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PHENOTYPIC PLASTICITY IN THE SAILFIN MOLLY, *POECILIA LATIPINNA* (PISCES: POECILIIDAE). II. LABORATORY EXPERIMENT

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Abstract.—Field studies indicate that the influence of environmental factors on growth rate and size and age at maturity in sailfin mollies (*Poecilia latipinna*) is inconsistent over time and suggest that the marked interdemic variation in male body size in this species is the result of genetic variation. However, the role of specific environmental factors in generating phenotypic variation must be studied under controlled conditions unattainable in nature. We raised newborn sailfin mollies from four populations in laboratory aquaria under all possible combinations of two temperatures, three salinities, and two food levels to examine explicitly the influence of these environmental factors. Males were much less susceptible than females to temperature variation and were generally less plastic than females in terms of all three traits. Members of both sexes matured at larger sizes and at later ages in less saline and in cooler environments. Food levels were not sufficiently different to affect the traits we studied. The effects of temperature and salinity were not synergistic. Males from different populations exhibited different average ages and sizes at maturity, but females did not. The magnitudes of the effects we found were not substantial enough to account for the consistent interdemic differences in male and female body size that have been observed previously. Our results also indicate that no single environmental factor is solely responsible for the environmental effects observed in field experiments on growth and development. These studies, together with other work, indicate that the strongest sources of interdemic variation are genetic differences in males and differences in postmaturation growth and survivorship in females.

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Variation among animal populations in life-history and morphological traits often has a substantial environmental component (James, 1983; Meyer, 1987; Patton and Brylski, 1987). In such cases, the spatial scale at which genetic differentiation exists may be very different from the scale at which phenotypic variation is observed. Substantial environmental effects, along with the possible effects of gene flow in "smoothing" differences among populations (Slatkin, 1973, 1978; Moody, 1981; Tachida and Cockerham, 1987), make it impossible to use observational data alone to answer the question, "at how fine a spatial scale can adaptive differences arise and persist?"

Correlative studies of environmental variation and trait variation cannot resolve the role of environmental factors. Correlations between graded differences among populations and differences in environmental variables have been used to infer both adaptive and nonadaptive differences (Ballinger, 1979; Chernoff, 1982). Historical effects cannot be separated from current environmental effects by survey data alone (Sokal, 1978), and even sophisticated statistical techniques are frequently ineffective at identifying one or a few key factors (Manly, 1985). In addition, the natural milieu of organisms is almost always a complex matrix of factors that may influence phenotypic variation in contrasting ways and covary among locations in a complicated fashion.

These considerations illustrate the need for an experimental approach in conjunction with survey studies to examine the problem of interdemic variation. Two kinds of experiments are necessary. The first focuses on the extent to which spatial variation in focal traits reflects spatial variation in environmental effects. Reciprocal-transplant experiments or common-garden experiments are examples. The second type of experiment attempts to identify specific factors in the environment that induce phenotypic variation. This is necessary if inferences from the first type of experiment are to be extended to the full range of environmental conditions a species experiences. Environmental factors that have opposite influences on a trait may covary positively among the "garden" conditions.

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At locations where one factor operates in the absence of the other, the phenotype may be very different from that supposed to be possible from the "known" effects of environmental variation. Experimental identification of key factors provides greater understanding of the outcome of both transplant experiments and correlative surveys of environmental variation and trait variation.

The sailfin molly, *Poecilia latipinna* (Pisces, Poeciliidae), offers an excellent opportunity to investigate the problem of interdemic variation. Populations exhibit a wide range of graded variation in body size and assorted other traits throughout the eastern half of the species' range (see references in the preceding paper [Trexler and Travis, 1990]). Differences among populations are independent of geographic proximity and are not strongly associated with any environmental differences (Trexler, 1986; Travis and Trexler, 1987). Experimental rearing in field enclosures indicates that, although environmental effects on juvenile growth rate and age and size at maturity exist, the differences induced by extremely different abiotic environments (relative to the range occupied by the species) are insufficient to account for the level of interdemic variation observed in natural populations (Trexler and Travis, 1990).

