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PHENOTYPIC PLASTICITY IN THE SAILFIN MOLLY, *POECILIA LATIPINNA* (PISCES: POECILIIDAE). I. FIELD EXPERIMENTS

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Abstract.—Sailfin mollies (*Poecilia latipinna*) display marked interdemic variation in body size. We employed "common-garden" experiments in field enclosures to explore the potential role of environmental factors in determining the interdemic phenotypic variation in growth rate, age at maturity, and size at maturity. The largest single, consistent source of variation for all traits was family identity within populations. Environmental effects acted predominantly through family × environment interactions. There was little evidence for any intrinsic variation among populations once family heterogeneity had been accounted for. In general, when statistically significant differences existed, fish raised in a saltwater pond grew faster than their broodmates raised in a freshwater pond. Both males and females tended to mature at a smaller size and later in the freshwater pond than in the saltwater pond. The effects of the environmental conditions differed among the three years in which we performed these studies. In only one year was there a substantial difference between fish raised under the two environmental conditions. These results indicate that direct environmental effects are not strong enough to account for the differences in body size among natural populations and that intrinsic differences among natural populations are due to different frequency distributions of genotypes that are present in all populations.

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Variation in life-history traits among conspecific populations is a ubiquitous phenomenon that raises two sets of questions. First, how much of the observed variation has a genetic basis, and what is the nature of that basis (number of loci involved, extent of fixed allelic differences, presence of distinct coadapted gene complexes)? Second, to what extent does any genetic differentiation represent an adaptive response to different demographic conditions that select for different life-history patterns?

A definitive answer to the first question is not easy to obtain. The initial problem is to quantify precisely the actual extent of phenotypic variation among populations. A single population can display annual (Tinkle et al., 1981; Healey and Dietz, 1984) or even seasonal (Hubbs et al., 1968; Bagenal, 1971; Nussbaum, 1981) variation in life-history traits, and differences among a set of populations may be observed in some surveys but not others (Wyatt and Antonovics, 1981). Once precise phenotypic distinctions are established, it may prove difficult to partition the total variance experimentally into independent "genetic" and "environmental" components. A variety of environmental factors directly influence the phenotypic expression of life-history traits (Dahlgren, 1979; Hirshfield, 1980; Reznick, 1983; Townsend and Wooton, 1984; Bernays, 1986), and genetic differences among populations in the developmental response to environmental factors can cause phenotypic differences among populations to be more pronounced under some conditions than others (Berven et al., 1979; Conover and Heins, 1987; Coyne and Beecham, 1987). In extreme cases, genetic differences may be expressed only under specific environmental conditions (Clare and Luckinbill, 1985).

The study of the sailfin molly, *Poecilia latipinna* (Poeciliidae), offers an excellent opportunity to examine these issues. Populations in the eastern half of the species' range occupy a wide variety of habitats and exhibit phenotypic variation in a variety of life-history traits. Variation among populations in reproductive traits (e.g., brood size, level of viviparity) is not extensive, and the repeatability of observed differences among populations is probably low (Trexler, 1985; Travis and Trexler, 1987). In contrast, male body size varies widely among individual

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populations (Hubbs, 1942; Kilby, 1955; Hubbs, 1964; Simanek, 1978; Snelson, 1985); differences among populations are repeatable despite seasonal variation, and those differences are completely unrelated to geographic proximity (Snelson, 1985; Trexler, 1986; Travis and Trexler, 1987). Variation in adult male size is almost completely determined by variation in size at maturity (Travis et al., 1989). Size of males at maturity is highly heritable; a series of Y-linked factors and autosomal modifiers govern the variation in size and age and maturity concomitantly, such that later maturation is tightly genetically correlated with larger size (Travis et al., 1990*a*). Female body size has patterns of interdemic variation that are similar to those for male body size, but the patterns in females are less repeatable over time (Travis and Trexler, 1987). Variation in female body size within a population is largely the result of age structure and adult growth; little genetic variation for size and age at maturity can be detected within populations (Travis et al., 1990*a*).

In this paper, we report the results of field studies designed to investigate the extent to which variation in juvenile growth rate, size at maturity, and age at maturity has an environmental basis. These studies consist of four "double common-garden" experiments; in each experiment we compared growth and development from birth in individuals from two different populations reared under two field conditions that represent the extremes from the range of environments that are normally experienced by the species. In the following paper, Trexler et al. (1990) report the results of a laboratory experiment designed to examine the responses to specific environmental factors that may be responsible for the results reported here.

Materials and Methods

Experimental Design

We raised fish in cages placed in two ponds at the St. Marks National Wildlife Refuge in northern Florida. These ponds represented the extremes of salinity and associated conditions that mollies experience in northern Florida (Travis and Trexler, 1987). One was a freshwater borrow pit with a sand and limestone bottom; it harbored emergent *Typha* sp. and a diversity of submerged plant species. The second was a tidally influenced marsh pond with a bottom of fine mud and flocculent material and a salinity of 12–20 ppt; it was bordered by emergent *Juncus roemerianus*. We refer to these ponds as "freshwater" and "saltwater" for brevity. The study ponds differ in many ways, and, therefore, no single environmental factor can be interpreted as influencing or failing to influence growth and maturation. These experiments examine the extent to which the extremes of the habitat gradient that mollies occupy affect these traits.

We collected gravid female mollies from two different locations for each experiment and maintained them in the laboratory until they gave birth. Females were chosen to represent the full size range of sexually mature females from each sampling location. Travis et al. (1990*b*) found that more than half (but not all) of the sailfin molly females they examined were multiply mated, so members of the families used in this experiment were related at least as half-sibs. Nongenetic maternal effects and genetic differences among families are confounded by use of field-collected females, but we chose to use them to examine the strength of any environmental effect on fish in relation to the ways in which genetic and maternal effects are expressed in natural populations.

