

## Original papers

# Phenotypic plasticity of life-history traits in clonal and sexual fish (*Poeciliopsis*) at high and low densities

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**Abstract.** Models of resource allocation strategies predict an array of life-history responses of individuals living in resource-stressed versus non-stressed environments. I tested a number of these predictions using three fish strains (a sexual and two clonal strains) in high and low density treatments. To examine the plasticity of life-history traits in females raised in these two environments, I measured survival, growth, egg production, egg size, and proportion mature at 10 weeks of age. Survival was not affected by density treatment. However, both growth and overall egg production were lower in females from the high density treatments, and reproductive maturity was significantly delayed at the high density for all strains. Egg production per unit size was not affected by density in any strain, signifying that differences in the numbers of eggs produced was merely a reflection of the differences in size of fish in the two density treatments. Egg size was also unaffected by density in all strains. These results are related to models of resource allocation in stressful environments. There was a consistent pattern of increased reproductive investment in the sexual strain relative to the two clonal strains. The sexual strain matured earlier, produced more eggs per unit body weight, and had larger eggs than either clone at both densities. These results are interpreted by considering the predicted adaptive responses of these three strains to the long-term environmental differences in their natural habitats.

**Key words:** Resource allocation – Livebearing fish – Growth – Reproduction – Egg size

Life-history theory predicts that organisms should allocate resources to the demands of maintenance, growth, reproduction, and storage in such a way that fitness is maximized (Gadgil and Bossert 1970; Smith and Fretwell 1974; Brockelman 1975; Giesel 1976; King and

Roughgarden 1982; Caswell 1983; Stearns and Crandall 1984; Stearns and Koella 1986; McGinley et al. 1987; Winkler and Wallin 1987; Schultz 1991). Although much life-history theory is framed in terms of evolutionary responses to different environments, the same expectations can be applied to responses that are the product of phenotypic plasticity. Environmental heterogeneity within an individual's lifespan should favor phenotypically plastic (i.e., environmentally sensitive) investment patterns, whereas environmental heterogeneity across generations should favor genetic variability for investment strategies (Giesel 1976). Strategies for timing and level of overall reproductive investment should be sensitive to trade-offs of current investment versus future reproductive success (Williams 1966; Schaffer 1974). For example, low adult survivorship indicates low likelihood of future reproductive success, and therefore should lead to increased current reproductive effort (Schaffer 1974). Different levels of age-specific mortality can also affect patterns of age and size at maturity (Stearns and Crandall 1984; Stearns and Koella 1986). Finally, environmental quality and juvenile survival can affect levels of investment per offspring, with "poorer" environments selecting for larger investment per offspring (Smith and Fretwell 1974; Reznick 1982; Reznick and Endler 1982; Morris 1985, 1987; McGinley et al. 1987; Schultz 1991).

Fish have proven useful in the examination of life-history theory, primarily due to their developmental plasticity and responsiveness to laboratory and field manipulations (Reznick 1981, 1982; Reznick and Endler 1982; Stearns 1983a, b, c; Meffe 1987, 1990, 1992; MacKay and Mann 1969; Rowe and Thorpe 1990; Thorpe et al. 1990; Trexler and Travis 1990a; Hutchings 1991). In a number of studies, plastic allocation patterns in fish under various levels of resource stress have been quantified (Scott 1962; Hester 1964; Bagenal 1969; Wootton 1973; Hislop et al. 1978; Trendall 1983; Reznick 1990; Trexler and Travis 1990b; Weeks and Quattro 1991). In the current study, I examined life-history plasticity in a sexual strain (*Poeciliopsis monacha*) and two clonal strains (*P. monacha-lucida*: strain S68–4 ML/VII

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and strain T70-3 ML/VIII; Vrijenhoek et al. 1978), under two density treatments. Populations of all three strains experience dramatic seasonal fluctuations in resource quality, resource abundance, and population size (Thibault 1974a; Moore and Eisenbrey 1979; Schenck 1988), and therefore should be characterized by individuals with phenotypically plastic investment strategies (Giesel 1976).

