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THE GENETIC BASIS OF DIFFERENCES IN LIFE-HISTORY TRAITS AMONG SIX POPULATIONS OF MOSQUITOFISH (*GAMBUSIA AFFINIS*) THAT SHARED ANCESTORS IN 1905

STEPHEN C. STEARNS
Biological Laboratories, Reed College, Portland, Oregon 97202

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Students of life-history evolution have relied for some time on inferences drawn from differences observed among populations and species. Such differences usually have both environmental and genetic components, but the studies in which the two components have been distinguished (e.g., Birch, 1953; Clatworthy and Harper, 1962; Birch et al., 1963; Keith et al., 1966; Gadgil and Solbrig, 1972; Hickman, 1975; Oka, 1976; Dawson, 1975; McCauley, 1978; Stearns and Sage, 1980) have remained a small, but important, part of the literature.

This paper documents genetically-based differences in life-history traits among six stocks of mosquitofish, *Gambusia affinis*, whose approximately 150 common ancestors were introduced to Hawaii in 1905 for mosquito control. Previous work (Stearns, 1983) has shown that 24 stocks of mosquitofish in Hawaiian reservoirs differ significantly in life-history traits in the field, that more of the variation in life-history traits is explained by differences among individual stocks than by classifying the reservoirs as stable or fluctuating in water level, and that three hypotheses could account for this pattern. The first, that the stable-fluctuating dichotomy misleads, concealing considerable diversity of types of fluctuations, is well-supported (Stearns, 1983). The second, that the differences contain a genetic component and have risen through either founder effects, drift, or local adaptation, is examined here. The third, that the differences are due to developmental plasticity, is evaluated in Stearns (1983). This paper demonstrates that there is a genetic component to many of the differences, and that some of the genetic differences are large and have arisen rapidly, but it does not isolate the evolutionary origin of the genetic differences.

The method used here to detect genetic differences between stocks is a compromise between power and difficulty. I held wild-caught fish in the laboratory for three months under similar conditions to reduce maternal effects, then raised their offspring on controlled rations and at constant temperatures in individual containers. This straight-forward method is best suited for surveys of a number of stocks; crosses between stocks and backcrosses to parental types would be required to rule out maternal effects definitively. The fish discussed in this paper are the F_1 generation born to wild-caught parents. I later reared an F_2 generation from full-sib/half-sib crosses within each of two stocks, and report on patterns of heritabilities elsewhere (Stearns, in press). In the F_1 generation I worked with six stocks, two from reservoirs with stable water levels and four from reservoirs with fluctuating water levels.

MATERIALS AND METHODS

Collection and Treatment of Parental Stocks.—The parents of the lab-raised fish were caught on 2–3 June 1980 at Reservoirs 31, 33, 40, and 81 of Hawaiian Commercial and Sugar Company, Inc., Puunene, Maui, Hawaii, and at Twin and Kay Reservoirs of Kohala Corporation, Inc., Kohala, Island of Hawaii. These stocks were selected because among them they spanned the range of phenotypic variation found in the field for fecundity and off-

spring weight. The reservoirs on Hawaii have water levels that do not vary; those on Maui have water levels that fluctuate dramatically with periods (within reservoirs) ranging from days to seasons (Stearns, 1983). The parental stocks consisted of more than 20 males and 20 females from each reservoir; they were shipped to Portland, Oregon, and maintained in 75 liter aquaria at 24–26 C on a daily diet of frozen brine shrimp in the morning and Tetramin flakes in the afternoon and evening. All fish were held under similar conditions for at least three months before giving birth to minimize maternal effects due to differences in recent physiological history. The experiments were conducted on their offspring.

Flow-through System.—Each lab-raised fish was housed in a 1.9 liter plastic container. The containers had holes in their bottoms and sides for water exchange and were suspended in eight large tanks (1.22 m × 2.44 m × 20.5 cm) in which 16 rows were set off by cross-pieces. Each of the eight tanks could hold 144 containers (1,152 total). A standpipe maintained the water level in the containers at about 1.5 liters. Water entered the system through a mixing valve which regulated the temperature of the incoming water at 25 ± 0.5 C. The water then went through a particulate filter, a carbon filter, and one of three solenoid valves controlled by timers that regulated the number of minutes the water was on each day. Each 1.9 liter container received an individual supply of water at 12.8 ± 3.1 ml/min; the timers that controlled the solenoids were set to supply water for 30 min/day. The rate of water flow was determined by a preliminary experiment that demonstrated that higher flow rates increased mortality. The water was replaced every 10–12 days. Oyster shells covered the bottom of each large tank to provide calcium ions and carbonate buffer.