In this paper, we report the results of a laboratory experiment in which we manipulated the levels of three environmental factors that vary across the locations occupied by sailfin mollies. Our goals were to identify which factors contribute to environmental effects, to evaluate the strength of each factor, and to determine whether factors combine synergistically either to reinforce or to cancel each other's effects. We used fish from four different populations to maximize the diversity of genotypes represented in the experiment and, thereby, to avoid bias with respect to the sensitivity of particular genotypes to environmental effects (i.e., to allow for as much genotype × environment interaction as possible). The results of this study, in conjunction with the results of field experiments and geographic surveys, allow us to evaluate how environmental factors contribute directly to population variation in this species.

Materials and Methods

Experimental Design

We raised fish drawn from four populations from birth to sexual maturity in aquaria in which we varied temperature (two levels), salinity (three levels), and food (two levels) in a fully factorial design. These factors were deemed most likely to influence growth and development; they vary widely across locations where sailfin mollies persist (Trexler, 1986; Travis and Trexler, 1987) and have been shown to be important in many other fishes (Brett, 1979). Field experiments indicated that there is extensive variation at the family level (i.e., among broods from different females from the same population) for size and age at maturity and juvenile growth rates (see preceding paper [Trexler and Travis, 1990]). Therefore, we nested family groups within populations by raising one offspring from each family under every combination of environmental conditions studied. This design did not have replication within family and environmental conditions, and, therefore, family differences were not tested for significance. However, the design is not subject to bias from familial variation in testing hypotheses regarding environmental effects. The populations studied were Melanie's Pond (MP), Boat Factory Pond (BF), Boat Ramp Pond (BR), and Lighthouse Pond (LP).

Variation among populations in size at maturity, age at maturity, or growth rate must be subtle, if it exists, because none was detected in our field experiment (Trexler and Travis, 1990). We have attempted to maximize our power to detect population differences and to maximize the range of genotypes used in our study by drawing fish from four populations that experience very different environmental conditions (Fig. 1) and also differ dramatically in the size distributions of sexually mature males (Fig. 2).

Laboratory Procedures

Individual fish were raised in 18.8-liter aquaria from their day of birth to time of sexual maturity. Tanks were equally divided between two rooms, one maintained at 23°C and the other at 29°C. Fish were kept in well water raised to salinities of 2, 12, or 20 ppt by the addition of commercial aquar-

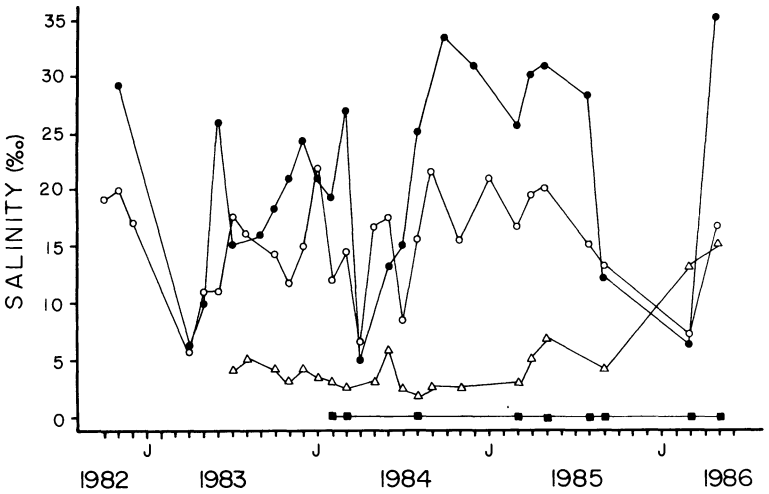

FIG. 1. Salinity over a four-year period in ponds from which pregnant female sailfin mollies were collected for this study. Different symbols represent different populations: △ = LP, ● = MP, ○ = BR, and ■ = BF.

ium seawater mix. The fish were fed one of two regimes: 1) the maximum ration the fastest-growing individuals of the initial cohort could eat in one day at a given age and 2) one-half that amount. Any excess food was removed daily before new food was added. Aerobic conditions were maintained by gentle stirring of the water as part of the daily food-removal procedure. The bottoms of all tanks were stirred and cleaned in this way irrespective of the obvious presence of food or wastes. Partial water changes were made at three-, six- and twelve-week points. When a fish reached six weeks of age, a commercial aquarium box filter containing activated carbon and aquarium filter floss was placed in its tank (six-week-old fish have reached a size that prevents them from becoming caught in the filter). The aquaria were illuminated by fluorescent aquarium bulbs on a 14L:10D cycle. The placement of tanks in each room was stratified to spread uncontrolled environmental variation as randomly as possible across treatments.

