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The Evolution of Life-History Traits in Mosquitofish Since Their Introduction to Hawaii in 1905: Rates of Evolution, Heritabilities, and Developmental Plasticity[1]

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SYNOPSIS. In 1905, mosquitofish were introduced to sugar plantation reservoirs in Hawaii. Collections of at least 250 fish from each of 24 reservoirs, 4 stable and 20 fluctuating in water level, demonstrated that there were small but significant differences in the life history traits of fish from stable and fluctuating classes of reservoirs, and large and significant differences among stocks from individual reservoirs. Fish from 2 stable and 4 fluctuating reservoirs were then raised in individual containers with controlled food and temperature. Age and length at maturity, growth rates, and size of offspring all differed significantly among stocks. Broad-sense heritabilities were significantly greater than zero for female age at maturity for fish from one of two stable reservoirs, and for male maturation traits for fish from two of four fluctuating reservoirs. Rates of evolution, calculated from the maximum difference between the means of lab-raised stocks and assuming 140 generations since 1905 and continuous change, ranged from 0.1% to 0.5% of the average value of the trait per generation. The traits that changed more rapidly were also more phenotypically plastic, thus suggesting that phenotypic plasticity cannot account for stasis in the fossil record. The concept of *plastic trajectories* is introduced and exemplified, and predictions are made about how age and length at maturity should alter under stress for organisms with different demographic histories.

INTRODUCTION

In this paper, I use data from a natural experiment to estimate rates of evolution for several life-history traits. I also introduce the idea of *plastic trajectories* to the analysis of developmental plasticity, and apply it to the evolution of plasticity in age and length at maturity.

Whether traits can evolve rapidly is of interest for at least two reasons. First, the more rapidly traits evolve, the better justified we are in asserting that populations are adapted to local circumstances, and the better chance we have of drawing valid connections between the problems posed by environmental circumstances and the solutions offered by the phenotypes we sample. Second, much has been made recently of stasis in the fossil record (*e.g.*, Gould, 1980), of the lack of morphological change over long periods of time within species, and we would like to know if the phenomenon is general, or if it is easy to find cases of rapid change in ecological rather than geological time. Three cases of rapid evolutionary change have been well-documented: industrial melanism in moths (Kettlewell, 1973), changes in the frequencies of chromosome inversions in *Drosophila pseudoobscura* (Dobzhansky *et al.*, 1966), and the acquisition of tolerance to toxic mine wastes in plants (Bradshaw *et al.*, 1965; McNeilly, 1968). None of these cases involved a trait that is both classically continuous (metric) and plastic.

One might think that developmental plasticity in a trait would slow the rate at which that trait could evolve by uncoupling genotype and phenotype. Wright (1931) argued that developmental plasticity "is not only of the greatest significance as a factor of evolution in damping the effects of selection . . . but is itself perhaps the chief object of selection" (p. 147). W. D. Hamilton has claimed (personal communication) that under most conditions the appropriately plastic type will beat any genetically fixed type in intraspecific competition. Thus we might expect developmentally plastic phenotypes to replace canalized phenotypes under many circumstances, and once they have been fixed in populations they should slow the rate of subsequent change (Stearns, 1980, 1982).

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[1] From the Symposium on *The Inter-face of Life-History Evolution, Whole-Organism Ontogeny and Quantitative Genetics* presented at the Annual Meeting of the American Society of Zoologists, 27–30 December 1981, at Dallas, Texas.

TABLE 1. *Summary of field evidence: Females sampled in January, 1974.*

		Mean value		Class effects	Stock effects	
Trait	n	Stable	Fluctuating	MW U-test	ANOVA	% variance
Standard length (mm)	[a]	33.6	35.3	0.05	0.001	31
Dry weight (mg)	[a]	153.6	195.0	0.05	0.001	33
Condition factor	[a]	4.7	20.0	0.025	0.001	97
Fecundity (188 mg female)	[a]	19.3	21.9	0.025	0.001	79
Reproductive allocation	[a]	22.0	23.0	0.025	0.001	18
Dry weight of early-eyed embryos (mg)	[b]	1.9	2.0	0.10	0.50	0

[a] 1,367; [b] 609.

Can developmental plasticity account for some of the stasis seen in the fossil record? That question can be answered by analyzing a case study in which there has been rapid evolution involving plastic traits.