Distribution of Stocks Among Tanks.—There were six stocks and eight large tanks. Ten days after they were born, fish were distributed into individual containers. Only broods of six or more were used, and if there were more than ten in a brood, ten were used and the rest were preserved to be weighed for estimates of birth weight. Broods were placed into the large tanks in rotation among the six stocks. Each tank held two or more broods of each stock, and all sibs were raised in the same large tank. This design allowed for the separation of tank effects and stock effects, while permitting direct comparisons among broods from the same stock raised in the same tank.

Temperature.—Water temperature was controlled by regulating the temperature of the entire room at 25 C and by having the water enter the room through a mixing valve at 25 C. A 5,600 BTU electric wall heater with fan supplemented the central heating of the building, and two fans circulated air through the room to reduce stratification. Mean temperatures in the eight tanks ranged from 24.2 C to 25.9 C over a 17 week period starting with the isolation of the first fish. Temperatures were taken in each tank once a week. The average temperatures in the eight tanks were (means ± 95% *CI*): 25.53 ± 0.64, 25.38 ± 0.72, 24.20 ± 0.78, 25.45 ± 0.76, 25.86 ± 0.70, 24.69 ± 0.78, 25.59 ± 0.80, 25.44 ± 0.64.

Handling and Feeding.—Fish were born in 1.9 liter containers that had been divided into upper and lower compartments by pulling a horizontal sheet of wide-mesh polyester fabric into four slits cut at the corners halfway up the sides. The mother was placed in the top, and the offspring fell through the fabric mesh into the bottom where they could not be eaten. On the day of birth, the mother and the fabric were removed, but the offspring were kept in the container for 10 days to reduce mortality induced by handling. From six to ten offspring per brood were then isolated in labeled containers. They were fed one drop of a standard dilution of San Francisco Brand frozen baby brine shrimp in the morning, and one shake of powdered Tetramin dispensed from a salt-shaker in the afternoon and again in the evening. No attempt was made to adjust the weight of food to the weight of individual fish

because so many (995) fish were raised. When the fish were 50 days old, the food ration was doubled.

Photography.—The same two fish from each brood were photographed from above at ten days, then every 14 days thereafter until they were 156 days old, for growth estimates. Every fish was photographed on the day it reached morphological maturity. The negatives were projected onto the screen of a Northwest Microfilm Inc. NMI 75 microfilm reader, and standard lengths were measured to the nearest 0.5 mm with a ruler. After conversion to actual lengths, this method is accurate to ±0.25 mm.

Maturation Criteria.—Fish were spot-checked for signs of maturity until 45 days old, then checked regularly until finally fish that were near maturity were checked every day. To check for maturity, I poured the fish from its container into a plexiglas chamber 10 cm × 10 cm × 1.5 cm, held it up to a light, and inspected the abdomen and anal fin closely. Males were judged mature when their gonopodium was clear, spikelike, with a small spine visible on the tip, and with a series of clear bony spindles leading outwards from the base. Turner (1941) presents details on gonopodial morphogenesis, and Kallman and Schreibman (1973) confirm that maturation of the gonad is well correlated with metamorphosis of the anal fin. At the start of the experiment, a few maturing males were examined under a dissecting microscope to confirm the completion of gonopodial morphogenesis, and from time to time maturing males were compared with known adults to refine my judgement. Females were judged mature when yolked, yellow eggs about 1 mm in diameter could be seen in the abdomen above the cloaca. Judgements of morphological maturity were accurate to ±1 day. I arrived at this estimate by performing double-blind spot-checks of maturing and recently-matured fish.

Artificial Insemination.—All F_1 females were artificially inseminated using a technique described by Vrijenhoek (pers. comm.). Each male was sacrificed and his testes were dissected, suspended in an aqueous solution of 0.7% NaCl in a depression slide, and minced. After examining the suspension of spermatophores under a compound microscope to verify the presence of active sperm, I drew the spermatophore suspension up into a fine pipette (0.5 mm diam.) to a length of 1–1.5 cm. Then I placed an unanaesthetized female on her back in a bed of damp paper towels, inserted the tip of the pipette into her genital passage (in some cases this was made easier by rubbing the genital papilla with the tip of the pipette), and forced the spermatophores into the female by blowing gently on surgical tubing attached to the pipette. Of 112 females inseminated, 111 survived the operation, and 98 gave birth. Sterile instruments and solutions probably account for this degree of success.