The standard length of each fish was measured at three weeks of age and weekly thereafter until maturation. Size and age at maturity were defined with the same criteria we used in the field studies (Trexler and Travis, 1990).

Data Analysis

Analysis of variance was used to analyze size at maturity, age at maturity, and growth rate; all factors were considered to be fixed effects, and family groups were nested within population. Both size and age at maturity were sufficiently skewed in distribution to require reciprocal transformation to fulfill assumptions of the analysis. Males and females were analyzed separately, because the genetic bases of size and age at maturity differ between the sexes (Travis et al., 1990). Growth rate was estimated from the slope of the curve of size versus age at an age two-thirds of that at maturity, following Travis et al. (1990). The use of growth rate at this point ensures that all fish are compared at the same developmental stage within each gender (see Bao and Kallman, 1982).

Males and females were randomly distributed across treatments, because the sex of newborns cannot be determined. This procedure unavoidably rendered the experimental design unbalanced. Sex ratios of broods are often skewed; it is not practical to replicate within families enough to balance the design of the experiment for the differences between genders.

The sums of squares for the various treatments obtained from a hierarchical extraction of terms are not orthogonal in an unbalanced design, i.e., the variation documented is not necessarily attributable to a single source (Sokal and Rohlf, 1981 pp. 293–308). Therefore, we undertook a series of hypothesis tests, each asking a different

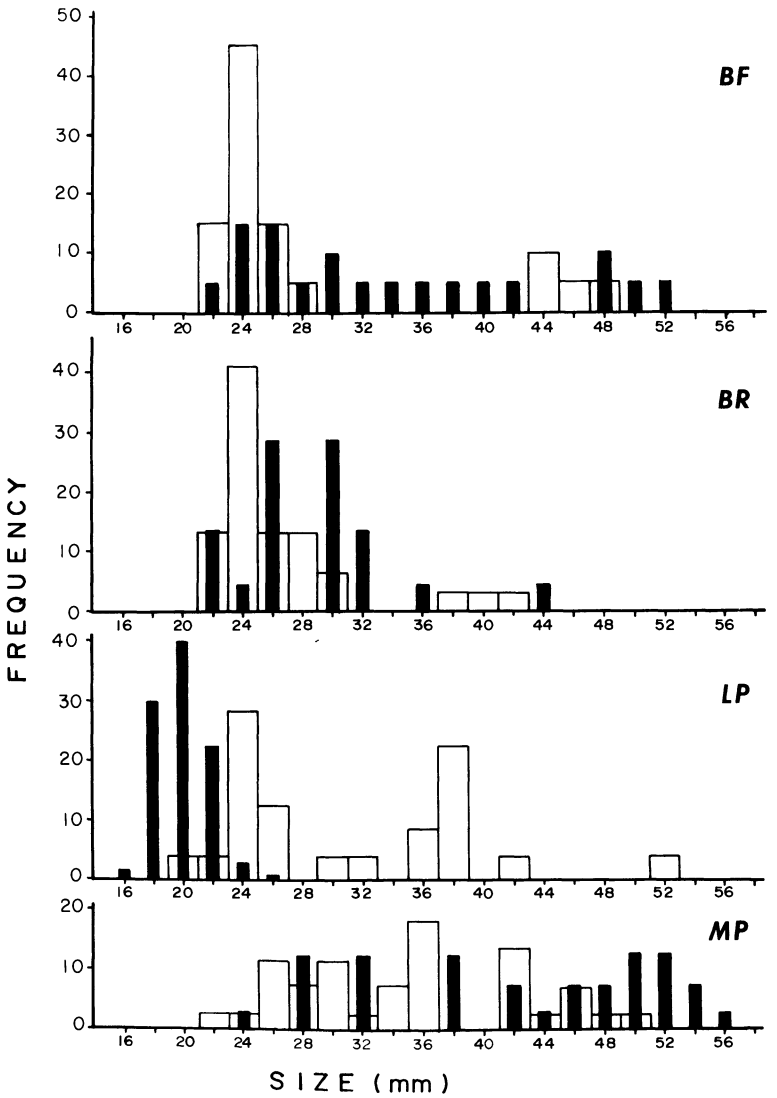

FIG. 2. Histograms of male size at maturity for each of the four study populations. Open bars represent laboratory-reared fish, and closed bars represent field-collected members of the same cohort used for lab study. Field data were obtained from males collected in July–August of the year; mothers of lab-reared fish were collected in April. Males grow little after attaining sexual maturity (Travis et al., 1989), so these sizes are indicative of their sizes throughout adult life.