THE INTRODUCTION OF MOSQUITOFISH TO HAWAII IN 1905

In 1905, about 150 *Gambusia affinis* were introduced from Texas to Hawaii for mosquito control (Seale, 1905), and by 1910 their descendents had been placed into sugar plantation reservoirs. In Hawaii, the water level in some reservoirs fluctuated because they were used for irrigation; other reservoirs were abandoned by 1910 because harvesting practices changed, and their water levels have remained essentially stable since then. In 1974 I collected at least 250 fish from each of 24 reservoirs, 4 stable and 24 fluctuating in water level, and analyzed their life-history traits. Subsequently I reared fish from 2 stable and 4 fluctuating reservoirs in the laboratory under constant conditions in individual containers to measure the genetic component of the differences between stocks and to estimate the heritabilities of life-history traits within stocks.

Field results

In the field, fish from stable reservoirs were shorter, lighter, and thinner than fish from fluctuating reservoirs, and they had slightly, but significantly, lower fecundities and reproductive allocations (100 × dry weight of embryos/dry weight of female's somatic tissue) (Table 1). This observation is consistent with three hypotheses. Either adult mortality is higher, more variable, or less predictable in the fluctuating reservoirs than it is in the stable reservoirs, or juvenile mortality is higher, more variable, or less predictable in the stable reservoirs than it is in the fluctuating reservoirs, or fish get less to eat in fluctuating reservoirs, or all three. These hypotheses have not yet been tested directly. Although the differences in the reproductive traits of fish from stable and fluctuating reservoirs were significant, they were small.

For every trait, more variation was accounted for by the effects of individual reservoirs than by the stable-fluctuating classification (Table 1). The stock means of pregnant females ranged from 30.1 to 43.6 mm for standard length, from 100.2 to 449.1 mg for somatic dry weight, from 0.4 to 178.6 for regular condition factor (rcf = 10e6 × dry wt. of fish in mg/power of standard length in mm, where power = slope of the regression of log(weight) on log(length)), from 9.6 to 44.0 for reproductive allocation, from 5.9 to 70.0 for number of embryos in a female weighing 188 mg, and from 1.1 to 2.4 mg for weight of early-eyed embryos (Stearns, 1975).

Both the stable-fluctuating classification and the individual reservoirs had significant effects on the expression of life-history traits in mosquitofish. The reservoir in which a fish is found has a much larger effect on its reproductive traits than does the stability or fluctuation of that reservoir's water level. Three hypotheses, not mutually exclusive, could account for this result. First, the stable-fluctuating dichotomy could mislead by masking significant differences among the types of fluctuations that characterize different reservoirs. This hypothesis is well-supported by evidence presented in Stearns (1975) and will not be discussed further here. Second, founder events, genetic and demographic drift (mortality and reproduction that is random with respect to age), and local adaptation could all have produced genetic differences among stocks. The stochastic parts of this hypothesis remain plausible in the face of available evidence (Stearns, 1975), but a stronger test requires extensive electrophoresis which has not yet been done. I next discuss evidence bearing on genetic differences per se and on the third hypothesis, that phenotypic plasticity accounts for some of the variation among stocks.

Stocks do differ genetically for life-history traits

To establish the extent of genetic divergence of life-history traits among stocks, I reared progeny of field-caught fish from six reservoirs, two stable and four fluctuating. As the fish were born, they were placed in containers in the eight tanks so that each stock was represented in each tank as equally as differing sample sizes would allow. Each fish was reared in a half-gallon plastic container suspended in one of eight large tanks. Each container received its own input of fresh water via an automatic timer. The fish were fed measured amounts of frozen baby brine shrimp in the mornings and powdered Tetramin flakes in the afternoon and evening. Some fish were photographed every 14 days; lengths were measured to 0.1 mm. From the length-age curve for each fish, I calculated the parameters of the Von Bertalanffy growth curve that best fit the data (Fabens, 1965).

As the fish neared morphological maturity, they were checked by eye each day. Males were judged mature when their gonopodium was clear, spikelike, with a small spinelike projection visible on the tip, and with a clear series of bony spindles leading outwards from the base. Females were judged mature when yolked eggs about 1 mm in diameter could be clearly seen in the abdomen above the cloaca when viewed against a strong light. All the fish born to a single female were reared in a single large tank. Thus I could estimate the effects of different tanks on fish from each stock; since tanks differed slightly in their mean temperatures, despite efforts to produce uniform temperatures throughout the room, this estimate was critical.