The habitats occupied by the populations from which we drew fish were similar to one or the other of our experimental ponds. The Melanie's Pond (MP) population (used in all four experiments) and the Boat Ramp Pond (BR) population (used in fall 1984 and summer 1985) occupy saline tidal marsh ponds (salinities range from 12 to 32 ppt) with muddy bottoms and emergent *Juncus roemerianus* and *Spartina alterniflora*. The Tram Road Pond (TR) population (used in summer 1983) occupies a brackish (0–4 ppt) canal atop a sand and limestone base, whereas the Boat Factory Pond (BF) population (used in summer 1984) occupies a freshwater springhead in the St. Marks River along a limestone bank. Thus, our experiments include two comparisons of populations from similar habitats and two comparisons of populations from different

habitats, each comparison being made under two environmental conditions (one corresponding to the habitat type occupied by MP and BR and the other corresponding to the habitat type occupied by BF and TR). We used the same experimental ponds in all four experiments; thus, we can examine the role of temporal variation in the environment by comparing the MP rearings across both environments in the four experiments.

The number of families studied varied among experiments, dependent upon availability of gravid female mollies in the field and limited by the number of cages available (60). In summer 1983, we used the offspring of four females from the MP population and four females from the TR population. In summer 1984, we used the progeny of six females from the MP population and five females from the BF population. Three females from the MP population and three females from the BR population provided offspring for the autumn 1984 study. Finally, in the summer 1985 experiment, the progeny of six MP females and five BR females were studied. In two instances, summer 1984 and summer 1985, more than 60 cages were required, but early-maturing fish and mortality provided the empty cages needed. Except in the fall 1985 experiment, all fish were placed in the field within a period of thirty days, and in general, the temporal separation among families was kept as low as possible.

The cages were 75 cm × 75 cm × 90 cm and were placed in water with an average depth of approximately 60 cm. The cages were constructed of wooden frames covered by linear polyethylene screen. Eighteen members of each brood were randomly distributed between two groups, one destined for the freshwater habitat and one for the saltwater habitat. Each of these groups was in turn divided into three smaller groups of three; each of these groups of three was placed in a different field cage. Thus, each family had three offspring in each of three different cages in each of two ponds. Each cage contained three fish, all from the same family and related at least as half-sibs. (In the summer 1983 experiment, five fish were placed in each cage. The number was reduced to three for subsequent experiments to allow the use of smaller broods and because three were found to be adequate to assure survival of at least one fish per cage.) Crowding was not considered to be a problem in these experiments. Farr and Travis (1989) have found no evidence for social effects on size or age at maturation among juvenile mollies raised in the laboratory at higher densities than we employed here.

In every experiment, fish were placed in cages within two days of birth. Two experiments were prematurely terminated: in 1983 we were able to study only juvenile growth patterns, and the summer 1985 experiment was destroyed after 14 weeks by Hurricane Elena.

Mollies in field cages were exposed to natural conditions with the exception that predators were excluded. Mollies are primarily herbivores (Harrington and Harrington, 1961), and experimental fish fed on the algae that grew in the cages. Once a fish reached three weeks of age, it was removed from its cage weekly, and its standard length was measured to the nearest 0.5 mm. Size at three weeks of age was used as a measure of juvenile growth rate. Size at maturity in males was defined as the size after which three succeeding weeks passed without measurable growth and after formation of a gonopodium was recorded. Age at maturity was that age at which a male first attained his final size, provided the gonopodium was completely formed, or the age at which the gonopodium was completely formed if that event did not precede the effective cessation of growth. Female maturity was marked by the appearance of a black spot over the gonopore. We measured size as standard length rather than as weight because weight confounds somatic growth with fat storage (Reznick, 1983).

Data Analysis

Juvenile growth rate, size at maturity, and age at maturity were examined for heterogeneity among family groups within and among populations by analysis of variance (ANOVA). Family groups were nested within population of origin for this analysis (Snedecor and Cochran, 1980 pp. 248–250). The data were log-transformed to fulfill the assumptions of the analysis. In autumn

1984, neonates were obtained over a period of two months, and those originating from MP were obtained before those of BR. Therefore, differences in origin were confounded with time of placement in the field for that experiment. The sum of squares for each term was extracted as the last one removed from the model, because all designs are unbalanced (type-III sums of squares; Milliken and Johnson, 1984 pp. 146–151). This is the most conservative method for testing each hypothesis. The sexes are strongly dimorphic and have different genetic bases for variation in size and age at maturity within a population (Travis et al., 1990*a*); therefore, we analyzed data for the sexes separately.

Univariate analysis of size and age at maturity indicated that there was extensive interfamily variation, such that tests of environmental effects had low statistical power. In addition, these analyses may not have detected strong bivariate effects resulting from small simultaneous shifts in both size and age. We have employed a multivariate analysis of variance (MANOVA) (Timm, 1975), pooled across families and populations, to test whether any effects of environment arise in this fashion. The pooling procedure yields a much larger error matrix for the statistical test of environment than we would normally have, thereby making this procedure a conservative one. We report the "canonical loadings" for each variable for each statistically significant result; these loadings are the correlations of the first discriminant-function score with each dependent variable (Timm, 1975).

Results

Juvenile Growth

The single most important influence on juvenile growth was family identity (Fig. 1, Table 1), which explained a minimum of 15–36% of the total variation, depending upon the experiment. In 1983 and 1985, environmental effects acted only through family × environmental interactions of varying strengths. The effects of differences in environment (as a main effect) were significant twice but never explained as much as 10% of the overall variance. Differences among populations approached statistical significance in the fall 1984 experiment, but this effect was more likely to be due to the difference in the time when fish from the different populations were placed in their cages than to any innate interpopulation differences. In 1985, the lack of a significant population effect was attributable to the relatively rapid growth of one family from BR (Fig. 1D).