Using these three strains, I was able to examine the plasticity of life-history strategies both within and between populations. I quantified fitness-related characters (growth, egg number, egg size, survivorship, and age at maturity) of these three strains under two levels of resource stress to quantify the plasticity of responses of the above life-history correlates to decreased resource availability. I examined reproductive allocation strategies by first considering the overall level and timing of reproductive investment, and then considering the pattern of that investment in many small or few large offspring. By using strains from two contrasting habitats, I was also able to correlate life-history strategies with habitat characteristics.

## Materials and methods

### Experimental organisms

The two clonal *P. monacha-lucida* strains are diploid, hybridogenetic "hemiclones" produced by the hybridization of a *P. monacha* female and a *P. lucida* male (Schultz 1969; Cimino 1972; Vrijenhoek 1972; Vrijenhoek et al. 1978; Avise and Vrijenhoek 1987; Quattro et al. 1991). During hybridogenetic oogenesis, only the haploid *P. monacha* genome is transmitted to the maturing oögonia. The paternal *P. lucida* genome is excluded during a premeiotic cell division, precluding synapsis and crossing over (Schultz 1969; Cimino 1972). Diploidy is restored following fertilization by a *P. lucida* male. For further information on this reproductive system, see Schultz (1969).

Clonal parents were artificially inseminated with sperm from isogenic *P. lucida* males (strain S68-4 PC; Angus and Schultz 1983), thereby standardizing the substitutable paternal genome and removing all among-individual genetically determined variation within a clonal strain (Wetherington et al. 1989). Previous studies have shown this inbred *P. lucida* strain shows no inbreeding depression in growth or fecundity over its many years in laboratory culture (Schultz 1982), and therefore should not adversely affect the offspring resulting from these crosses. Sexual females were naturally inseminated by *P. monacha* males in large rearing tanks.

### Experimental design

All treatments were started with juvenile fish between 3 and 21 days of age. Juveniles were collected from 20 adult females kept in a flow-through aquatic incubator (25° C, 12L:12D photoperiod) throughout their gestational period to homogenize the juveniles' developmental environment (see Wetherington et al. 1989). Juveniles were temporarily placed in three 356-liter tanks until 108 juveniles had been collected from each strain. Fish were weighed immediately before random assignment to treatments (Table 1). The experiment consisted of a randomized block design, crossing the three fish strains with two density treatments (high = 24 and low = 12 fish per tank). The entire design was conducted in two blocks of three replicates each.

Aquaria were housed in a greenhouse in a recirculating freshwater system that simulated small-scale heterogeneous conditions in natural Sonoran desert streams. Each 75 liter glass aquarium had a standpipe allowing approximately 37 liters of standing water. Plastic mesh was used to cover the openings of all standpipes so that no fish could escape the tanks. All aquaria were divided into a U-shaped design using a Plexiglass divider. Each aquarium had a single water input dropping onto a Plexiglass "ramp" which provided areas of fast current near the inlet and slow current near the outlet. The bottom of each aquarium was covered with 2 cm of sand. Three substrates were provided in different regions of each tank: (1) water-soaked straw, (2) pebbles (1–2 cm diameter), and (3) an aquatic moss. Recirculated water from all 18 experimental aquaria was collected in a 1125 liter sump. Treatments ran for 70 days. The photoperiod was set at 15L : 9D by supplementing natural sunlight with broad-spectrum fluorescent light. To simulate natural fluctuations, temperature was systematically varied throughout the experiment on a three-week cycle using refrigeration and heating elements in the sump. Temperature was set at 30° C for two weeks followed by one week at 20° C. Temperature differences among replicate tanks within a block were negligible (< 1° C) throughout the experiment.

The fish in all experimental treatments were fed brine shrimp nauplii, ground Purina trout chow, live chironomid larvae, live tubifex worms, and live brine shrimp adults added once daily (see Weeks and Quattro 1991). When live chironomid larvae were unavailable, frozen chironomid larvae were substituted. The same quantity of food was added to all treatments. Food was added through a series of 12 mm diameter, vinyl feeding tubes from a remote location so the fish were not disturbed by the feeder.