Stocks displayed significant differences in age and length at maturity and in growth rates for both males and females (Table 2, in which all values within stocks have been adjusted to remove tank effects). Weights of offspring also differed significantly among stocks. Whether the fish came from a reservoir with a stable or a fluctuating water level made a significant difference to the life-history traits expressed in the laboratory (Table 2, in which the stable reservoirs are Twin and Kay, from the island of Hawaii, the fluctuating reservoirs are 31, 33, 40, and 81, from the island of Maui, and the effect of water level fluctuations is indicated in the ANOVA table as the island effect).

Island effects (effects of stable *vs.* fluctuating water levels) were significant for age and length at maturity and for weights of offspring, where sample sizes were large, but not for growth rates, where sample sizes were smaller. Both males and females from stable reservoirs matured earlier than did their counterparts from fluctuating reservoirs. The females from stable reservoirs were longer at maturity than those from fluctuating reservoirs, whereas the males were shorter (Table 3). Males from stable reservoirs did grow faster than those from fluctuating reservoirs, but the difference was not significant ($0.10 < P < 0.25$). The fish from stable reservoirs had significantly smaller young than those from fluctuating reservoirs (Table 3).

The differences between stable and fluctuating classes observed in the laboratory are thus not consistent with the hypothesis that fluctuating environments select for early maturity and many small young (*e.g.*, Gadgil and Solbrig, 1972). However, the rankings of these traits in the field could well be reversed. As Berven *et al.* (1979) showed for the green frog, selection can act in the field to counter phenotypic plasticity induced by environmental stress. In this case, the fish in the stable reservoirs

TABLE 2. *Summary of genetically-based differences among stocks.*

Trait		Rank order of stock means							ANOVA			
									Source	df	F	*P*
1. Age at maturity												
Females		Kay	33	Twin	81	31	40	[a]				
	n	40	89	60	74	29	72		Island	1	8.82	<0.005
	days	78	82	86	87	90	97		Stock	5	5.50	<0.001
Males		Twin	Kay	81	33	31	40	[b]				
	n	74	57	78	58	28	79		Island	1	51.78	<0.001
	days	71	74	80	84	85	87		Stock	5	2.44	<0.05
2. Length at maturity												
Females		81	33	Kay	40	Twin	31	[a]				
	n	74	89	40	72	60	29		Island	1	8.82	<0.005
	mm	18	19	19	19	20	20		Stock	5	5.50	<0.001
Males		Kay	81	Twin	33	40	31	[b]				
	n	57	78	74	58	79	28		Island	1	39.12	<0.001
	mm	17	17	17	18	19	19		Stock	5	10.39	<0.001
3. Growth rates, K												
Females		31	Twin	40	81	33	Kay	a				
	n	7	19	17	17	22	11		Island	1	0.26	NS
	1,000 × K	4	5	7	7	8	9		Stock	5	2.59	<0.05
Males		33	40	31	Kay	Twin	81	[c]				
	n	10	23	5	15	19	18		Island	1	1.62	NS
	1,000 × K	14	17	19	20	20	22		Stock	5	2.71	<0.05
4. Dry weight of young												
		31	Kay	81	Twin	40	33	[c]				
	n	48	63	83	61	130	94		Island	1	26.32	<0.001
	mg	0.96	0.99	1.03	1.06	1.14	1.19		Stock	5	13.99	<0.001

Tests for equality of means: [a] $P < 0.05$ by Games and Howell method, Sokal and Rohlf (1981, p. 409). [b] $P < 0.01$ by Games and Howell method. [c] $P < 0.05$ by Student-Neuman-Keuls procedure, Sokal and Rohlf (1969, p. 242).

TABLE 3. *Summary of island effects.*

Sex	Trait	Hawaii (stable)		Maui (fluctuating)	% difference
Females	Age at maturity (days)	82.5	<	88.3	7
	Length at maturity (mm)	19.5	>	18.9	3
	Growth rate, K	0.0066	<	0.0071	8
	Dry weight of offspring (mg)	1.00	<	1.12	12
Males	Age at maturity (days)	72.6	<	84.0	16
	Length at maturity (mm)	17.0	<	18.0	6
	Growth rate, K	0.020	>	0.018	11

have probably been living under food stress induced by intraspecific competition; certainly the field data on condition factors support this inference. When they are brought into the laboratory, they may grow more rapidly and mature earlier, at smaller sizes, than fish from fluctuating reservoirs, but not because they normally do so in the wild.