In three of the four repetitions, the data generally indicated more rapid growth in the saltwater pond (Fig. 1A, B, C). In 23 of 24 families in those three experiments, siblings either grew faster in the saltwater environment or grew equally well in both environments, depending upon specific family identity. The differences were statistically significant in the summer 1984 and fall 1984 experiments (Table 1). There is no convincing evidence from these experiments that families from one population grew faster than those from other populations and no evidence that fish from "saltwater" and "freshwater" populations were differentially adapted to grow best in the "correct" environment.

The results of the summer 1985 experiment are different. Three of the five BR families and two of the six MP families grew better in the freshwater pond (Fig. 1D). In addition, family performance was more clearly related to source population. The data from this repetition provide the only evidence for any biologically significant family × environment interactions; there is no evidence, however, that the different family responses to the environmental conditions represent differentiation of the source populations.

The comparative performance of MP fish across the four experiments suggests that annual environmental variation plays a large role in juvenile growth patterns (Table 2). First, fish born late in the breeding season grow poorly (fall 1984 data compared with others). Second, the extent to which the two environments induce different growth rates varies across years (three summer repetitions). In only one year (1984) did the growth differences between environments appear to be substantial enough to be both statistically and biologically significant (Table 1: fall 1984, row 2).

We draw four conclusions about juvenile

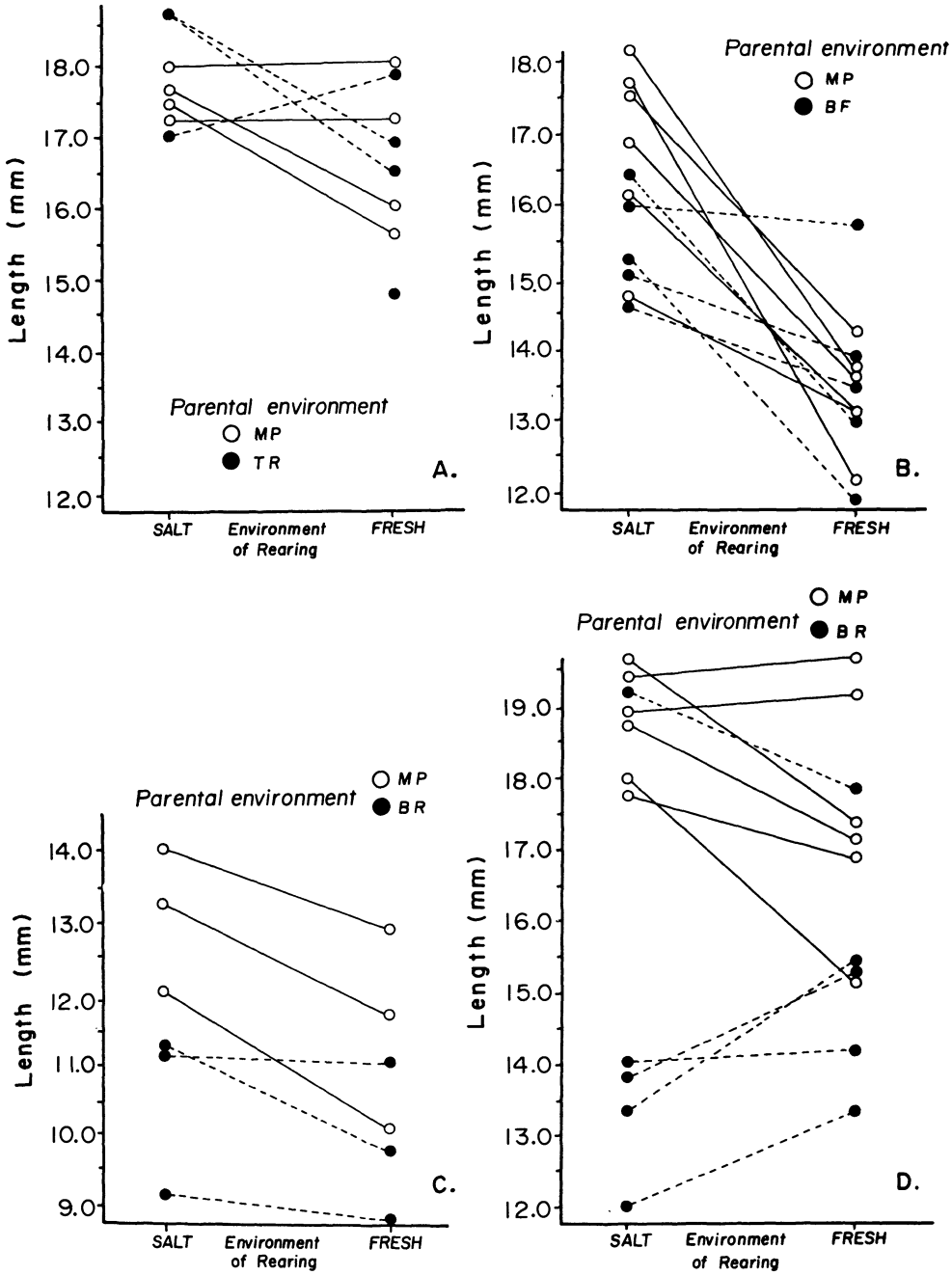

FIG. 1. Juvenile growth rates, measured as standard length at three weeks of age, by population of origin and environment experienced during rearing. Family averages are plotted. Parental environment is indicated by open or closed symbols as noted in each graph. Dashed and solid lines connect family averages from different populations, unless no fish survived in one of the two ponds. A) Summer 1983 experiment; B) summer 1984 experiment; C) fall 1984 experiment; D) summer 1985 experiment.

TABLE 1. Analysis of variance for juvenile growth rate. Results from four experiments are reported. The habitat types compared in each analysis are indicated at the top of each ANOVA table. Numbers given in parentheses for denominator mean square correspond to row numbers. CD = coefficient of determination.