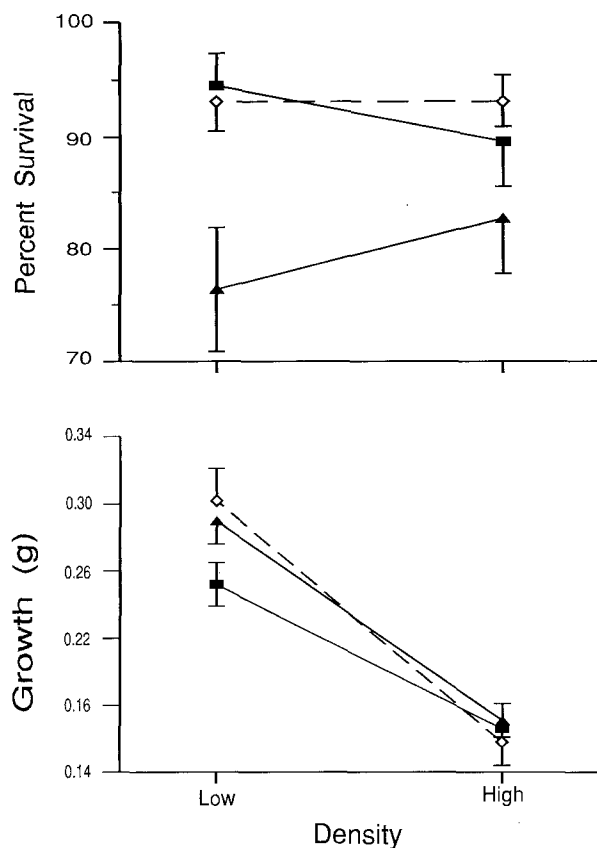
On the 70th day of all trials, survivors were sacrificed by placing them in icewater 45 min after feeding. The fish were counted, weighed, and dissected. Eggs were categorized as either atretic (post-mature), mature, or immature (see Wetherington et al. 1989). Mature eggs were measured with an ocular micrometer at 20× magnification. Egg volumes were estimated by assuming each ovum to be a sphere with a radius equal to the average calculated from the minimum and maximum measured diameters (Quattro and Weeks 1991). Egg volumes have been shown to be a good measure of energy investment per egg in *Poeciliopsis* (Quattro and Weeks 1991; Weeks and Quattro 1991).

### Statistical methods

Data were analyzed with the General Linear Models and Univariate procedures of the SAS statistical package (SAS Institute, Inc. 1985). Male *P. monacha* exhibited determinate growth, whereas female growth was indeterminate. Therefore, to simplify the comparisons of sexual to asexual productivity, among-strain comparisons of growth and reproductive measures were reported for females only.

Growth per female was estimated by subtracting the average wet weight of the juveniles added to a tank from the wet weight for each female at the completion of the experiment (Table 1). Proportion mature was calculated by calculating the proportion of females that produced mature or older (i.e., atretic) eggs per replicata tank. Fecundity was determined by totaling the number of mature and atretic eggs per female. Egg size per female was estimated by averaging the volumes of three randomly chosen mature eggs (when available).

Univariate analyses of variance and covariance were used to test for significant effects of density and fish-strain on growth, fecundity, egg size, proportion mature, and survival. An analysis of variance was also used to determine differences in starting size among treatments. Statistical analyses of survival percentages and proportion mature required arcsin, square-root transformations, and egg number required log<sub>e</sub> transformations to normalize distributions. Survival and proportion mature were measured on a per-tank basis, whereas growth, egg production and egg size were measured on a per-female basis. Survival was not a significant covariate of average



**Fig. 1.** Percent survival and growth of the three strains in high and low density treatments. Dashed lines are for the sexual strain, and solid lines are for clones. Error bars portray one standard error of the mean (—■— ML/VII; —▲— ML/VIII; -◇- *P. monacha*)

**Table 1.** Average values, sample sizes, and standard deviations of dependent variables. Weights are reported in milligrams wet weight, and egg volume is in microliters. Means with different superscripts are significantly different ( $P < 0.05$ )