These genetically-based differences have arisen rapidly

One measure of the minimum rate of evolution is based on the maximum genetically-based difference found among the means of a set of populations that shared a common ancestral stock at a known time in the past. This method cannot discriminate between change that occurred gradually and continuously over that period and change that occurred rapidly when the stocks were founded, nor can it discriminate among founder effects, drift, and local selection as causes of change. However, it can establish a minimum rate at which genetic differences arise among stocks for whatever reason.

Using this method, and assuming that 140 generations had elapsed, on average, since the stocks diverged, I found changes that were significant in ecological time and that would appear to be very rapid if extrapolated into geological time. For example, females from Kay Reservoir (stable) matured, on average, at 78 days, and females from Reservoir 40 (fluctuating) matured at 97 days. The difference of 19 days corresponded to 24% of the mean age at maturity, or a divergence of 0.17% per generation. The maximum difference between any two stocks (Reservoirs 81 and 31, both fluctuating) for length at maturity of females was 1.51 mm, a change of 8%, or 0.06% per generation. In general, growth rates changed the most, from 0.4 to 0.8% per generation, ages at maturity and weight of offspring changed at about 0.2% per generation, and lengths at maturity changed the least, less than 0.1% per generation. These estimates, of course, assume that the changes occurred gradually and continuously, not in a rapid burst after the stocks diverged.

Thus genetically-based differences among stocks can arise rapidly for metric traits determined by many loci, or possibly by a single locus in the case of male age and length at maturity (Kallman and Borkoski, 1978). Local adaptation is not restricted, in this case, by limits on the rate of genetic change for traits like age at maturity, growth rates, and size of young. Length at maturity changed more slowly. One interpretation is that some traits respond rapidly with genetic change to novel environmental challenges, while others respond more slowly and may constrain the responses of the traits with potential for more rapid change. A second interpretation is that selection pressures differ for the different traits, and there is no difference in genetic constraints.

Heritability estimates and inferences about selection

If a metric trait remains under constant selection pressure, whether directional or stabilizing, for a sufficient period, then selection should exhaust the additive genetic variance for that trait. When we measure the heritability of traits with such history, it should not differ significantly from zero.

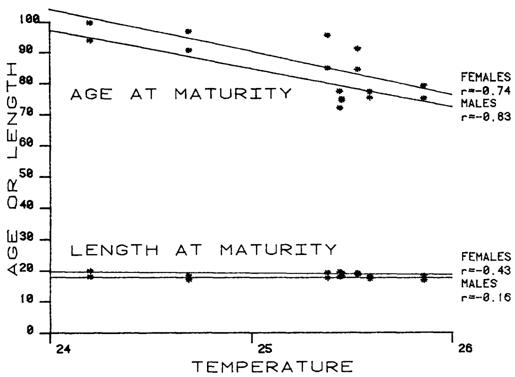

FIG. 1. The relationship of age and length at maturity to temperature at which mosquitofish, *Gambusia affinis*, are raised. The asterisks indicate the means for fish from 6 stocks raised at that temperature; the straight lines are linear regressions. The correlations are significant for age at maturity but not for length at maturity. Each asterisk is the mean of 50–60 observations.

Thus we can use the pattern of heritabilities to infer the relative strength of selection on different traits. Those under strong selection should have low heritabilities; those under weak selection should have higher heritabilities.

In the first laboratory-reared generation, I had sample sizes large enough to estimate heritabilities from family effects for age and length of maturity. Here heritabilities are broad-sense for two reasons. First, the estimate given is the covariance of full sibs, which has two additional components:

$$\text{Covariance of full sibs} = \tfrac{1}{2}\text{Va} + \tfrac{1}{4}\text{Vd} + \text{Vec}$$

where Va indicates additive genetic variance, Vd indicates interaction effects from dominance and pleiotropy, and Vec indicates the effects of common environment, in this case maternal effects and environmental effects induced in the first 10 days of life before the fish were placed in isolated containers. Thus estimates of heritability based on the covariance of full sibs tend to overestimate the true value because the effects of interactions and common environment have not been subtracted.