biological question. First we asked whether any observed variation was attributable to the joint effects of our treatments (Draper and Smith, 1981 pp. 97–98). A finding of statistically significant joint effects would justify testing for specific treatment effects. When the joint effect of all treatments was significant, we proceeded to examine the relative contribution of the treatments by extracting sums of squares attributable to each treatment in four ways: 1) each term extracted individually as the first term in the model, 2) each term extracted second, after the effects of families within population were removed as a first term, 3) each term extracted after extraction of those other terms that were found significant by method 1, and 4) each term extracted as the last term, i.e., adjusted for all others regardless of whether the others were significant by method 1. The first method ignores confounding among variables to yield the

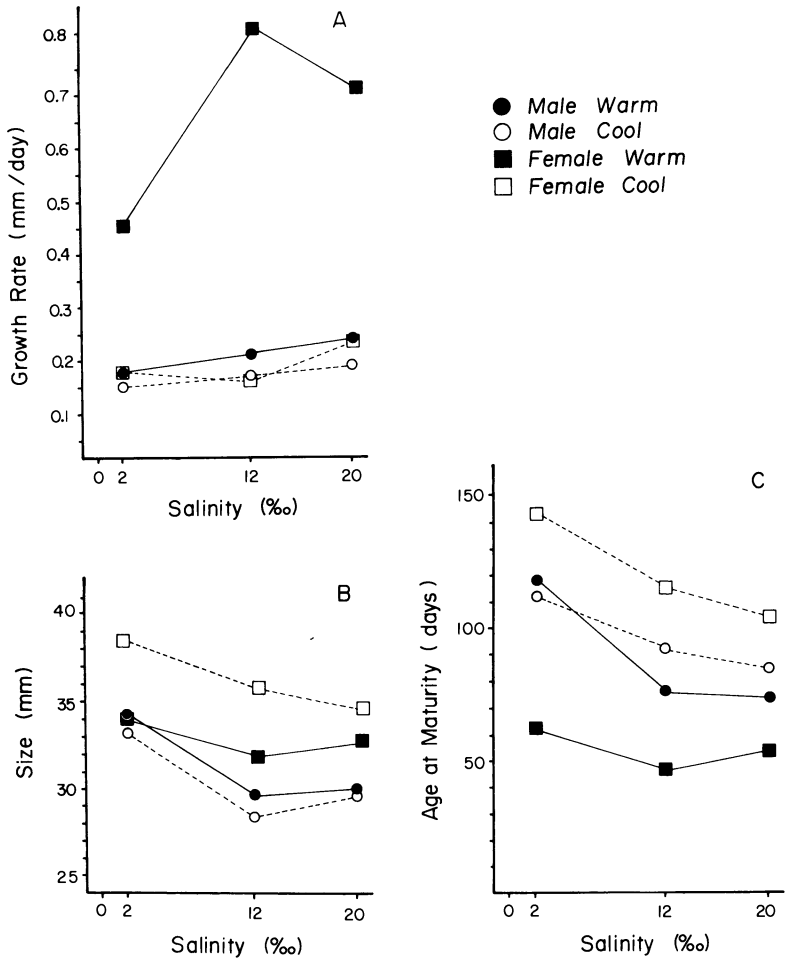

FIG. 3. Growth rate (A), size at maturity (B), and age at maturity (C) for male and female sailfin mollies reared from birth at warm (29°C) and cool (23°C) temperatures at three different salinities (reprinted from Trexler [1989]). Symbols are identified on the figure.

most powerful test of each term. The second method also ignores confounding among variables but attributes a major share of overall variation to families within populations. The third method assumes that variation attributable to terms not significant by the most powerful test should be considered to be merely random noise. The fourth method is extremely conservative. Because of the unbalanced design and the consequent complexity of the F tests, the probability levels for hypothesis tests cannot be applied strictly, and therefore we report in which of the four models a given hypothesis was significant at the $P = 0.05$ level.

Multivariate analysis of variance was used to explore the bivariate relationship between size and age at maturity. This technique can detect bivariate changes in size and age at maturity that may be small enough in each individual variable to remain undetected by univariate analysis (Timm, 1975). We used canonical loadings, the correlations of each variable with the score of the first discriminant function separating main effects, to evaluate the importance of each variable to any bivariate effect.

