Size, Age and Demography of Metamorphosis and Sexual Maturation in Fishes

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SYNOPSIS. Understanding what determines the timing of transitions between life-history stages in fishes is crucial to an understanding of their demography. Most theoretical treatments assume that these transitions are age dependent, but evidence accumulating from a variety of organisms indicates that size is an important variable also. In the starry flounder, Platichthys stellatus (Pallas), the onset of metamorphosis is more closely related to size than age. In the platyfish, Xiphophorus maculatus (Günther), the onset of sexual maturation depends on both size and age. I compare these results with those reported for other organisms, and outline the expected ecological correlates of age- and size-dependent transitions between life history stages in general.

INTRODUCTION
The life histories of many animals and plants are divided into well-defined stages. For example, many angiosperms go through the stages of seed, seedling, immature, and flowering adult. Many animals, including crustaceans, molluscs, echinoderms, and fish go through most of the following stages: egg, one or more larval stages, sexually immature (juvenile), and sexually mature (adult).

An understanding of the life histories and population biology of these organisms depends crucially on an understanding of the timing of these stages. This is because the behavior of populations will be different for different timing mechanisms. For example, if a transition is triggered by the attainment of a certain age, conditions unfavorable to growth will result in a population of smaller individuals. On the other hand if the transitions are triggered by size, conditions unfavorable to growth will delay the transitions. If one of the stages involves dispersal, conditions unfavorable to growth will increase dispersal, decrease local recruitment, perhaps increase gene flow, etc. If the transitions are triggered by a combination of age and size the effects of conditions unfavorable to growth will be different from those associated with purely size- or purely age-triggered transitions.

Most theoretical treatments consider the onset of these stages to be age determined (e.g., Leslie, 1945; Futuyma, 1979). This seems to be due to two factors. Firstly, it is easier to treat ages than sizes, because age increases linearly with time, while size need not. Secondly, until recently, there has been little experimental evidence indicating otherwise, and the detailed studies of Alm (1959) have been overlooked.

Alm was interested in the relationship between maturity, size and age in fishes. His survey of fisheries literature covering a period of about 80 years revealed much confusion on these topics. His experiments on freshwater fishes did not completely resolve the confusion, because of his experimental conditions and the fish he used. Nonetheless, his work did show clearly that the onset of maturation in fishes was related to genetic constitution and size, in addition to age.

In many other organisms, recent evidence suggests that the stages are not merely age dependent. For plants, Werner and Caswell (1976), Sohn and Policansky (1977), Policansky (1981), and Solbrig (1982) have shown that size is a better predictor of an individual's fate than is age. In other words, the onset of sexual reproduction (flowering), reproductive success, sexual state, and mortality have all been shown to be more closely correlated with size than with age. Wilbur and Collins (1973) and Smith-Gill and Berven (1979)
have shown that neither size nor age alone predicts metamorphosis in amphibians, and the latter authors argued that differentiation rate is the best predictor. Nijhout and Williams (1974), Nijhout (1975), and Blakely and Goodner (1978) have shown that the onset of metamorphosis in two insect species is determined by size, while in other insect species (Beck, 1971) neither age nor size appears to be the determining factor. Frisch and McArthur (1974) have shown that there is a minimum critical weight required for the onset and maintenance of reproductive activity in human females. Some molluscs and other marine invertebrates are able to delay metamorphosis depending on environmental conditions (Jackson and Strathmann, 1981; Pechenik, personal communication) and in the American Plaice (Hippoglossoides platessoides (Fabricius)) sexual maturity is probably at least partially size dependent (Pitt, 1975).

On the other hand, some organisms do have age-determined onset of life-history stages. Berven and Gill (1983) showed that under certain conditions metamorphosis in frogs is more closely related to age than to size. The most striking case of an age-determined transition is that of the pink salmon, Oncorhynchus gorbuscha (Walbaum), which nearly always matures in its second year, at sizes ranging from 1 to more than 6 kg (Scott and Crossman, 1973).

I have been studying metamorphosis in the starry flounder, Platichthys stellatus (Policansky, 1982), and, with colleagues, sexual maturation in the platyfish, Xiphophorus maculatus (McKenzie et al., 1983). We are interested in the determinants, or at least the ecological correlates, of the onset of these life-history stages, in particular the influences of age and size. We also want to know how much genetic variability there is for these traits. In this paper I will briefly present the results of the work with these fish species, and then discuss what conditions I believe will favor age- versus size-determined onset of transitions between important life-history stages.