Second, these estimates were made on offspring born to mothers whose mating was not controlled. Like other poeciliid fish, *Gambusia* has the potential for multiple insemination, and if estimates from other species hold here (Constanz, personal communication), then it is likely that the offspring in each brood were fathered by about 2–3 males. Since the covariance of half-sibs is ¼Va, estimates of heritability which assume that unknown half-sibs are in fact full sibs will tend to underestimate the true value. Thus the confounding factors have opposite effects of unknown magnitude, but at least their opposition lends more confidence to the estimates.

In 4 of 24 cases (2 sexes × 2 traits × 6 stocks), broad-sense heritabilities were significantly greater than 0: for female age at maturity in fish from Twin Reservoir (49% of variance accounted for by family effects, $P < 0.001$), for male age and length at maturity in fish from Reservoir 31 (60%, $P < 0.001$; 29%, $P < 0.005$), and for male length at maturity in fish from Reservoir 40 (17%, $P < 0.05$). The existence of genetic and possible social control of male age and size at maturity known from other poeciliids (Kallman and Borkoski, 1978; Borowsky, 1973; Sohn, 1977) complicates interpretation of male heritabilities.

In the case of the females, it appears that selection on age at maturity has been strong in all but one stable reservoir. Lewontin (1965) predicted that populations subjected to repeated episodes of exponential growth, in which the intrinsic rate of natural increase, *r*, was an appropriate definition of fitness, would be under strong directional selection to mature as early as possible and would display low heritabilities for age at maturity. These results support the inference that the fish living in fluctuating reservoirs experience episodes of exponential growth more frequently than do the fish living in Twin Reservoir, which has a stable water level, and they suggest that fish in the other stable reservoir, Kay, also experience episodes of exponential growth. An alternative hypothesis is that genetic drift and the founder effect have reduced genetic variability in the fluctuating reservoirs, but this is not consistent with the evidence, because it requires that drift be important for female

TABLE 4. *Rates of evolution measured by the maximum difference between any two stocks.*

Sex	Trait	Difference	%	Per generation (%)
Females	Age at maturity	18.9 days	24	0.17
	Length at maturity	1.51 mm	8	0.06
	Growth rate, K	0.00479	117	0.84
	Dry weight of young	0.23 mg	24	0.17
Males	Age at maturity	16.0 days	23	0.16
	Length at maturity	2.00 mm	12	0.09
	Growth rate, K	0.00788	56	0.40

traits in the fluctuating reservoirs, but not for male traits, and for male traits in the stable reservoirs, but not for female traits.

Another mechanism producing strong selection for a particular age at maturity is the balance between fecundity gained by females that delay maturity, and the additional risks of mortality they take while still juveniles (Stearns and Crandall, 1981). If we ignore the females from Twin Reservoir, which appear not to have been under strong selection for age at maturity, then the series of stocks with increasing ages at maturity—Kay, 33, 81, 31, 40—should also form a series in which more and more fecundity is gained as maturity is delayed, or in which mortality risks for late juveniles decline, or both. That prediction can be tested by field measurements of age-specific mortality rates and of growth and fecundity.

The more rapidly evolving traits are also more plastic

This set of data permitted two measures of developmental plasticity. In the first, the environmental stress was induced by temperature differences among the 8 tanks in which individual containers were suspended. For the second, the environmental stress was induced by differences in the degree of crowding to which fish were subjected in the first 10 days of life. In the first generation, broods were kept in the container in which they were born for the first 10 days to reduce losses due to handling; in the second generation, fish were placed in their individual containers on the day they were born.

The average temperature in the eight tanks ranged from 24.2 to 25.8°C. For both males and females, age at maturity was much more sensitive to temperature than length at maturity (Fig. 1). For females, the correlation of age at maturity with temperature was $r = -0.74$ ($P < 0.05$); for males, it was $r = -0.83$ ($P = 0.01$). In contrast, the corresponding correlations of length at maturity with temperature were -0.43 and -0.16, neither of which is significant.