Row	Source	SS	*d.f.*	Denominator MS	*F*	*P*	CD
Summer 1983; saltwater versus freshwater population (MP vs. TR):							
1	Population (P)	0.016	1	(4)	1.63	ns	—
2	Environment (E)	0.000	1	(5)	0.00	ns	—
3	P × E	0.008	1	(6)	2.13	ns	—
4	Family within P	0.059	6	(6)	2.45	0.05	0.21
5	(Family within P) × E	0.056	5	(6)	2.79	0.04	0.20
6	Within cells (error)	0.112	28				
Summer 1984; saltwater versus freshwater population (MP vs. BF):							
1	Population (P)	0.004	1	(4)	0.27	ns	—
2	Environment (E)	0.086	1	(5)	8.25	0.02	0.09
3	P × E	0.022	1	(6)	3.92	0.05	0.02
4	Family within P	0.149	9	(6)	2.89	0.01	0.15
5	(Family within P) × E	0.093	9	(6)	1.81	ns	—
6	Within cells (error)	0.195	34				
Fall 1984; two saltwater populations (MP vs. BR):							
1	Population (P)	0.269	1	(4)	5.58	0.06	0.38
2	Environment (E)	0.027	1	(5)	7.77	0.04	0.04
3	P × E	0.000	1	(6)	0.00	ns	—
4	Family within P	0.241	5	(6)	12.05	0.00	0.34
5	(Family within P) × E	0.017	5	(6)	0.87	ns	—
6	Within cells (error)	0.092	23				
Summer 1985; two saltwater populations (MP vs. BR):							
1	Population (P)	0.002	1	(4)	0.03	ns	—
2	Environment (E)	0.025	1	(5)	2.79	ns	—
3	P × E	0.000	1	(6)	2.79	ns	—
4	Family within P	0.464	9	(6)	18.85	0.00	0.36
5	(Family within P) × E	0.079	9	(6)	3.21	0.01	0.06
6	Within cells (error)	0.101	37				

growth rate: 1) growth rate is low for fish born late in the season; 2) environmental effects on growth rate are biologically significant only in some years; 3) when environmental effects are significant, fish grow better in the saltwater environment; and 4) variation among family groups, which is sometimes (but not usually) related to source populations, is the major source of growth-rate variation and any genotype × environment interactions.

TABLE 2. Average size of sailfin mollies from Melanie's Pond (MP) at three weeks of age from each of four experiments.

Experiment	Standard length (mm)	
	Fresh water	Salt water
Summer 1983	16.7	17.6
Summer 1984	13.3	16.8
Fall 1984	11.5	13.1
Summer 1985	17.5	18.7

Female Size and Age at Maturity

Variation among families, regardless of source population, was the only significant source of phenotypic variance in female size and age at maturity, accounting for ~35% of the variance in age at maturity and up to 50% of the variance in size at maturity (Fig. 2, Table 3). There is no indication of intrinsic distinctions among populations in these traits.

The bivariate analyses indicated an environmental effect that acted jointly on age and size at maturity, but only in 1984. Females matured sooner and at a larger size in the saltwater environment than in the freshwater environment in 1984 (bivariate analysis, Wilks' lambda $P = 0.007$; Table 4, Fig. 3). There were no such effects de-