**Platyfish**

The genetics of this species has been much studied. For the present discussion, the greatest interest of this fish is the presence of a locus, P, that is involved in control of sexual maturation (Kallman et al., 1973). At least six alleles can be distinguished at this locus (Kallman and Borkoski, 1978) which cause male platyfish of different P genotypes to mature at different ages and weights. Under certain conditions the onset of maturation appears to be a function of the age of the fish (Schreibman and Kallman, 1977; Kallman and Borkoski, 1978) while under different conditions it appears the onset of maturation is size determined (Sohn and Crews, 1977). To clarify the nature of the relationship between age and size at maturation, McKenzie et al. (1983) raised male platyfish of two maturation genotypes (P^P^3 and P^P^4) under a wide variety of environmental conditions. We raised the fish in isolation to minimize the effects of social interactions on maturation (Borowsky, 1973; Sohn, 1977), and varied their food, light and temperature environments. The fish were weighed and examined for signs of maturation at least as often as once per week. Sexual maturation in platyfish is associated with the transformation of the anal fin into an intromittent organ, the gonopodium (Grobstein, 1940).

When the fish grew extremely rapidly, it appeared that there was a minimum age below which they would not mature (Fig. 1). For completion of maturation, this age was about 9 wk for P^P^3 males and about 14 wk for P^P^4 males, and there was great variation in the weights of these fish. As the fish grew more slowly, they matured later, and the slowest growing fish appeared not to mature until they reached a minimum weight, however long it took (Fig. 1). These weights were about 50 and 100 mg for the P^P^3 and P^P^4 genotypes, respectively, and one P^P^4 fish took 45 wk to complete maturation (not shown on Fig. 1).

In spite of the enormous environmentally induced variation in age and weight at maturation the position of each maturing fish in an age-weight space specified its genotype (with one exception). In other words, of 76 P^P^3 and 104 P^P^4 fish, it was possible to identify the genotype of all but one individual correctly by its age and weight at maturation.
DEMOGRAPHY OF LIFE-HISTORY STAGES

1.8

10 20 30 40
Age(weeks)

Fig. 1. Age and weight at completion of maturation of two genotypes of platyfish. Outlines contain all points representing the two genotypes; the diamond represents one P'P' fish. There were 76 P'P' and 104 P'P* fish.

STARRY FLOUNDER

Members of the order Pleuronectiformes (flatfishes) have a striking metamorphosis. They hatch as externally symmetrical, cod-like larvae. At ages ranging from a few weeks to many months and sizes ranging from less than 0.5 cm to more than 12 cm (Amaoka, 1971; Policansky, 1982) the neurocranium of the larva rotates through 90° carrying one eye with it, and the now asymmetrical little flatfish settles on the bottom. This metamorphosis usually involves a change from a pelagic life to a benthic one, and thus has important ecological consequences.

I have been studying metamorphosis in the starry flounder, a commercially important member of the family Pleuronectidae (Policansky, 1982). The fish occurs along the Pacific coast of North America and Asia from southern California to Japan. There has been no previous work designed to correlate metamorphosis with age and size in fishes. With this in mind I have raised the progenies of individual crosses of starry flounders at different temperatures and recorded their ages and sizes at metamorphosis.

I obtained live flounders from San Francisco and Monterey Bays, from Puget Sound, and from Japan, held them at the New England Aquarium in Boston, crossed them and raised the progenies of the crosses. The fish were fed on unicellular algae and rotifers at first, and later on brine shrimp nauplii. The tanks were examined daily for metamorphosing larvae; all larvae showing signs of eye migration were removed from the tanks, and measured to the nearest 0.05 mm standard length. The process of metamorphosis was very quick, occupying only 3–5 days. Technical details are given in two earlier papers (Policansky and Sieswerda, 1979; Policansky, 1982).

The mean temperatures in the tanks varied from 9.55 to 13.0°C. In 1977, only 92 progeny from three crosses completed metamorphosis, and they were considered together. In 1980 and 1981 the progenies were raised in individual 19 liter tanks. The progenies of four crosses in 1980 had 27, 32, 34, and 35 larvae that completed metamorphosis; in 1981 1,877 larvae from eight crosses were measured at metamorphosis. The number of metamorphosing larvae per tank ranged from 26 to 487.