Comparison of the first and second generations leads to a similar conclusion (Table 5). Fish subjected to crowding in the

TABLE 5. *Differences at maturation between first and second generations.*

Trait	Sex	Gen.	Stock		ANOVA			
			Twin	33	Source	df	F	*P*
Age	Female	1	85.6 (60)	81.9 (89)	Generation	1	42.11	<0.001
		2	46.5 (46)	40.6 (60)	Stock	1	4.19	<0.05
	Male	1	71.3 (74)	84.4 (58)	Sex	1	2.57	NS
		2	38.7 (39)	36.8 (49)	Within	471		
Length	Female	1	19.8 (60)	18.5 (89)	Generation	1	0.12	NS
		2	21.4 (46)	18.3 (60)	Stock	1	0.29	NS
	Male	1	17.3 (74)	18.5 (58)	Sex	1	0.56	NS
		2	19.4 (39)	17.1 (49)	Within	471		

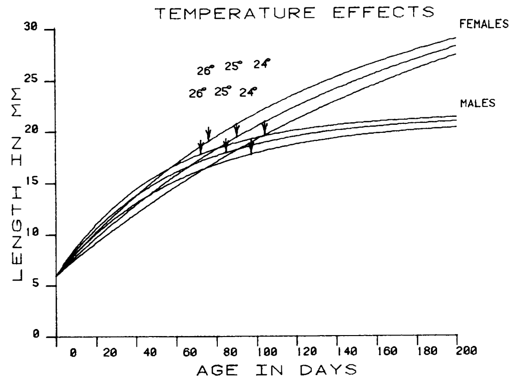

FIG. 2. Growth curves for males and females at three different temperatures calculated from the average effect of temperature on growth and age and length at maturity for 6 stocks. The sample size from which the growth equation was estimated was 100–120 fish for each line. The arrows indicate morphological maturity.

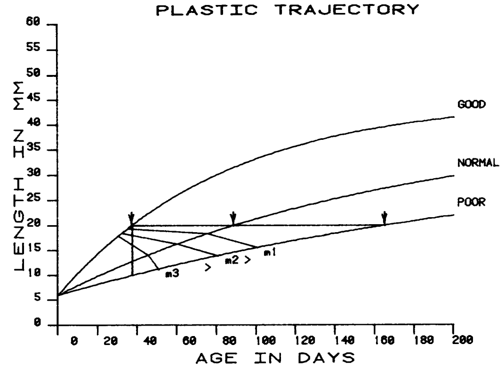

FIG. 3. A schematic illustration of the concept of plastic trajectories. The three growth curves contrast growth under good, normal, and poor conditions. An organism following the rule "mature at a fixed size" would describe a trajectory through changing conditions indicated by the horizontal line along which maturation is marked with arrows. An organism following the rule "mature at a fixed age" would describe the trajectory indicated by the vertical line. More realistic trajectories are labeled m1, m2, and m3, in increasing order of the adult mortality rates expected in the field for populations whose response to stress follows the trajectories indicated.

first 10 days of life in Gen. 1 matured at about 80 days; fish isolated in individual containers on the day they were born matured at about 40 days. However, the differences between the generations had no impact on length at maturity.

For both types of stress, and for both sexes, the more rapidly evolving trait, age at maturity (*cf.*, Table 4) was also more plastic than the more slowly evolving trait, length at maturity (*cf.*, Fig. 1, Table 5). Thus both Wright (1931), who thought that plasticity damps the effects of selection, and I (1980, 1982), who suggested that plasticity uncouples phenotype from genotype, were wrong. Plastic traits can also evolve rapidly, and this study suggests that phenotypic plasticity cannot be invoked to explain the stasis seen in the fossil record in any straightforward way. The possibility remains that plasticity in some traits could promote stasis in others (Ashby, 1956; Bradshaw, 1965; also see Caswell, this volume), but that is a more complex problem to which these data do not speak.

Plastic trajectories

The average growth curves for fish raised at different temperatures, calculated by removing stock effects from the data, suggest that the plastic response to stress is lawlike and potentially predictable from life-history arguments (Fig. 2). As temperature drops, maturity is delayed in both sexes, and by approximately the same amount—a 2°C drop in temperature produces a 28 day delay in maturity in females and a 25 day delay in males.

Now consider how age and length at maturity should change as the organism is placed under increasing stress. In Figure 3, I have plotted three growth curves to indicate good, normal, and poor conditions. Enviromental factors commonly affecting growth in this way are temperature and food. The organism could follow the rule, "Always mature at the same size," in which case its maturation events would fall along the horizontal black line on which age at maturity is marked with arrows. Under the conditions plotted, such an organism would delay maturity from 40 days under good conditions to 175 days under bad conditions, while maintaining a constant length at maturity of 20 mm. On the other hand, the organism could follow the rule, "Always mature at the same age," in which case its maturation events would fall along the vertical line at 40 days. Under the conditions plotted, such an organism would mature at 20 mm under good conditions and at 10 mm under bad conditions.