RESULTS

In all, 231 fish were raised to sexual maturity in this experiment: 108 males and 123

TABLE 1. Lists of statistically significant factors from ANOVA of males. Sums of squares were extracted in four ways: 1) each term extracted individually as the first term in the model, 2) each term extracted second, after the effects of family within population were removed as a first term, 3) each term extracted after extraction of those other terms that were found significant by method 1, and 4) each term extracted as the last term, i.e., adjusted for all others regardless of whether the others were significant by method 1. Method 1 is the least conservative, and 4 is the most conservative; methods 2 and 3 are intermediate. Dashes indicate that no factor was statistically significant. (Population differences could not be tested by method 2.)

Trait	Method of extracting sums of squares			
	1	2	3	4
Growth rate	salinity temperature × food salinity × food population × food	—	salinity temperature × food	—
Size at maturity	population salinity	salinity	population salinity	—
Age at maturity	population temperature salinity	temperature salinity	population salinity	—

females. All 48 combinations of population, temperature, salinity, and food level were represented for at least one male and one female. The joint effect of these four factors was significant for juvenile growth rate, size at maturity, and age at maturity for both males and females ($P < 0.025$ in each of the six cases). Therefore, we proceeded with the analysis of individual treatment effects.

Males

The growth rates of juvenile males do not vary among populations and are little influenced by environmental effects (Table 1). Salinity explains at most 8% of the total variation in male growth rates. Fish grew 35% faster at 20 ppt salinity than at 2 ppt and 13% faster at 20 ppt than at 12 ppt (Fig. 3A). Food level has a small effect through interactions with other factors (Table 1) but never explains more than 5% of the total variation. Only the temperature × food interaction is significant by a method of extraction other than method 1.

Male size at maturity differs among populations (Table 1, Fig. 2), and population differences may explain as much as 22% of the total variation in this trait. Size is affected by salinity, but the effect is small. Size at maturity is largest at the lowest salinity (Fig. 3B; 15% greater than at the two higher salinities), but salinity variation explains at most 4% of the total variation.

Age of males at maturity differs among populations (Table 1) and is also influenced by environmental effects: the influence of salinity is significant by three methods of analysis and that of temperature by two methods (Table 1). Temperature explains a greater amount of variation in this trait than does salinity (8% and 4%, respectively) when both terms are significant (method 1). In the high-temperature treatment, age at maturity was 44% higher at 2 ppt salinity than at 20 ppt; in the low-temperature treatment, this difference was 6% (Fig. 3C). Population differences exceed environmentally induced variation in these data (variation among populations explains 17% of the total variation in analysis by method 1).

Bivariate analysis indicates that salinity and temperature do not affect size and age at maturity similarly. No effect is significant when variance attributable to all other sources is removed first (method 4). According to analysis by method 1, temperature has a highly significant impact on the joint distribution of size and age at maturity (Wilks' lambda, $P < 0.0001$), primarily because of its influence on age at maturity (canonical loadings were approximately 0 for size and 0.47 for age). Population differences and salinity effects are less pronounced than temperature effects (Wilks' lambda, $P = 0.06$ and 0.07, respectively) and influence both size and age at maturity

TABLE 2. Lists of statistically significant factors from ANOVA of females. Sums of squares were extracted four ways: 1) each term extracted individually as the first term in the model, 2) each term extracted second, after the effects of family within population were removed as a first term, 3) each term extracted after extraction of those other terms that were found significant by method 1, and 4) each term extracted as the last term, i.e., adjusted for all others regardless of whether the others were significant by method 1. Method 1 is the least conservative, and method 4 is the most conservative; methods 2 and 3 are intermediate. Dashes indicate that no factor was statistically significant. (Population differences could not be tested by method 2.)

Trait	Method of extracting sums of squares			
	1	2	3	4
Growth rate	temperature salinity	temperature salinity	temperature salinity	temperature
Size at maturity	temperature salinity	temperature salinity	temperature salinity	—
Age at maturity	population temperature salinity	temperature salinity	temperature salinity	temperature

concordantly (canonical loadings for both factors exceeded 0.85).