	N	Low Density	N	High Density	Mean
<b>a Starting weight</b>					
ML/VII	72	10.8 ± 6.8	144	12.4 ± 9.0	11.9 ± 8.3 <sup>b</sup>
ML/VIII	72	10.5 ± 10.5	144	8.8 ± 6.9	9.4 ± 8.3 <sup>a</sup>
<i>P. monacha</i>	72	17.6 ± 10.7	144	17.7 ± 11.2	17.7 ± 11.0 <sup>c</sup>
Mean		13.1 ± 10.0 <sup>a</sup>		13.1 ± 9.9 <sup>a</sup>	
<b>b Ending weight</b>					
ML/VII	68	262.6 ± 76.4	129	176.4 ± 72.9	206.2 ± 84.6 <sup>a</sup>
ML/VIII	55	296.9 ± 102.3	116	179.6 ± 81.8	216.7 ± 104.0 <sup>a</sup>
<i>P. monacha</i>	32	317.1 ± 97.6	61	176.2 ± 69.2	224.7 ± 104.2 <sup>a</sup>
Mean		286.0 ± 92.9 <sup>a</sup>		177.6 ± 75.6 <sup>b</sup>	
<b>c Fecundity</b>					
ML/VII	18	3.4 ± 3.1	13	2.8 ± 2.4	3.2 ± 2.8 <sup>a</sup>
ML/VIII	20	5.0 ± 3.8	22	3.0 ± 1.5	4.0 ± 3.0 <sup>a</sup>
<i>P. monacha</i>	30	3.9 ± 2.6	30	2.1 ± 1.4	3.0 ± 2.2 <sup>a</sup>
Mean		4.1 ± 3.1 <sup>b</sup>		2.6 ± 1.7 <sup>a</sup>	
<b>d Egg volume</b>					
ML/VII	14	3.5 ± 0.7	8	3.4 ± 0.8	3.5 ± 0.7 <sup>b</sup>
ML/VIII	17	2.7 ± 0.8	8	2.9 ± 0.7	2.8 ± 0.7 <sup>a</sup>
<i>P. monacha</i>	24	5.5 ± 0.8	19	5.3 ± 1.0	5.4 ± 0.9 <sup>c</sup>
Mean		4.1 ± 1.5 <sup>a</sup>		4.3 ± 1.4 <sup>a</sup>	

growth, fecundity, or egg size. Residual analyses revealed both the size-corrected fecundity and egg size data were normally distributed, but the growth data was found to be non-normally distributed (leptokurtic). Therefore, the reported  $p$ -values for growth should be considered conservative.

End weight (weight at completion of the experiment) was found to be a significant covariate of egg production, and therefore was included as a covariate in one of the analyses of the fecundity data. The effect of end weight on egg production was similar in the three strains and at both densities, which satisfies the assumptions of the analysis of covariance test. Only females with mature or atretic eggs were included in the fecundity analysis. Neither end weight nor total egg production was found to be a significant covariate of egg size, and average end weight per replicate tank was not a significant covariate of proportion mature.

Density and strain treatments were considered fixed effects, whereas blocks and replicate tanks were considered random. No block-by-treatment interactions were found for any of the fitness measures analyzed. Therefore, treatment main effects were compared to the overall mean square error in the survival and proportion mature analyses, and to the tank mean square error in all other analyses.