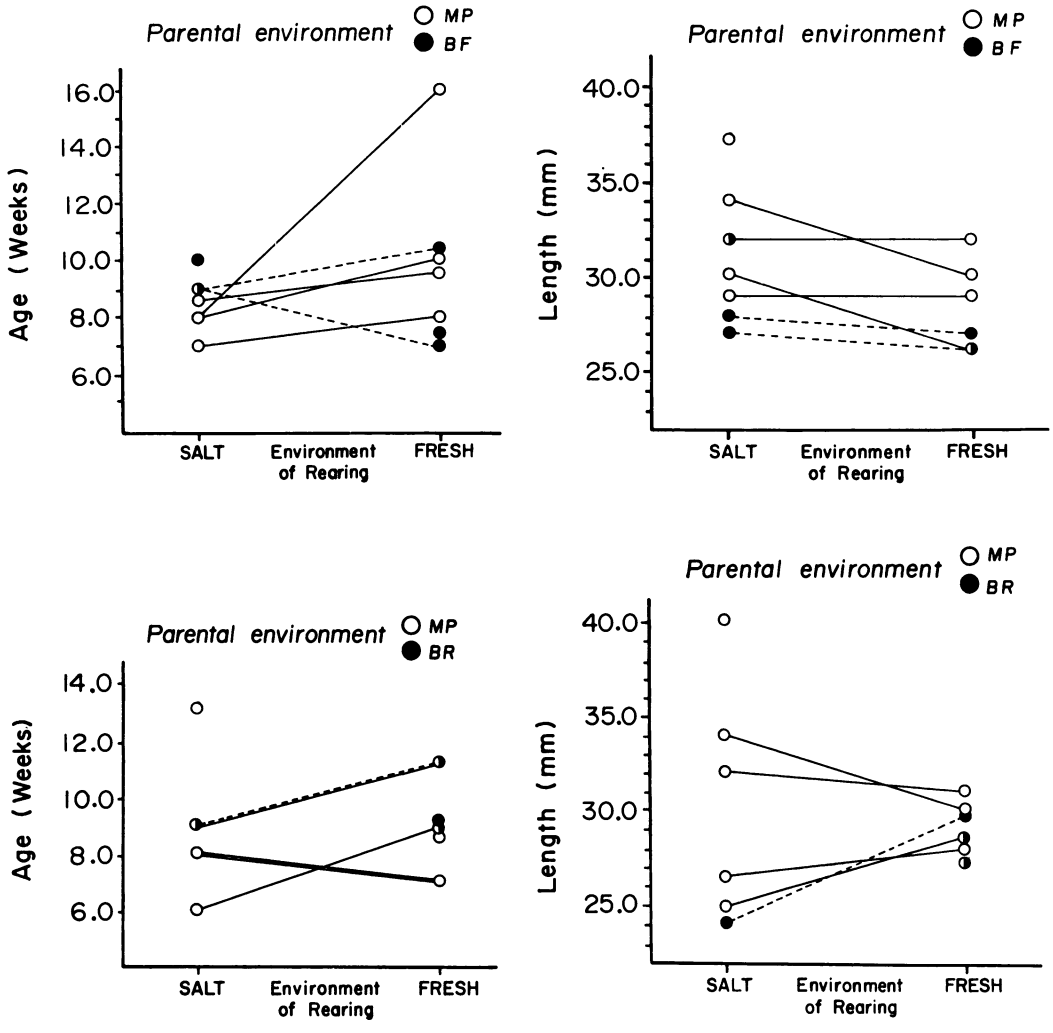

FIG. 2. Age (left-hand panels) and standard length (right-hand panels) of females at sexual maturity by population of origin and environment experienced during rearing. Family averages are plotted. Parental environments are indicated by open and closed symbols as noted on the figure. Dashed and solid lines connect family averages from different populations, and half-closed circles indicate overlapping points from different populations. Isolated points represent replicates in which no fish survived in one environment. The upper two graphs represent the summer 1984 experiment; the lower two graphs represent the summer 1985 experiment.

tectable in 1985 (bivariate analysis, Wilks' lambda $P = 0.493$; Table 4, Fig. 3). Size and age at maturity contributed equally, though in opposite ways, to the significant result observed in 1984 (canonical loadings: size $= -0.599$, age $= 0.483$).

Male Size and Age at Maturity

Families within populations represented the major source of variance in male size and age at maturity (Fig. 4, Table 5). There was no indication of further differentiation among populations. The average sizes of field-collected males from each of the three populations in these experiments are larger than the mean for all populations (Trexler, 1986; Travis and Trexler, 1987), so this experiment is a very weak test for local genetic differentiation. Family-level variation accounted for 50% of the variance in age and 33–64% of the variance in size. Family × environment interactions contributed an additional ~25% of the variance in age and 20% of the variance in size.

TABLE 3. Analysis of variance of female size and age at maturity from the summer 1984 and summer 1985 experiments. One population inhabiting salt water (MP) and one inhabiting fresh water (BF) were studied in 1984, and two saltwater-inhabiting populations (MP and BR) were studied in 1985. Numbers given in parentheses for denominator mean square correspond to row numbers. CD = coefficient of determination.

Row	Source	SS	*d.f.*	Denominator MS	*F*	*P*	CD
Age at maturity; summer 1984:							
1	Population (P)	0.055	1	(4)	1.11	ns	—
2	Environment (E)	0.005	1	(5)	0.10	ns	—
3	P × E	0.005	1	(5)	0.10	ns	—
4	Family within P	0.346	7	(6)	3.93	0.02	0.35
5	(Family within P) × E	0.202	4	(6)	4.00	0.03	0.20
6	Within cells (error)	0.139	11				
Size at maturity; summer 1984:							
1	Population (P)	0.032	1	(4)	2.92	ns	—
2	Environment (E)	0.000	1	(5)	0.14	ns	—
3	P × E	0.000	1	(5)	0.14	ns	—
4	Family within P	0.077	7	(6)	1.04	ns	—
5	(Family within P) × E	0.011	4	(6)	0.26	ns	—
6	Within cells (error)	0.116	11				
Age at maturity; summer 1985:							
1	Population (P)	0.004	1	(4)	0.07	ns	—
2	Environment (E)	0.049	1	(5)	1.15	ns	—
3	P × E	0.000	1	(5)	0.00	ns	—
4	Family within P	0.505	8	(6)	3.97	0.02	0.34
5	(Family within P) × E	0.128	3	(6)	2.69	ns	—
6	Within cells (error)	0.191	12				
Size at maturity; summer 1985:							
1	Population (P)	0.071	1	(4)	3.19	ns	—
2	Environment (E)	0.002	1	(5)	0.35	ns	—
3	P × E	0.038	1	(5)	5.36	ns	—
4	Family within P	0.177	8	(6)	4.45	0.01	0.49
5	(Family within P) × E	0.021	3	(6)	1.42	ns	—
6	Within cells (error)	0.060	12				

The family × environment interaction terms for males must be interpreted with caution. Figure 4 shows what appear to be extensive interactive effects involving age and size; however, several factors must be kept in mind. Some families comprise full sibs, while some are half-sibs; male age and size at maturity are highly heritable within populations (Travis et al., 1990*a*). Furthermore, the vagaries of mortality and random assignments to environments can combine to produce small sample sizes and a pattern of age and size at maturity that is very erratic with respect to specific family-environment combinations, even without any direct environmental effects. These factors may be responsible for the "patterns" seen in Figure 4, and there may be no true genotype × environment interactions in the data. The lack of any consistent, strong direct effect of environment on age or size is clear, however, and this result indicates that direct environmental effects at the extremes of molly habitat do not have strong influences on male age or size. Certainly, envi-

TABLE 4. Average size (standard length) and age at maturity of all male and female fish raised in saltwater and freshwater ponds (pooled across families). Results for summer 1984 and summer 1985 experiments are reported.