The successful use of Vrijenhoek's technique for artificial insemination is notable because it makes controlled matings of a single male to several females practical.

Fecundity Estimates.—Pregnant females were checked daily from 16 days after insemination. On the day of birth, the offspring were collected, and both female and offspring were photographed for length measurements. The offspring were counted, dried, and weighed. Fecundity was estimated by calculating the regression of litter size on length within each stock, then calculating the length-adjusted fecundity of each female. I used analysis of covariance to test for differences among stocks. Fecundities were measured on fish that were 7–15 months old. Thus all females who gave birth were well past maturity, and some were quite old. The rankings of stocks for fecundity in mid and late life are not necessarily the rankings that would have been found for fecundity in the two or three litters delivered immediately after maturity was achieved.

Longevity Estimates.—After delivering her second litter, or 45 days after delivering her first, each female was transferred from her brood trap to a regular container, then fed three times a day and checked each week to see if she was alive

or dead. Longevity was estimated as the mean age at death of all fish that had not escaped or been lost and that died before 581 days of age. That age was taken as a cut-off point because there were still some fish alive at the time the estimate was made.

Statistics.—In all statistical calculations, I followed the recommendations and procedures laid out in Sokal and Rohlf (1981). For analysis of covariance, I used BMDP program P1V (Dixon and Brown, 1977). All estimates presented here are based on the F_1 generation. I did not nest sibships within stocks in the analyses of variance, but I did nest stocks within islands. Thus the component of variance attributable to differences among families was part of the error mean square, making the estimates of stock effects conservative. I treated both island effects and stock effects as fixed (Model I), and used error mean square in the F-tests for both (Brownlee, 1965 p. 508). For the analysis of covariance of fecundity with length as the independent variable, I did a one-way analysis to test for stock effects.

Results

Age and Length at Maturity.—For both females and males, age and length at maturity differed significantly both among stocks and between islands (Tables 1, 2). For females, the range between the earliest- and latest-maturing stocks was 19 days; for males, it was 16 days. Females matured, on average, at 87 days, males at 80 days. Both females (at 82.5 days) and males (at 72.6 days) from stable reservoirs matured earlier than did females (at 88.3 days) and males (at 84.0 days) from fluctuating reservoirs.

For females, the range between the smallest- and largest-maturing stocks was 1.51 mm; for males, it was 2.00 mm. Thus the divergence among stocks in length at maturity as a percentage of the overall mean (8% for females and 11% for males) was less than the divergence among stocks in age at maturity (22% for females and 20% for males). Females matured, on average, at 19.04 mm, males at 17.69 mm; thus males matured at a length 1.35 mm shorter than females. Females from stable reservoirs were larger at maturity (19.51 mm) than were females from fluctuating reservoirs (18.86 mm), but males from stable reservoirs were smaller at maturity (17.01 mm) than males from fluctuating reservoirs (18.05 mm).

Growth Rates.—For both females and males, none of the parameters of the Von Bertalanffy growth equation differed between stable and fluctuating classes, and only one parameter, K, differed among stocks (Tables 1, 2). Sample sizes for growth rates were 24–26% as large as sample sizes for age and length at maturity. Differences between length at maturity and asymptotic length (Von Bertalanffy parameter A) were large for females and smaller for males, reflecting the general poeciliid pattern of indeterminate growth in females and determinate growth in males (Figs. 1, 2). However, males from all stocks grew slightly after morphological maturation of the gonopodium, and males from Reservoir 33 grew from 17 mm at maturity (for the sub-sample of fish photographed for growth) to an asymptotic length of 26 mm (Fig. 2).