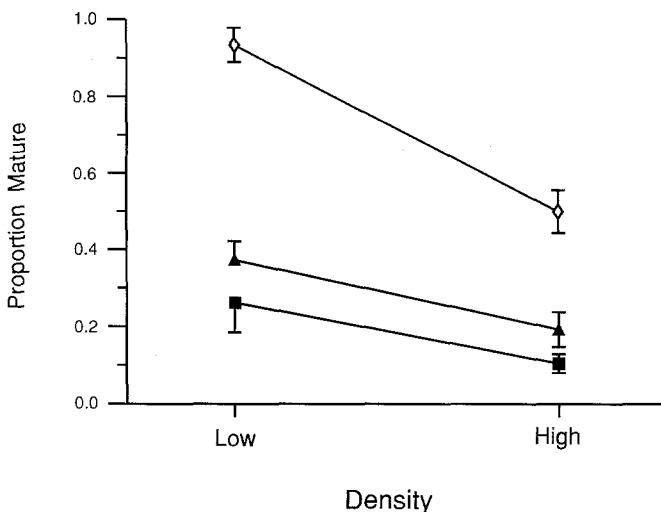
## Results

Survival was uniformly high in all three strains at both densities, ranging from a low of 58% to a high of 100% (Fig. 1). Both *P. monacha* and ML/VII had higher survivorship than ML/VIII ( $F_{(2,29)} = 7.28$ ,  $P = 0.003$ ). Survivorship was not affected by increased density ( $F_{(1,29)} = 0.05$ , NS), and all three strains were equally unaffected ( $F_{(2,29)} = 1.08$ , NS).

Initial weight of the three strains was consistent with offspring size at birth and egg size in these three strains

**Table 2.** ANOVA results for growth data. Mean-squared errors for block, density, strain, and density by strain interaction were tested against the tank mean-squared error to calculate appropriate F-ratios

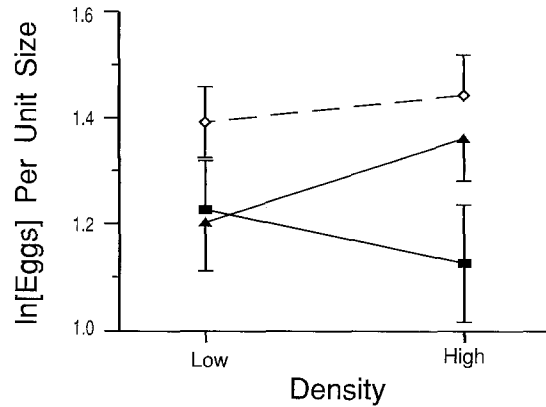
Source	df	Sum of Squares	F ratio	P-value
Block	1	0.001	0.11	0.7454
Density	1	1.203	107.25	0.0001
Strain	2	0.044	1.96	0.1584
Density*Strain	2	0.051	2.29	0.1190
Tank	29	0.325	1.79	0.0081
Error	428	2.687		



**Fig. 2.** Proportion of females in all three strains at high and low density that were reproductively mature. Dashed lines are for the sexual strain, and solid lines are for clones. Error bars portray one standard error of the mean (—■— ML/VII; —▲— ML/VIII; —◇— *P. monacha*)

(Weeks and Gaggiotti, 1993), in that *P. monacha* were larger than ML/VII, which in turn were larger than ML/VIII (Table 1). These initial differences in weight were unapparent at the end of the experiment (Table 1). Since growth rate (measured as an increase in biomass) was more sensitive to end weight than starting weight, there were no among-strain differences in overall growth (Table 2). However, growth was 70% greater, on average, at the low relative to the high density for all three strains (Fig. 1), and all three strains reacted similarly to increased density (Table 2).

The proportion of females sexually mature was significantly lower in the high relative to the low density treatments for all three strains ( $F_{(1,30)} = 39.03$ ;  $P < 0.0001$ ; Fig. 2). *Poeciliopsis monacha* had a greater proportion of reproductively mature females than either clone across densities ( $F_{(2,30)} = 56.50$ ;  $P < 0.0001$ ), but the decline in the proportion mature at the higher density was more pronounced in this strain ( $F_{(2,30)} = 6.54$ ;  $P < 0.004$ ; Fig. 2). These data indicate that *P. monacha* began investment in reproduction at an earlier age than the two clones at both densities, and the lack of a significant



**Fig. 3.** Least-squared means of the analysis of covariance of egg production corrected for body weight. Dashed lines are for the sexual strain, and solid lines are for clones. Error bars portray one standard error of the mean (—■— ML/VII; —▲— ML/VIII; —◇— *P. monacha*)

**Table 3.** ANOVA results for fecundity data. Mean-squared errors for block, density, strain, and density by strain interaction were tested against the tank mean-squared error to calculate appropriate F-ratios

Source	df	Sum of Squares	F ratio	P-value
Block	1	0.874	2.17	0.1515
Density	1	2.445	6.07	0.0199
Strain	2	0.994	1.23	0.3057
Density*Strain	2	0.302	0.38	0.6905
Tank	29	11.676	1.94	0.0086
Error	97	20.115		

