeny of a single individual, and yet significant resource partitioning was still not demonstrable in this experiment. Thus, if spatial heterogeneity and resource partitioning are important in reducing the levels of sib-sib competition in natural populations of these shrimp, the degree of heterogeneity needed to produce such partitioning is significantly greater than that provided by a laboratory simulation of a single patch at one point in time.

It is possible that the laboratory conditions did not properly simulate a heterogeneous environment, and therefore resource partitioning was impossible given the levels of phenotypic variability. This argument can be levied against any laboratory experiment in which resource partitioning is not found, and may indeed prove to be an insurmountable barrier to such experimental endeavors. Nevertheless, it is important to understand the level of environmental variability that is sufficient to maintain sexuality in the short term. The tangled bank hyypothesis leads us to believe that the environment is composed of numerous, partitionable "microniches" which may not be obvious to human observers (Bell 1982, 1985). Obvious environmental factors, such as predators, parasites, competitors, and larger scale environmental fluctuations, may have been necessary to provide the level of heterogeneity upon which these three inbred lines could have subdivided niche-space.

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