Females

Variation in environmental factors had a large impact on female growth rates. Females grew 257% faster under warm conditions than under cool conditions and 50% faster at 12 and 20 ppt salinity than at 2 ppt (Fig. 3A). These effects were additive; no interactions were significant by any method (Table 2). Temperature variation explained as much as 47% of the total variation. Salinity influenced growth rate much less than did temperature, accounting for at most 4% of the total variation.

Size at maturity was influenced by the environment. Both temperature and salinity effects were statistically significant in analyses by three of the four methods (Table 2). Female size at maturity was 10% larger at 23°C than at 29°C and 8% larger at low salinity (Fig. 3B). There was no significant interaction of temperature and salinity. At most, temperature differences explain 9% of the total variation in size at maturity, and differences in salinity account for 7%.

Environmental factors also influenced the age at which females matured. Temperature effects were statistically significant by every method of analysis, and salinity effects were significant by all but the most conservative method (Table 2). The temperature effect dwarfed the salinity effect (by method 1, temperature differences accounted for 56.4% of the variation in female age at maturity, and salinity differences accounted for 4.1% of the variation). Females matured 127% later at 23°C than at 29°C. At both temperatures, maturation in the low-salinity treatment was delayed 30% compared to the two higher salinity treatments (Fig. 3C). There is some indication of population differences in these data, but these are statistically significant only by method 1.

In females, bivariate analysis reveals temperature and salinity effects in the joint distribution of size and age at maturity. Temperature effects were statistically significant by the most conservative analytical approach (method 4; Wilks' lambda, $P = 0.009$) and primarily affected age at maturity (canonical loadings: size = 0.19, age = 0.97). The salinity effect was less notable (method 4; Wilks' lambda, $P = 0.07$) and resulted from effects on both size and age at maturity (canonical loadings: size = 0.97, age = 0.63). The testing of hypotheses following method 1 gives similar results in this case.

DISCUSSION

Comparison of Males and Females

Females were much more labile than males in terms of all three traits examined. Over 50% of the total variation observed in female age at maturity and growth rate can potentially be explained by environmental factors. In males, less than 12% of the vari-

ation in age at maturity and less than 9% of the variation in growth rate can be explained by environmental factors. Size at maturity is a less labile trait than age at maturity or growth rate in both males and females, but the difference between the sexes persists. Environmental factors explain as much as 12% of the total variation in female size at maturity but no more than 4% of the variation in that trait in males.

Females were much more susceptible to temperature effects than were males, especially in terms of age at maturity and juvenile growth rate. Males and females were influenced similarly by salinity, but its effect appears to be larger in males because of the lack of temperature effects. The direction of temperature and salinity effects is similar, on average, in the two sexes for each trait studied.

The variation among families in size and age at maturity is greater for males than for females. The average sum of squares (SS) attributed to variation among families within populations in males is more than twice as large as that in females ($SS_{males} = 1.063$ and $SS_{females} = 0.437$ by method 1). As a result, the test of the hypothesis that there are no effects of population is more conservative for males than for females, because the family-within-population mean square is the denominator for that test. Nonetheless, male size and age at maturity differed significantly among populations, but neither trait did so in females. It seems likely that the differences in average size at maturity among populations reflect differences in the frequency of male maturation genotypes (Travis et al., 1990). This interpretation must be made with caution, however, as maternal environmental effects are confounded with population differences in this study. The mothers of the fish we raised were collected from the field in an advanced stage of pregnancy.

We do not believe that maternal effects are likely to yield differences among populations in male size at maturity of the magnitude that we have observed. If maternal effects were the source, they would have to affect males and females differently. Forster-Blouin (1989) documented maternal effects on the poeciliid *Heterandria formosa* by raising females from birth to parturition of their offspring under markedly different temperatures and then raising the offspring in a common environment. She observed a statistically significant effect of maternal environment on age at maturity, but the magnitude of the effect was small, and it explained only about one percent of the total variation. Additionally, the effect was limited to female offspring and only one of several life-history parameters examined was affected.