Clearly, there are problems with both rules. An organism that always matures at a fixed size must wait a long time under poor conditions before reproducing, and during that period it undergoes a risk of mortality proportional to the length of the delay. An organism that always matures at a fixed age will mature at a very small size under poor conditions, and will have much lower fecundity as a result if fecundity scales with size. We should expect organisms to adopt an intermediate course, maturing somewhat earlier, at a somewhat smaller size, under poor conditions to avoid some of the mortality risk without giving up too much size-related fecundity.

Furthermore, if we sample populations ranked by increasing adult mortality, then the organisms from the populations with higher adult mortality will show this effect more strongly. I have indicated this prediction on Figure 3 by drawing three lines—m1, m2, and m3. Their relative positions are my qualitative predictions of how age and length at maturity should change when organisms from three such populations are raised under three conditions of food or temperature stress. If organisms have encountered high pre-maturation mortality rates in the field, then they should respond to stress by maturing at much smaller sizes with a small delay in maturity (m3); if they have encountered relatively low pre-maturation mortality rates in the field, then they should respond to stress with a relatively small reduction in size but a larger increase in age at maturity (m1). This prediction is contingent on the assumption that juvenile mortality of offspring is not affected by age or size at maturity of parent, and that the mortality of small organisms, *e.g.*, newborn offspring, is much less affected by poor conditions than is the mortality of large organisms, *e.g.*, reproductive adults.

These predictions are testable, and more easily testable than most life-history predictions, for they concern the response of stressed and non-stressed organisms in a single generation. Note that the qualitative predictions say nothing about the shape of the curve; it could be linear, convex, or concave, for example. Elsewhere in this volume, Policansky (1983, his Fig. 1) presents envelopes on the plastic trajectories of two genotypes of *Xiphophorus maculatus*, a platyfish. Both envelopes are concave, and one lies entirely below and to the left of the other. The implication, from the argument presented above, is that adult mortality rates are higher for the genotype that matures earlier and at smaller sizes.

I call each line a *plastic trajectory*, *plastic* because the changes represented by the line are caused by developmental plasticity, and *trajectory* because we can imagine organisms following the line as a law-governed path through changing conditions. The concept applies to other traits and other observations. For example, if one applies food stress to flour beetles, they decrease their reproductive effort and live longer (Mertz, 1975; Boyer, 1978), presumably because adult mortality is less affected by food stress than is juvenile mortality. In contrast, stressed triclad flatworms increase reproductive effort, presumably because juveniles resist starvation better than adults (Calow, 1979).

These observations suggest that if different types of stress produce different effects on adult and juvenile mortality, they should also produce different plastic trajectories. In other words, the plastic response should be specific to the stress applied if the stress has served as a dependable cue to age-specific shifts in mortality and fecundity. Many would agree that one has to understand life-history evolution and the heritabilities of life-history traits to predict genetic change. I suggest that we should add plastic trajectories for the components of fitness to the minimal definition of the phenotype necessary to understand genetic change.

CONCLUSION

The introduction of mosquitofish to Hawaii in 1905 has provided a case study in which an unusual amount of information can be developed about the processes underlying evolutionary change in life-history traits. To date, this natural experiment has provided data bearing on life-history evolution, on rates of evolution, and on the evolutionary significance of developmental plasticity.

Three hypotheses could explain why individual reservoirs accounted for much more of the variation in life-history traits of the fish living in them than whether their water levels were stable or fluctuating: (1) the stable-fluctuating dichotomy might mislead, (2) the fish differ genetically from stock to stock, whether through founder events, drift, or local adaptation, and (3) the fish are developmentally plastic. All three hypotheses are well-supported by evidence.

Phenotypic plasticity did not uncouple genotype and phenotype in this case; it did not blunt the force of selection. The more plastic traits also evolved more rapidly. This weakens the case I made previously (Stearns, 1980, 1982) for developmental plasticity as one cause of stasis in the fossil record. I no longer think that explanation works.

Plastic trajectories are important and little-recognized adaptations that explicitly combine problems of growth and development with life-history theory. Life-history traits and plastic trajectories form part of the minimal representation of the organism necessary to understand genetic change, or lack of it.

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