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Genetics

Size-mediated onset of genetically determined maturation in the platyfish, *Xiphophorus maculatus*

(nutrition/weight at maturation/age at maturation/critical weight)

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ABSTRACT A single sex-lined gene that controls the maturation process had previously been identified in *Xiphophorus maculatus*. It was presumed that this gene controls the age of onset of maturation. We demonstrate that the gene is either activated or not inhibited from activity by the attainment of a critical weight rather than age.

There exists considerable doubt as to whether an individual's size or age is most important in determining the onset of maturation in fishes (1–3). Maturity is frequently presumed to be associated with the attainment of a critical size (1–3), although many demographic models are age dependent (4–6). Fishery biologists have observed that faster-growing fish mature at an earlier age than slower-growing fish, but in many cases the fastest- and slowest-growing individuals mature at sizes smaller than individuals growing at intermediate rates (1–3). The difficulties in understanding the maturation process stem from the confounding effects of seasonality on growth and spawning, and the lack of a simple genetic mechanism that affects maturation.

Kallman *et al.* (7, 8) reported the discovery of a sex-linked gene in the platyfish, *Xiphophorus maculatus*, that affects the maturation process. According to Kallman *et al.*, the gene controls the age of onset of maturation. We report that individuals homozygous for "early maturation" initiate the maturation process only after a critical body weight is achieved. Because the time of attainment of a critical body weight is dependent upon the growth rate and the initial size of an individual, the age of onset of maturation is affected.

Individuals of *X. maculatus* homozygous for "early maturation," P^eP^e, complete the maturation process between 10 and 16 weeks of age. Heterozygous individuals, P^eP^l, require 16 to 25 weeks for completion of maturation and "late maturation" homozygotes, P^lP^l, require between 20 and 32 weeks to mature. Because males of *X. maculatus* stop growing at maturity, there is almost no overlap in the sizes of males of these three genotypes. In this species, as well as in other poeciliids, the anal fin transforms into an intromittent organ. This transformation of the anal fin is correlated with testicular differentiation and the organization of the gonadotropic zone of the adenohypophysis (7–9). Thus, it is possible to determine the time of onset of sexual maturation and its completion from external examination of the anal fin.

If the activity of the *P* gene is related to the attainment of a critical weight as opposed to critical age, then (*i*) the weight at initiation of maturation should be constant with respect to time at initiation, and (*ii*) changing the growth rate and initial size should change the timing of onset of the maturation process. That is, slower-growing fish of the same genotype and similar starting weights should initiate maturation at a later age than fish of a larger starting weight. To explore the activity of the *P* gene, we caused variation in the growth rate and initial size of individuals.

METHODS

All fish used in our experiment were derived from stocks that Kallman *et al.* (7) had identified as the "early maturing" genotype, P^eP^e. Four broods were used in the experiment; all derived from different females. One YY male of the Belize stock (3492s) was mated to two XX females of the Rio Jamapa stock ($163A^{50}$) and one XY male derived from the cross (3492s × $163B^{47}$) was mated to two XX females of the Rio Jamapa stock ($163B^{48}$). After birth, all members of a brood were transferred from their birth tank and placed in a 20.1-liter tank. Fish were fed frozen brine shrimp twice daily from birth to separation. Each member of a brood was placed in a separate, shielded, 1.89-liter jar. Unfortunately, it was impossible to begin members of different broods at the same age. Brood 1 was started on day 17 after birth, brood 2 on day 3, brood 3 on day 20, and brood 4 on day 14 after birth. Fish were anesthetized with Finquel weekly and examined for anal fin metamorphosis, and their weights and standard lengths were recorded. The laboratory temperature was maintained at 25° ± 2°. The natural photoperiod was not supplemented during the course of the experiment, which lasted from May 19, 1976 to November 5, 1976. To cause variation in the growth rate of individuals, some fish were fed once a day while others were fed once a week; each feeding consisted of approximately 30 frozen brine shrimp.