Comparison with Other Poeciliids

The patterns of plasticity that we have documented for *P. latipinna* are similar to those found in some poeciliid species but different from those in others. *Xiphophorus maculatus* males mature at similar sizes in different densities of conspecifics, though maturation is delayed and growth rate is decreased under high-density conditions. Female *Xiphophorus maculatus* were plastic in terms of both size and age at maturity (Kallman and Borkoski, 1978). Borowsky (1987) reported a pattern of plasticity for *Xiphophorus variatus* that is similar to that reported here for *P. latipinna,* but results for females were not reported. Stearns (1983) found that *Gambusia affinis* mature later under freshwater conditions than under more saline conditions (as do *P. latipinna*) but at a similar size (unlike *P. latipinna*). Male and female *G. affinis* respond similarly, again unlike the pattern in mollies. Both male and female *G. holbrooki* mature sooner and smaller at 32°C than at 25°C. The percentage decrease in size is similar in the two sexes (G. K. Meffe, unpubl.). The direction of the response to temperature variation in these fish is similar to that in *P. latipinna,* but the similarity of the response between sexes is unlike the pattern in *P. latipinna.*

The Significance of Environmental Effects in P. latipinna

Repeated geographic surveys of size variation in sailfin mollies have not established a consistent relationship between habitat characteristics and size variation (Trexler, 1989). Qualitative surveys on more limited spatial and temporal scales have suggested that average male size increases with increased salinity (Hubbs, 1942; Swift et al.,

1977; Loftus and Kushlan, 1987). The effect of salinity found by Zimmerer (1983) seemed to support this conclusion. These studies have focused on male size because males grow very little after reaching sexual maturity (Snelson, 1982, 1985; Travis et al., 1989), and variation among populations is, therefore, not confounded with age structure. We have shown that male size is relatively uninfluenced by environmental conditions and that genotypic differences are much more pronounced than the direct effects of salinity. Male size variation is based on a Y-linked allelic series and autosomal modifiers (Travis et al., 1990). If average male size is relatively large in habitats that are more consistently saline, it is because genotypes that produce large males are common in those sites. The local distribution of such sites indicates that this reflects some type of adaptive differentiation (Trexler, 1986, 1989). The phenomenon is certainly not a case of direct environmental induction. Female size is highly correlated with male size in natural populations (Travis and Trexler, 1987), despite different genetic bases of size variation (Travis et al., 1990) and large differences in the level of plasticity between the sexes. We interpret this correlation as suggestive that some size-selective factor is determining male and female size variation in adult sailfin mollies (Trexler, 1989).

Our results suggest that temperature variation has a greater impact on the traits studied than does salinity. However, before making such a claim, we must demonstrate that we varied these factors on a scale relevant to variation in nature (Lewontin, 1974). We varied salinity within the range of salinities experienced by mollies in the populations from which we collected our stocks (Fig. 1). Our temperature range was also within that experienced by most molly populations in northern Florida in the spring and summer, although we have collected sailfin mollies from water as warm as 36°C. We have not been able to assess natural food levels, so our ability to relate our results from this experiment to nature is limited. Our experimental results suggest that seasonal temperature fluctuation should yield greater environmentally induced variation in the traits we studied than should natural levels of salinity variation, particularly for females. This conclusion is supported by the marked seasonal effects we have observed for fish raised in field cages (Trexler and Travis, 1990).

Our field study (Trexler and Travis, 1990) produced results that differ from those that would be predicted from the laboratory results reported above. The field study documented that, on average, fish raised in a freshwater pond mature later and at a smaller size than those raised in a saltwater pond. The laboratory study indicates that size and age at maturity are positively correlated across a range of temperature and salinity variation; a pattern of decreased size with increased age at maturity is not predicted. It is possible that patterns of survival, rather than growth, produced the different results in these two studies. In the laboratory, there was less than 5% mortality prior to maturation; mortality in the field cages was on the order of 60%, and was generally of unknown cause.

In the laboratory, the average size of males at maturity differed among populations, but the differences do not mirror those seen in the parental populations (Fig. 2). In particular, we raised males of a much larger range of sizes from LP than were ever collected there, and we raised males from BR that were smaller on average than males usually collected there (see also Farr et al. [1986]). These two populations are closely adjacent, and they are very similar allozymically (Trexler, 1988). The limited plasticity in male size at maturity suggests that the difference between lab and field involves a change in the frequencies of the male maturation genotypes between birth and the subsequent adult cohort. This scenario is compatible with a hypothesis of a balance between gene flow and selection that maintains local distinctions in male size and age at maturity. Extensive gene flow would also preclude evolution of independent norms of reaction in each population; there is no evidence of any such distinctions among populations, although there are genotype × environment interactions within populations that could provide the raw material for such distinctions. Estimations of the actual levels of present-day gene exchange among populations and the ecological bases for local

selection should be the object of future research into interdemic variation in these animals.

Acknowledgments

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