**Table 4.** ANCOVA for fecundity data. Mean-squared errors for block, density, strain, and density by strain interaction were tested against the tank mean-squared error to calculate appropriate F-ratios

Source	df	Sum of squares	F ratio	P-value
End weight	1	11.181	120.15	0.0001
Block	1	0.027	0.23	0.6333
Density	1	0.028	0.24	0.6303
Strain	2	0.892	3.78	0.0349
Density*Strain	2	0.232	0.98	0.3865
Tank	29	3.427	1.27	0.1940
Error	96	8.934		

correlation with end weight reveals that this maturity response was not merely a reflection of differences in size.

Not only did the number of females producing eggs decrease at the high density, but the number of eggs per reproductive female was also reduced at the high relative to the low density in all three strains (Tables 1 and 3). When differential size was considered, it was clear that the decrease in egg production was due to decreased body size (Table 4, Fig. 3). The size-corrected egg production

**Table 5.** ANOVA results for egg size data. Mean-squared errors for block, density, strain, and density by strain interaction were tested against the tank mean-squared error to calculate appropriate F-ratios

Source	df	Sum of Square	F ratio	P-value
Block	1	0.387	0.62	0.4372
Density	1	0.069	0.11	0.7416
Strain	2	91.308	73.34	0.0001
Density*Strain	2	0.546	0.44	0.6493
Tank	28	17.430	0.80	0.7340
Error	55	42.710		

also revealed that *P. monacha* produced more eggs per unit weight than either clone at both densities (Table 4; Fig. 3). Egg size was not affected by increased density, but was different among strains (Tables 1 and 5). *Poeciliopsis monacha* had the largest eggs, being 96% larger than ML/VIII and 55% larger than ML/VII, on average (Ryan-Einot-Gabriel-Welsch multiple range test,  $P < 0.05$ ). ML/VII's eggs were an average of 26% larger than ML/VIII's eggs ( $P < 0.05$ ). It is possible that the differences in egg size were due to the two clones not having sufficient time to fully yolk their eggs. However, the observed differences are consistent with differences in starting size (Table 1), as well as previously reported differences in egg size between ML/VIII and *P. monacha* (Quattro and Weeks 1991) and differences among all three strains in offspring size at birth in a previous study.

## Discussion

This study clearly revealed different life-history responses in the three fish strains studied. In what follows, I will examine these life-history responses from two perspectives. First, I will examine how well the observed phenotypic plasticity within each strain is explained by life-history theory. Second, I will try to account for the obvious differences in reproductive investment between *P. monacha* and the two clones by considering the different habitats in which these three strains naturally exist.

### Within-strain comparisons

By examining life-history traits under various environmental conditions, one can quantify their environmental sensitivity, and note whether the observed plasticity appears adaptive or is merely "developmental noise" (Smith-Gill 1983; Reznick 1990; Travis 1992). Deciding whether observed plasticity is adaptive can be accomplished in a number of ways. One method is to show that the observed plasticity consistently responds to a set of environments, and that the resulting reaction norms are explainable in terms of current life-history theory (Reznick 1990; Travis 1992). A stronger case for an adaptive

plastic response is to observe a change in the underlying developmental processes determining the response (Smith-Gill 1983) or a change in energy allocation patterns associated with the response to different environments (Travis, 1992). Neither of these methods can unequivocally prove that the observed plasticity is truly adaptive, but they are steps in the right direction. Finally, the best method for deciding that a norm of reaction is adaptive is to demonstrate that the consequences of the plastic response positively impact individual fitness (Reznick 1990). In the current study, I use the first of these three methods by quantifying the phenotypic plasticity under these two density treatments, and then relate this plasticity to that predicted by life-history theory. The latter two methods must be left for more detailed future experiments.