Fecundity, Weight of Offspring, Interbrood-interval, and Longevity.—Weight of offspring, for which there were large sample sizes, differed significantly among stocks and islands. Offspring dry weights ranged from 0.96 mg (Res. 31) to 1.19 mg (Res. 33), a difference of 0.23 mg or 21%. Fish from stable reservoirs weighed 1.02 mg at birth; fish from fluctuating reservoirs weighed 1.06 mg at birth. Mean values of fecundity adjusted for length did not differ among stocks, but the slopes of the fecundity-length relation did (Table 1). Sample sizes for the other traits were small, and some of the F-values from the ANOVA's were large enough to suggest that with sample sizes as large as those attained for age and length at maturity or weight of offspring, significant differences would have been detected among stocks for interbrood interval and between islands for survival. Interbrood intervals ranged from 18 to 24 days, a difference of

TABLE 1. *Life-history traits ranked as means (±95% CI) for six stocks. Values have been adjusted for tank effects. See Table 2 for ANOVA results. A: asymptotic length in Von Bertalanffy growth equation; B: 1 − B = length at birth/asymptotic length in Von Bertalanffy growth equation; K: growth rate in Von Bertalanffy growth equation—Length = A(1 − B × exp(−K × age)). Fecundity: mean = number of offspring adjusted for length, slope = slope of regression of fecundity on length; Wt. off.: dry weight of offspring in mg; I.B. int.: interbrood interval in days; Longev.: average age at death in days. Twin and Kay Reservoirs, on Kohala Corp. land on the Island of Hawaii, have stable water levels; Reservoirs 31, 33, 40, and 81, on Hawaiian Commercial and Sugar Co. land on Maui, have fluctuating water levels. Means joined by a horizontal line are not significantly different (P > .05).*

Sex trait	Ranks of stocks					
Females						
Age at maturity (days)	Kay 77.95 ± 5.60	33 81.94 ± 3.82	Twin 85.57 ± 4.51	81 86.87 ± 3.47	31 90.14 ± 7.16	40 96.86 ± 5.13
N	(40)	(89)	(60)	(74)	(29)	(72)
Length at maturity (mm)	81 18.34 ± 0.39	33 18.53 ± 0.43	Kay 19.01 ± 0.44	40 19.40 ± 0.46	Twin 19.84 ± 0.52	31 19.85 ± 0.66
A	Kay 39.18 ± 2.39	33 50.49 ± 13.23	31 53.43 ± 5.36	40 60.26 ± 18.72	81 60.63 ± 14.37	Twin 60.91 ± 15.35
N	(11)	(22)	(7)	(17)	(17)	(19)
B	40 0.853 ± 0.042	Twin 0.861 ± 0.023	81 0.866 ± 0.023	Kay 0.867 ± 0.004	31 0.884 ± 0.021	33 0.913 ± 0.122
K × 100	31 0.409 ± 0.074	Twin 0.535 ± 0.087	40 0.698 ± 0.213	81 0.720 ± 0.149	33 0.801 ± 0.232	Kay 0.888 ± 0.177
Fecundity	Kay	31	40	Twin	33	81
Mean	16.9 ± 11.7	16.6 ± 10.4	17.5 ± 7.0	21.1 ± 8.3	21.9 ± 8.2	30.2 ± 9.1
Slope	−1.76	1.95	−0.38	−0.88	−0.02	3.54
N	(10)	(13)	(30)	(21)	(21)	(17)
Wt. off.	31 0.96 ± 0.03	Kay 0.99 ± 0.05	81 1.03 ± 0.05	Twin 1.06 ± 0.06	40 1.14 ± 0.05	33 1.19 ± 0.06
N	(48)	(63)	(83)	(61)	(130)	(94)
I.B. int.	81 18.3 ± 1.2	31 19.3 ± 2.0	Kay 22.0 ± 1.0	40 22.5 ± 1.2	33 23.8 ± 1.0	Twin 23.5 ± 0.5
N	(6)	(4)	(2)	(8)	(4)	(2)
Longevity	40 240 ± 44	81 254 ± 38	Kay 259 ± 66	33 268 ± 51	Twin 296 ± 41	31 309 ± 70
N	(24)	(39)	(17)	(34)	(39)	(17)
Males						
Age at maturity (days)	Twin 71.32 ± 2.34	Kay 74.16 ± 3.47	81 79.76 ± 3.93	33 84.38 ± 5.06	31 85.18 ± 2.39	40 87.37 ± 3.18
N	(74)	(57)	(78)	(58)	(28)	(79)
Length at maturity (mm)	Kay 16.64 ± 0.33	81 17.09 ± 0.42	Twin 17.30 ± 0.23	33 18.46 ± 0.46	40 18.50 ± 0.37	31 18.64 ± 0.49
A	Kay 20.51 ± 0.75	31 20.68 ± 1.01	Twin 20.94 ± 0.97	40 21.41 ± 0.81	81 23.70 ± 6.81	33 25.75 ± 5.94
N	(15)	(5)	(19)	(23)	(18)	(10)
B	Kay 0.749 ± 0.030	Twin 0.751 ± 0.021	31 0.752 ± 0.046	33 0.766 ± 0.047	40 0.768 ± 0.029	81 0.792 ± 0.053
K × 100	33 1.40 ± 0.42	40 1.73 ± 0.18	31 1.91 ± 0.42	Kay 1.99 ± 0.41	Twin 2.00 ± 0.29	81 2.19 ± 0.27