		Fresh water		Salt water	
Sex	Year	Age (weeks)	Size (mm)	Age (weeks)	Size (mm)
Female	1984	9.7	28.2	8.4	30.8
	1985	8.7	28.4	8.0	28.5
Male	1984	10.4	26.1	9.5	30.2
	1985	8.9	24.9	7.2	24.3

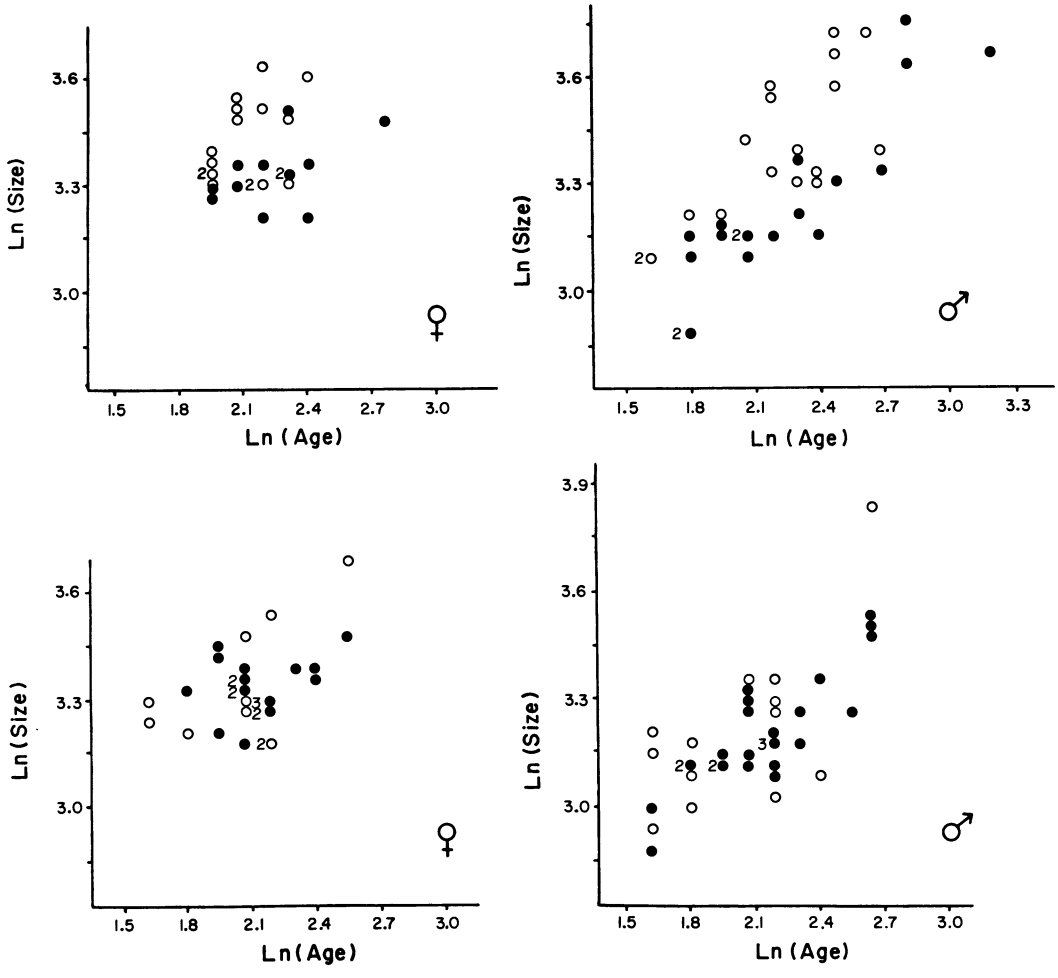

FIG. 3. Standard length (mm, log scale) at sexual maturity plotted against age (weeks, log scale) at sexual maturity for females (left-hand panels) and males (right-hand panels). Fish reared in salt water are indicated by open circles, and those reared in fresh water are indicated by closed circles. Numbers to the left of circles indicate the number of overlapping points. The upper graphs represent the summer 1984 experiment; the lower graphs represent the summer 1985 experiment.

ronmental effects are very weak compared to family-level effects.

Males were about 16% larger at maturity in the saltwater pond than in the freshwater pond in 1984, but ages at maturity in the two ponds were similar (bivariate analysis, Wilks' lambda $P \simeq 0.00$; canonical loading: size = -0.461, age = 0.083; Table 4, Fig. 3). In 1985, males matured about 19% earlier in the saltwater pond but at sizes similar to those of fish reared in the freshwater pond (bivariate analysis, Wilks' lambda, P = 0.021; canonical loadings: size = 0.241, age = 0.817; Table 4, Fig. 3).

Statistical Power

The high level of variation among families and the small sample sizes at maturity suggest that the statistical power to detect habitat and population differences may be low (Tables 3, 5). The power to detect population effects is greater for female traits than for male traits (appropriate mean-square errors for female traits are about 25% the size of those for male traits, whereas sample sizes for females are about 70% those of males), but no effects were detected for either sex. The sums of squares attributable to