Because the fish initiate maturation between observation periods and grow at an approximately exponential rate, we estimated the weight at initiation by the antilogarithm of $(\log W_i + \log W_{i-1})/2$, in which W_i is the weight recorded when the fish was first observed to have initiated maturation and W_{i-1} is the weight recorded at the previous observation period. The age of initiation was estimated as $(A_i + A_{i-1})/2$ in which A_i is the age at discovery of initiation and A_{i-1} is the age at the last observation before initiation. Because individuals of the different broods began the experiment at different ages, it was necessary to use the transformation T^* = age at initiation − age at start of the experiment, to examine correctly the effects of growth rate and intitial size on time and weight at intitiation.

RESULTS

Fig. 1 shows the relationship of weight at intitiation to age at initiation. The regression equation of weight on age is $W = 77.6$

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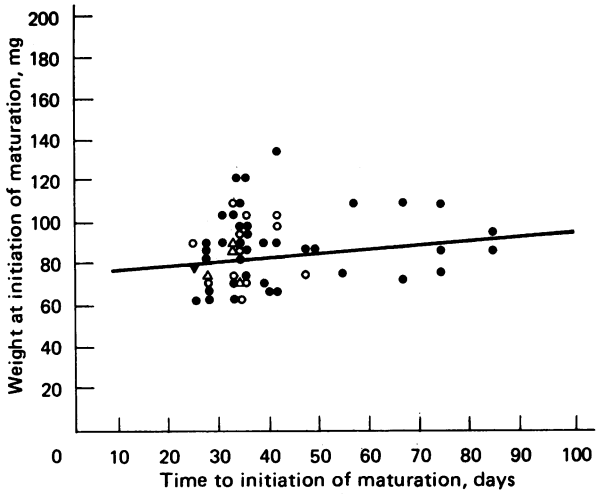

FIG. 1. Body weight and age at initiation of sexual maturation in *Xiphophorus maculatus* homozygous for "early maturation" following manipulation of growth rate. The regression equation of weight on age is $W = 77.6 + 159T$ (degrees of freedom = 73, $t = 1.08$, $P > 0.10$). ● = 1 individual; ○ = 2 individuals; △ = 3 individuals.

$+ 0.159T$, the slope of the regression is not significantly different from zero (degrees of freedom = 73, $t = 1.08$, $P > 0.10$). Thus, maturation is intitiated at a constant weight. The partial correlation coefficient between age at initiation T^* and growth rate (with initial size constant) is −0.742 (degrees of freedom = 72, $P < 0.001$). The partial correlation coefficient between age at initiation T^* and initial size (with growth rate constant) is −0.7218 (degrees of freedom = 72, $P < 0.001$). Thus, a smaller starting size or slower growth rate increases the time to initiation. Even when the correction is not applied, the results are robust. The partial correlation coefficient between age at initiation (actual) and the growth rate is −0.682 (degrees of freedom = 72, $P < 0.001$) and the partial correlation coefficient between age at initiation (actual) and initial size is −0.6982 (degrees of freedom = 72, $P < 0.001$).

The results demonstrate that the onset of maturation takes place only after an individual achieves a body weight of approximately 70 mg; this finding indicates that the timing of initiation is not genetically determined, but is a function of growth rate and initial size. At present, we have not tested fish that are heterozygous for maturation, P^eP^l, but evidence (7, 8) indicates that at a size when P^eP^e individuals have initiated maturation, P^eP^l individuals have not. We suggest, therefore, that the P gene is either activated or not inhibited by the attainment of a critical body weight, which reflects a critical metabolic state (9, 10).

DISCUSSION

Studies on some mammals (10) demonstrate that the initiation of maturation is a function of body weight rather than age. In reptiles (11–13), molluscs (14, 15), holothurians (16), protozoans (17), crustaceans (18–21), and polychaetes (22) the association of a critical body weight or length with the maturation process has been documented. If in these groups as in the platyfish, maturation depends upon size rather than age, then life-history theory and demography based solely upon age-specific variables must be reexamined (23).

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