TABLE 2. *ANOVA results for traits listed in Table 1.*

Sex	Trait	N	Island effects (d.f. = 1) F	Island effects (d.f. = 1) P	Stock effects (d.f. = 5) F	Stock effects (d.f. = 5) P
Females	Age at maturity	364	7.24	<.001	6.30	<.001
	Length at maturity	364	8.82	<.005	5.50	<.001
	A	93	0.26	NS	1.12	NS
	B	93	0.29	NS	0.39	NS
	K	93	0.26	NS	2.59	<.050
	Fecundity	112				
	adj. mean		—	—	1.22	NS
	slopes		—	—	2.98	<.020
	Offspring	479	26.32	<.001	13.99	<.001
	I.B. int.	26	1.05	NS	2.14	NS
	Longevity	147	0.93	NS	0.99	NS
Males	Age at maturity	374	51.78	<.001	2.44	<.050
	Length at maturity	374	39.12	<.001	10.39	<.001
	A	89	1.93	NS	0.70	NS
	B	89	2.37	NS	0.40	NS
	K	89	1.61	NS	2.71	<.050

24%; longevities ranged from 240 to 309 days, a difference of 16%. Females from stable reservoirs lived, on average, 285 days; females from fluctuating reservoirs lived, on average, 263 days.

Correlations Between Stock Means.— Only one correlation between stock means was significant (Table 3); stocks whose females matured at large sizes also survived a long time ($r = 0.850$). Correlations among several other traits, although not significant, were large enough to suggest that with a larger sample of stocks a significant association would be detected. Stocks with long female survival had slow female growth rates ($r = -0.774$); stocks with high fecundity matured at small sizes ($r = -0.695$); stocks with large offspring had long interbrood intervals ($r = 0.659$).

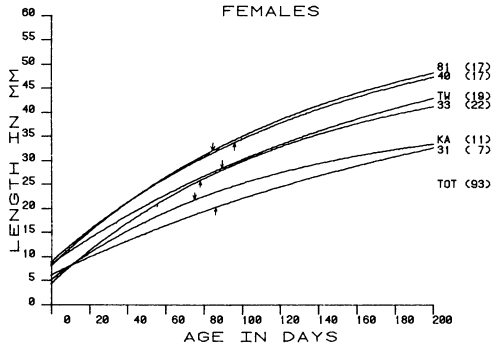

FIG. 1. Von Bertalanffy growth curves for females from each of six stocks, calculated by first fitting a least-squares estimate to the length-age data for individual fish, then calculating stock means for the parameters of the equation from the parameter estimates for individual fish. These data have been adjusted for effects arising from temperature differences among the large tanks in which individual containers were placed. Ages at maturity for this subsample of fish measured for growth are indicated with arrows; sample sizes in parentheses.

FIG. 2. Von Bertalanffy growth curves for males from each of six stocks, calculated as in Figure 1. Ages at maturity indicated with arrows; sample sizes in parentheses. Note the difference between Figures 1 and 2 in scale on the ordinate.

TABLE 3. *Product-moment correlations among stocks calculated from the stock means for females. Trait labels: as in Table 1.* * $P < .05$; ⇄ $P > .05$ *but* r *large enough to merit attention.*

	Alpha	L(alpha)	K	Longev.	Fec.	Wt. Off.
L(alpha)	0.395					
K	−0.514	−0.748				
Longev.	0.176	0.850*	−0.774⇄			
Fec.	−0.035	−0.695⇄	0.146	−0.347		
Wt. off.	0.157	−0.352	0.368	−0.264	0.151	
I.B. int.	−0.208	0.139	0.292	0.216	−0.420	0.659⇄

One correlation between male and female traits stood out. Stocks whose females matured early had males that matured late ($r = -0.700$). There was no significant association between age at maturity and longevity ($r = 0.176$) or fecundity and logevity ($r = 0.347$) calculated from stock means.