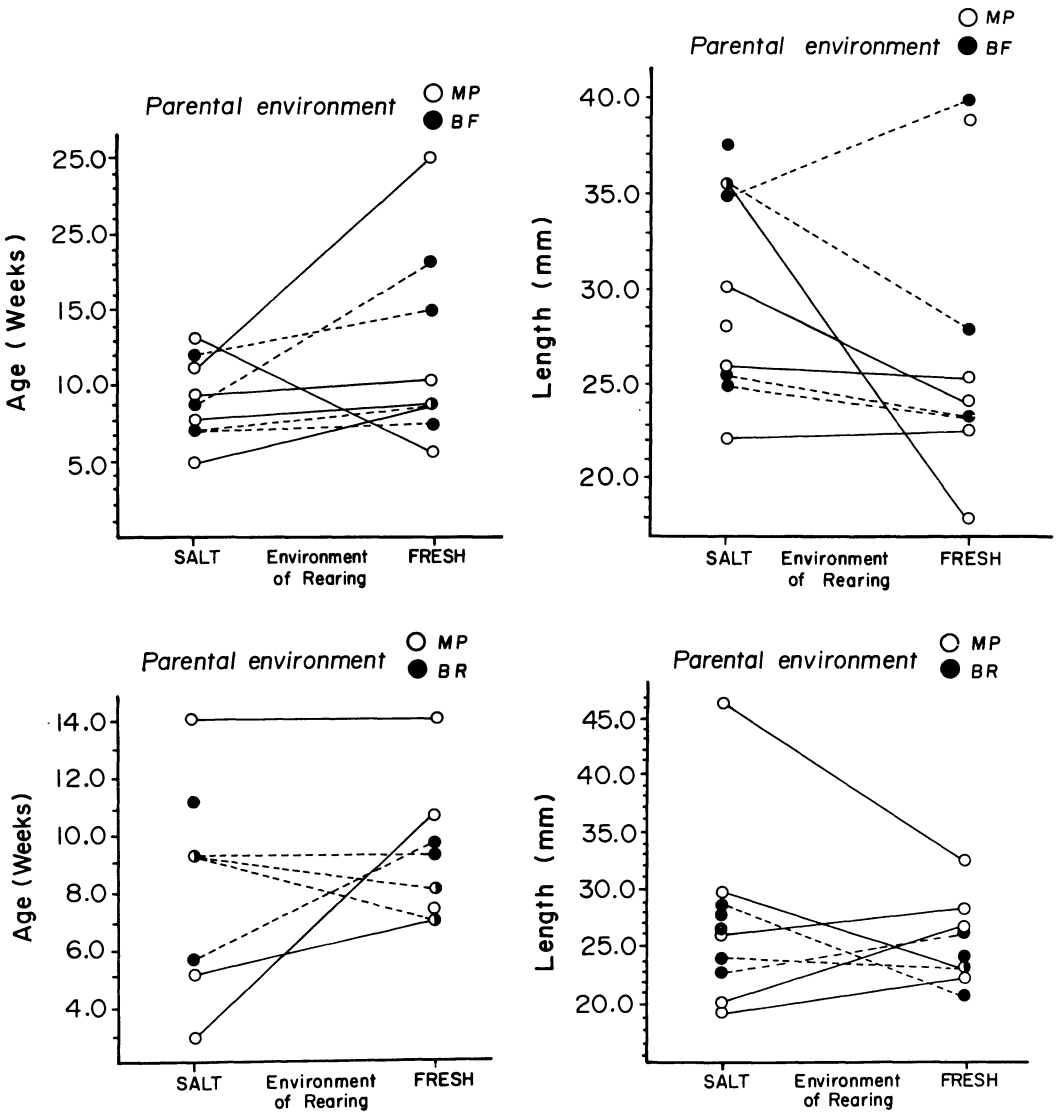

FIG. 4. Age (left-hand panels) and standard length (right-hand panels) of males at sexual maturity by population of origin and environment experienced during rearing. Family averages are plotted. Parental environment is indicated by open or closed symbols as noted on the figure. Dashed and solid lines connect family averages from different populations, and half-closed circles indicate overlapping points from different populations. Isolated points represent replicates in which no fish survived in one environment. Upper graphs represent summer 1984 experiment; lower graphs represent summer 1985 experiment.

population and environment main effects are very small in every case, suggesting that the lack of significance of these effects is not solely due to a lack of power.

The residual mean square is inversely proportional to the statistical power to detect interfamily variation, and there are some notable patterns in this regard. The power to detect variation among families in age at maturity was similar between years for both sexes. However, the power to detect variation in size at maturity was less for both sexes in 1984 than in 1985. The power to detect size variation was comparable between the sexes in both years, but the power to detect age variation was greater in females than in males in both years. These patterns are similar to those seen in labo-

TABLE 5. Analysis of variance of male size and age at maturity from the summer 1984 and summer 1985 experiments. One population inhabiting salt water (MP) and one inhabiting fresh water (BF) were studied in 1984, and two saltwater-inhabiting populations (MP and BR) were studied in 1985. Numbers given in parentheses for denominator mean square correspond to row numbers. CD = coefficient of determination.

Row	Source	SS	*d.f.*	Denominator MS	*F*	*P*	CD
Age at maturity; summer 1984:							
1	Population (P)	0.018	1	(4)	0.06	ns	—
2	Environment (E)	0.013	1	(5)	0.07	ns	—
3	P × E	0.052	1	(5)	0.29	ns	—
4	Family within P	2.500	8	(6)	8.42	0.00	0.50
5	(Family within P) × E	1.250	7	(6)	4.81	0.003	0.25
6	Within cells (error)	0.705	19				
Size at maturity; summer 1984:							
1	Population (P)	0.045	1	(4)	0.57	ns	—
2	Environment (E)	0.043	1	(5)	0.71	ns	—
3	P × E	0.000	1	(5)	0.00	ns	—
4	Family within P	0.634	8	(6)	4.50	0.01	0.33
5	(Family within P) × E	0.424	7	(6)	3.44	0.01	0.22
6	Within cells (error)	0.335	19				
Age at maturity; summer 1985:							
1	Population (P)	0.387	1	(4)	1.52	ns	—
2	Environment (E)	0.295	1	(5)	1.40	ns	—
3	P × E	0.870	1	(5)	4.13	ns	—
4	Family within P	2.550	10	(6)	6.41	0.00	0.50
5	(Family within P) × E	1.264	6	(6)	5.30	0.002	0.25
6	Within cells (error)	0.755	19				
Size at maturity; summer 1985:							
1	Population (P)	0.002	1	(4)	0.03	ns	—
2	Environment (E)	0.000	1	(5)	0.01	ns	—
3	P × E	0.103	1	(5)	2.42	ns	—
4	Family within P	0.847	10	(6)	14.52	0.00	0.64
5	(Family within P) × E	0.256	6	(6)	7.31	0.00	0.19
6	Within cells (error)	0.111	19				

ratory studies (Trexler et al., 1990) and make the lack of significance for female size striking, given how strong family effects were in males.