Decreased growth rate is expected to affect both age and size at maturity (Gadgil and Bossert 1970; Stearns and Crandall 1984; Stearns and Koella 1986). How these two traits are affected depends on the effects of growth rate on age-specific survival (Stearns and Crandall 1984; Stearns and Koella 1986). Size at maturity was not measured in the current experiment, and therefore differences in size at maturity cannot be addressed. However, the prediction that decreased growth delays time to maturity (Gadgil and Bossert 1970; Stearns and Koella 1986) can be tested with the current data. All three lines decreased the proportion of mature females with increased density, reflecting increased age at maturity in females experiencing resource stress. Decreased food ration has also been shown to increase maturation time in a number of other studies (Scott 1962; Bagenal 1969; MacKay and Mann 1969; Hislop et al. 1978; Reznick 1990; Rowe and Thorpe 1990; Thorpe et al. 1990). Nevertheless, there are a number of reports of decreased growth associated with decreased age at maturity (Alm 1959; Pinhorn 1969; Meffe 1992), which is not predicted in any of the submodels of Stearns and Koella (1986). Therefore, either the organisms in the latter experiments were somehow constrained from exhibiting adaptive plastic responses, or the notion that decreased growth should concomitantly increase age at maturity needs to be modified to account for situations in which the opposite result holds.

Different environments can also cause differences in the patterns of resource allocation in growth and reproduction after investment in reproduction has begun. Decreased growth can cause lower residual reproductive value, and thus trigger higher current reproductive investment, if it causes reduced future survival (Fisher 1930; Williams 1966; Schaffer 1974). On the other hand, if growth has no effect on survival, increased resource availability is predicted to cause increased reproductive investment at all ages (Gadgil and Bossert 1970). Bagenal (1969) and Hester (1964) report increased reproductive effort with increased resource availability in brown trout and guppies, respectively, and Dahlgren (1979) reports increased gonadosomatic ratio with decreased density in guppies, which are consistent with Gadgil and Bossert's predictions. In the current study, increased density caused a nearly twofold reduction in growth and a 25% reduction in egg production in all three lines, but did not

cause a change in the relative investment in reproduction per unit body size. The lack of plasticity in size-specific reproductive allocation in the two density treatments for all three strains is contrary to expectations of Gadgil and Bossert (1970), but has no bearing on the reproductive value argument, since decreased growth had no effect on survival. The current results are consistent with those of Wootton (1973) in which sticklebacks reared on three dietary treatments showed decreased growth and egg production with increased resource stress, but exhibited constant reproductive allocation across all diets. Similarly, Reznick (1983) found that guppies raised on three dietary regimes decreased their absolute energy allocations to both reproductive and somatic tissues, but the ratios of the two remained constant across diets.

Another way in which an organism can respond to resource stress is by altering its packaging of reproductive investment per offspring. Environments with "poor" conditions might select for increased investment per offspring if that increase in investment confers increased offspring survival (Smith and Fretwell 1974; McGinley et al. 1987; Morris 1987; Winkler and Wallin 1987; Schultz 1991). This prediction has recently been supported by experiments with brook trout (Hutchings 1991). Organisms with high investment per offspring should be selected in highly competitive environments (Brockelman 1975; Morris 1987) or in environments with size-selective predation on smaller size classes (Reznick 1981, 1982; Reznick and Endler 1982). In the current study, there was no evidence that increased competition had any effect on egg size, nor was there a pattern of correlation of egg size and number. These results are consistent with a previous study on ML/VIII that showed no effect of either density or diet on egg size (Weeks and Quattro 1991). Since the differences in egg sizes among strains in this study exactly match the differences in offspring size of these same strains in a previous study (Weeks and Gaggiotti, 1993), we can predict that the observed egg sizes correctly reflect eventual offspring sizes, and therefore, that increased competition did not affect offspring size in these strains over the densities examined.

There is no consistent trend of changes in egg or offspring size with increased resource competition in other studies on fish. Bagenal (1969) found that brown trout produce smaller eggs when experiencing conditions of increased resources. Hislop et al. (1978) and Trendall (1983) found increased investment per offspring with increased resources in haddock (*Melanogrammus aeglefinus*) and mosquitofish (*Gambusia affinis*), respectively. Scott (1962), Hester (1964), and Wootton (1973) found no effect of food rations on reproductive investment per offspring in rainbow trout, guppies, and sticklebacks, respectively. Dahlgren (1979) found no consistent effect of ovum diameter with increased density in guppies. As for overall reproductive effort, experimental evidence on investment per offspring in resource-stressed fish remains ambiguous.