DISCUSSION

When mosquitofish were introduced to Hawaii in 1905, they entered into a natural experiment that has provided an unusual amount of information on the processes underlying the evolution of life-history traits and the rates at which they can occur. These experiments demonstrate that there are significant genetically-based differences in life-history traits among six stocks that shared common ancestors in 1905. The divergence, measured as the range of the stock means divided by the overall mean, was 69% for female growth rate, 64% for fecundity, 42% for male growth rate, 24% for interbrood interval, 22% for female age at maturity, 21% for weight of offspring, 20% for male age at maturity, 16% for longevity, 11% for male length at maturity, and 8% for female length at maturity. Not all divergences were significant (Table 2).

The possible causes of genetic divergence include founder effects, drift, and adaptation to local environments. These data cannot distinguish among those causes nor weigh their relative impact. They do establish that differences among populations in life-history traits can arise rapidly, for whatever reason. In Hawaii, mosquitofish have 2–3 generations per year. Thus there were 140–210 generations between the introduction of the fish to the reservoirs between 1907 and 1914 (Stearns, 1975) and the collection of their descendants in 1980. For female growth rates, if we assume 140 generations elapsed, that the divergence was gradual and continuous, and that it occurred in response to local selection pressures, then the rate of evolution was 0.49% per generation. For female age at maturity, it was 0.16% per generation, and for female length at maturity it was 0.06% per generation. The changes could have occurred rapidly soon after the introductions, then stopped, or the traits could still be diverging gradually, and part of the divergence could be due to founder effects. In any case, these estimates of the rate of evolution should not be quoted or used without appropriate qualification.

Females from stable reservoirs were larger and younger at maturity and had smaller offspring than females from fluctuating reservoirs. Males from stable reservoirs were smaller and younger at maturity than males from fluctuating reservoirs. In the field, there was no difference in the length at which 50% of females were pregnant between four stable (29.1 mm) and 20 fluctuating (28.3 mm) stocks that included those analyzed in this paper. However, males collected from stable reservoirs in January, 1974, were significantly smaller (21.2 mm) than males from fluctuating reservoirs (22.9 mm, $N = 1{,}398$, $P < .05$, nested ANOVA; Stearns, 1975). There are two ways to interpret these results: either the laboratory data reflect the field situation, or, as Berven et

al. (1979) documented for the green frog in Maryland and Virginia, the field situation is exactly the opposite of the laboratory situation because of counter-gradient selection on developmentally plastic traits. Under the first interpretation, the results imply that both females and males gain fecundity more slowly with size in the stable reservoirs than in the fluctuating reservoirs (Stearns and Crandall, 1981). Under the second interpretation, in the field both sexes mature later in the stable reservoirs than in the fluctuating reservoirs. These data cannot resolve the issue, which can be settled with age estimates from otoliths of fish collected in the field.

One of the earliest generalizations of life-history theory, drawn largely from comparisons among species and higher taxa, was that life-history traits tend to be associated in two patterns (Pianka, 1970): early maturation, a short life, high reproductive effort, and many small young, on the one hand, and late maturation, a long life, low reproductive effort, and a few large young, on the other. That idea was challenged with a review of 35 studies in which 18 fit the generalization and 17 did not (Stearns, 1977). It can also be tested with correlations among the stock means in this study. The only significant correlation (Table 3) is between longevity and length at maturity ($r = 0.850$); the correlation between longevity and age at maturity is much lower and insignificant ($r = 0.176$). There were suggestively large, but statistically insignificant, correlations between fecundity and length at maturity ($r = -0.695$), longevity and growth rate ($r = -0.774$), and interbrood interval and weight of offspring ($r = 0.659$), but not between fecundity and size of young ($r = 0.151$) or between fecundity and age at maturity ($r = -0.035$). Thus comparisons among populations of mosquitofish cannot be fitted neatly into the "accepted scheme" (Stearns, 1977).