DISCUSSION

The Nature of Environmental Effects

A variety of environmental factors influence growth in poeciliid fishes (Trexler, 1989), and it is not possible to identify the specific factors responsible for the results of this field study. Slower growth, later maturation, or smaller size at maturity in fresh water than in salt water are consistent with laboratory reports (Zimmerer, 1983) and observational studies (Hubbs, 1942; Swift et al., 1977; Loftus and Kushlan, 1987; cf. Kilby, 1955; Snelson, 1985) of *P. latipinna*. However, the ponds used in our study differed in temperature, food quantity and quality, types of pathogens present, and presumably other factors. Growth rate is set by a balance between the energy demands of the environment and the productivity of the habitat available to the organism, the "scope" for growth (Schmidt-Nielsen, 1983). The energetic regime experienced by fishes involves many factors that can combine in an additive or a synergistic fashion to influence the scope for growth (Heuts, 1947; Kinne, 1960; Alderdice and Forrester, 1968; Peters and Boyd, 1972; Otwell and Merringer, 1975; Hetler, 1976). The low salinity in the freshwater pond may have imposed a high maintenance demand (Evans, 1973, 1975; Gustafson, 1981), but stress may have been mitigated by a higher quantity or quality of food. Alternatively, temperature stress may have been greater in the saltwater pond and may have acted to counterbalance salinity stress. The temperature of the salt-

water pond often exceeded 36°C, whereas that of the freshwater pond seldom exceeded 34°C. These types of interactions among factors may reduce or obscure correlations of truly important variables with variation in life-history traits (Trexler, 1989). In addition, 60% of the fish in our cages died before reaching sexual maturity, but our sample sizes are too small to reveal how this mortality influenced the distribution of traits observed in the survivors. We will report an analysis of patterns of mortality elsewhere.

The fall 1984 experiment suggests that there is a large effect of season on the growth of juvenile sailfin mollies. Fish placed in cages in September were much larger at three weeks of age than those placed in cages in early October. These data accurately reflect the fate of fish born in nature, as their dams, collected from natural populations, would have given birth naturally at these times. None of the fish born in fall survived to sexual maturity; all died during mid-winter.

The annual variation in growth rates for MP fish suggests that conditions were less conducive to growth in 1984 than in 1983 or 1985. In particular, the growth rates for all five families in fresh water in 1984 are lower than those of any families raised in fresh water in 1983 or 1985 (Fig. 1). Sampling variation alone seems to be an unlikely explanation for this pattern. Because genetic factors are unlikely to have changed so quickly, this annual variation must have resulted from changing environmental effects. We cannot determine, however, whether the environment in the ponds where the fish were raised was different or whether maternal effects differed in 1984 as a result of different conditions in the pond where the mothers were collected. Maternal nutritional contribution to ova and embryos may vary across years in MP females (Trexler, 1985).

These experiments indicate that there is some genetic variation in the response to environmental factors in northern Florida populations of *P. latipinna* and that the full range of that variation can be observed within a local population. Our results suggest that the lack of population differences in plasticity is real, because the sums of squares attributable to these sources are universally small and the environmental effects within families operate in the same direction for the vast majority of families. The lack of any evidence for differential plasticity is notable. Mollies live in a variety of habitats, and some habitat types certainly exhibit different sets of common conditions from others. Some habitats are relatively constant with respect to temperature, water chemistry, and, to a lesser extent, productivity (e.g., springheads such as that occupied by BF population), whereas others are typically widely variable estuarine situations (e.g., those occupied by MP and BR populations). These situations should select for different patterns of plasticity (Via and Lande, 1985; Stearns and Koella, 1986), and there is evidence that differential plasticity has evolved in response to similar differences in other animal species, albeit on a geographic scale (Bradshaw, 1986; Conover and Heins, 1987; Coyne and Beecham, 1987; for plants see Quinn and Hodgkinson [1983] and Scheiner and Goodnight [1984]). However, divergent patterns of plasticity may be precluded by even moderate gene flow (Via and Lande, 1985), and mollies appear to have extremely high gene-flow rates (Trexler, 1988).

The Control of Local Variation

If family effects are taken as evidence of broad-sense genetic differences, then the patterns we have found may have simple interpretations. Family-level variation was extensive and generally uncorrelated with source population. In some instances (e.g., juvenile growth rate in the summer 1985 experiment) there appeared to be some general associations marred by one or two "atypical" families. If there are true genetic differences among these populations for these traits, they are differences of degree. In other words, the populations we employed may vary only in the relative frequencies of maturation genotypes but not between extremes. The occasional atypical families provide evidence for that interpretation.

We did not use populations from opposite extremes of male size distributions (Farr et al., 1986). Our goal in these experiments was to examine the extent to which environmental effects mold variation in life-history traits and, secondarily, to examine the extent to which populations occupying dif-

ferent types of environments differ in their performance in each type of environment. It is clear that, although we found environmental effects on all the traits we examined, those effects are not strong enough to account for the wide repeatable variation observed among natural populations. Exactly which factors produced the observed effects and whether individual factors with dramatic effects cancelled each other, are the subjects of the following paper (Trexler et al., 1990).

There are lessons to be learned from the repetition of this experimental design. Growth rate was affected by environment in only one of four experiments. Biologically significant genotype × environment interactions in growth rate, a trait for which there are no differences between sexes and few problems with sample size, were observed only once in the four experiments, and not in the same experiment in which environment was significant as a main effect. No single experiment was sufficient to suggest general conclusions, and conclusions drawn from only one experiment could have been misleading. In part, this variation reflects the vagaries of sampling from natural populations, but it no doubt also reflects the very real importance of a variable environment in determining genotypic expression from one experiment to the next.

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