The lack of a consistent investment pattern in response to parental resource stress may be explained in three ways. First, the above patterns may indicate variable parent-offspring environmental correlations. The

current life-history models assume that resource stress for the parents is positively correlated with resource stress on their offspring. This need not be true. The strategies outlined above would be consistent with theory if natural parental conditions were positively correlated, negatively correlated, or uncorrelated with juvenile conditions, respectively. Accordingly, the current results with *Poeciliopsis* would be consistent with theoretical expectations if natural parental conditions were not correlated with juvenile conditions. Second, parents might be ineffective at perceiving offspring environmental conditions, or be constrained to develop a certain egg or offspring size regardless of environmental conditions, and therefore the prediction of an "adaptive response" of offspring size to environmental conditions may not be feasible for such parents (Via and Lande 1985; Morris 1987). Finally, the prediction that poor environments select for increased offspring size may be incorrect. Future examinations of investment per offspring should relate parental investment to offspring environmental conditions to better predict the adaptive responses of offspring size in the organisms examined.

#### *Among-strain comparisons*

As was repeatedly mentioned above, the lack of fit of the observed life-history plasticity to a number of theoretical predictions might be explained by either a lack of appropriate environmental "cues" for the appropriate parental investment or a developmental constraint on these characters. Yet, a consistent, long-term pattern of environmental differences in natural habitats should select for a suite of genetically determined life-history characters that are adaptive in these environments (Giesel 1976). Unfortunately, the manipulation of such long-term environmental conditions is difficult in long-lived organisms such as fish (but see Reznick et al. 1990), and therefore comparative analyses of populations assumed to have experienced long-term environmental differences are commonly used (e.g., Stearns 1983a, b, c).

In the current study, measurements of reproductive effort revealed a regular difference in investment strategies among strains over both treatments. *Poeciliopsis monacha* showed a consistent pattern of increased early reproductive effort relative to either ML/VII or ML/VIII; *P. monacha* matured earlier, had a higher investment in eggs per unit body size, and produced larger eggs than either clone. Clearly, *P. monacha* has a greater investment in early reproduction than either clone under these conditions. There were no consistent differences in any fitness related characters between the two clonal lines (but see Schultz and Fielding 1989).

There are a number of differences between these three strains that may account for such divergent reproductive schedules. It is possible that the observed differences are merely a reflection of phylogenetic differences among lineages, since the two clones are hybrids between *P. monacha* and another sexual strain, *P. lucida*. Of course this begs the question of why the closely related parental lineages have such dissimilar reproductive

schedules. Conversely, it is possible that these reproductive differences reflect different selective pressures in the environments in which these three strains naturally exist. The upstream habitats in which *P. monacha* are found are typically resource-poor and harsher than the downstream habitats of the two clones (Thibault 1974a; Thibault and Schultz 1978; Schenck and Vrijenhoek 1986). Thus, one might expect a shorter average lifespan in this environment, which is predicted to select for increased early reproductive effort (Williams 1966; Schaffer 1974). This could explain the observation of a decreased average age at maturity and increased investment per unit weight in *P. monacha* relative to the two clones. The upstream habitats may also have a higher likelihood of size-selective predation on the smaller size classes of *Poeciliopsis* due to the nearly 40-fold increase in numbers of predaceous aquatic insects (esp., *Buenoa arizonis*, see Thibault 1974a) and the cannibalistic tendency of *P. monacha* and its associated clones, which is significantly lower in the downstream habitats (Thibault 1974b; Weeks and Gaggiotti, 1993). Increased size-selective mortality in the upstream habitats should select for increased investment per offspring (Reznick 1981, 1982; Reznick and Endler 1982), which was found in this study. Therefore, it appears that the predictions of life-history theory are better reflected in the among-strain comparisons than in the within-strain comparisons. Future ecological examinations of these strains in their native environments should be undertaken to get a clearer picture of the differences in age-specific survival in these habitats so that precise life-history predictions can be tested.

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