It has been argued (e.g., Caswell, 1983) that it matters little if such differences are genetically based or the result of developmentally plastic interactions with the environment, since in either case the response is assumed to be an adaptation shaped by demographic pressures. However, at least three arguments suggest that the distinction is critical. First, one purpose of life-history studies is to predict how life-history traits will change in an altered environment. Plastic traits will change in the next generation; genetically-based traits will change much more slowly. Second, experiments are much more easily done on the nature of the plastic response, which can be elicited in a single generation, than on the causes of genetic differences, which are quite difficult to isolate. Third, the differences may not be adaptations and may have nothing to do with demographic pressures (Stearns and Sage, 1980).

In Stearns (1983) I gave an analysis of patterns of water level fluctuation in the set of fluctuating reservoirs, and described their impact on life-history traits in the field. Their primary effect was on the short-term expression of fecundity. What was the correlation of long-term patterns of water level fluctuation with the life-history traits as expressed under constant conditions, where differences among stocks have some genetic basis? There were only four stocks from fluctuating reservoirs, and a canonical correlation revealed no significant relation between water level measures and life-history traits. However, some individual correlations were significant.

The following measures of water level fluctuation in the reservoirs were taken from records of daily measurements spanning 16 years: volume of the reservoir (in million gallons), average percent full, percent of power in significant peaks (where power is defined by the Fourier transform, see Stearns, 1983, for details), ratio of power at periods of one week to power at periods of one year, ratio of power at periods of one week to power not in significant peaks, and ratio of power at periods of one year to power not in significant peaks.

Female length at maturity was negatively correlated with power in significant peaks ($r = -0.88$, $P < .05$) and with the strength of yearly fluctuations ($r = -0.95$,

$P < .01$). Female longevity was negatively correlated with reservoir volume ($r = -0.85$, $P < .05$). Weight-adjusted fecundity was quite strongly correlated with power in significant peaks ($r = 0.99$, $P < .01$), with the ratio of weekly to yearly power ($r = 0.94$, $P < .01$), with the ratio of weekly to background power ($r = 0.96$, $P < .01$), and with the ratio of yearly to background power ($r = 0.97$, $P < .01$). Offspring size was positively correlated with reservoir volume ($r = 0.83$, $P < .05$), and inter-brood interval was negatively correlated with average percent full ($r = -0.90$, $P < .05$).

These correlations indicate that strong, frequent fluctuations in water level select for fish that mature at small sizes and have high fecundities. Fish from larger reservoirs, which cannot fluctuate rapidly, have large offspring. Fish from reservoirs that have high average water levels, which also tend to be reservoirs that do fluctuate rapidly, had short inter-brood intervals. These inferences are consistent with field observations which indicate that rapid fluctuations select against large fish, while long periods of low water select against small fish (Stearns, 1983).

Summary

This study documents the degree to which six populations of mosquitofish that shared common ancestors in 1905 had diverged by 1980. Seven hundred thirty-eight fish were raised to maturity in individual containers with controlled feeding and closely regulated water temperatures. The two populations from Hawaii inhabited reservoirs whose water level did not vary; the four populations from Maui inhabited reservoirs whose water level fluctuated dramatically on periods ranging from days to seasons.

Island effects (effects of stable vs. fluctuating water levels) were significant for male and female age and length at maturity and for offspring weight. Females from stable reservoirs were larger and younger at maturity and had smaller offspring than females from fluctuating reservoirs. Males from stable reservoirs were smaller and younger at maturity than males from fluctuating reservoirs. Stock effects (effects associated with particular reservoirs) were significant for male and female age and length at maturity and growth rates, for the slope of the fecundity-length relation, and for offspring weights. No significant effects were observed for length-adjusted fecundity, interbrood interval, and longevity, for which sample sizes were smaller.

The degree of divergence among stock means ranged from 69% for female growth rate to 8% for female length at maturity, corresponding to a rate of evolution ranging from 0.49% to 0.06% of the value of the trait per generation, assuming 140 generations since 1905 and gradual change.

The only significant correlation among stock means was between longevity and length at maturity. Correlations between age at maturity and longevity, age at maturity and fecundity, and fecundity and weight of offspring were low and insignificant. These results do not fit neatly into any scheme that dichotomizes life-histories into a group of early-maturing, highly fecund organisms that have short lives and small young, and late-maturing, long-lived organisms that have a few large young. Correlations between measures of water level fluctuations in the reservoirs and the life-history traits of the fish whose parents had lived in those reservoirs were significant and consistent with field observations of the impact of fluctuations on mortality rates.

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