There was a great range in the age at metamorphosis, which began as early as 27 days after fertilization of the egg, at 13°, and as late as 104 days, at 10.3°. The mean times ranged from 33.5 days, at 13°, to 75.3 days, at 10.7°. There was a correlation between temperature and time to metamorphosis (Fig. 2); the regression equation was time (days) = -8.9 X temperature + 153;

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 r = -0.69, \text{ } n = 14, \text{ } P < 0.005.
\]

It is clear from examination of Figure 2 and Table 1 that there was a considerable amount of variation in time to metamorphosis that was not explained by temperature, but no clear genetic component could be shown. One aspect of Figure 2 that probably does have a genetic component is the absence of any progeny raised at temperatures above 10° from crosses where both parents were from Japan. Al-
FIG. 2. Mean times to metamorphosis of larvae from 14 crosses raised at different temperatures. Open circles denote U.S. fish; closed circles denote Japanese fish; open circles with triangles denote hybrids.

though such tanks were set up, the larvae all died before metamorphosis when the water temperature exceeded 10°. Since all the adults had been in the New England Aquarium for up to three years, it seems that differential physiological adaptation of the females, and thus their eggs, was not to blame. This conclusion is supported by the fact that hybrids between Japanese and U.S. fish developed well at higher temperatures even when the mother was from Japanese waters.

The standard length at metamorphosis varied from 4.8–9.0 mm, but there was very little correlation between size and age at metamorphosis as can be seen from Table 1. This table also shows that mean sizes at metamorphosis varied much less than mean ages. The cross 82 × 98, whose progeny were raised at two temperatures, bears this out (Table 1). Since there can be no genetic difference, the large difference in times to metamorphosis is due to the temperature difference. The mean sizes at the two temperatures, on the other hand, were only slightly different. Thus it appears that metamorphosis in this species is more closely correlated with size than with age.

**DISCUSSION**

The aim of this research is to gain an understanding of the general pattern of transitions between important life stages. There is no reason to consider metamorphosis and sexual maturation as different in a general sense, although the specific ecological considerations may differ. In the following attempt to generalize conditions under which the transitions may be size determined or age determined the arguments apply to any important transition, although it may be easiest to imagine the case for sexual maturation.

The experiments show that the correlates of important transitions are different in platyfish and flounders. In male platyfish, the onset of sexual maturation is apparently influenced both by the fish’s size and by its age, depending on the conditions. There is also great genetic variability in the size and age of maturation due to allelic substitutions at a single locus. In the starry flounder the onset of metamorphosis is much more closely related to the size than to the age of the larvae. Furthermore I found no evidence of genetic variability in the size and age at metamorphosis, even between fish from as far apart as northern Japan and central California.

These differences are perhaps related to the fishes’ environments. When platyfish grow very rapidly, it appears as if the factor limiting the onset of maturation is the differentiation rate, and thus the fish do not initiate maturation until a minimum age is reached. As they grow more slowly, then apparently either the differentiation rate slows down as well as the growth rate, or there is a switch to a different triggering mechanism. When growth is very slow, it appears that there is a minimum weight below which metamorphosis will never occur. The combination of these two (or more) regimes produces the characteristic concave curves shown in Figure 1, called “plastic trajectories” by Stearns (1983).

Platyfish in nature live in very variable environments (Gordon and Gordon, 1954; Kallman et al., 1973; Kallman, 1974). It is thus not surprising that there is a great deal of genetic variability and phenotypic plasticity for age and size at maturation. Under stable conditions with abundant food, the fish should grow rapidly and mature as soon
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TABLE 1. Relationships between age and standard length at metamorphosis of starry flounder larvae.

<table>
<thead>
<tr>
<th>Parents (F X M)</th>
<th>Mean temp. ºC*</th>
<th>Mean age* (days)</th>
<th>Mean SL  † (mm)</th>
<th>Regression coefficient</th>
<th>r</th>
<th>N</th>
<th>P (slope = 0)</th>
</tr>
</thead>
<tbody>
<tr>
<td>91 X 59†‡</td>
<td>10.6 ± 0.8</td>
<td>66.3 ± 8.9</td>
<td>7.43 ± 0.44</td>
<td>-0.0062</td>
<td>-0.127</td>
<td>487</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>91 X 87</td>
<td>10.6 ± 0.8</td>
<td>67.4 ± 9.9</td>
<td>6.79 ± 0.35</td>
<td>-0.0068</td>
<td>-0.192</td>
<td>127</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>91 X 89</td>
<td>10.5 ± 0.7</td>
<td>66.1 ± 9.3</td>
<td>7.06 ± 0.37</td>
<td>-0.0105</td>
<td>-0.265</td>
<td>364</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>91 X 98</td>
<td>10.7 ± 0.9</td>
<td>75.3 ± 10.2</td>
<td>6.95 ± 0.49</td>
<td>-0.0160</td>
<td>-0.334</td>
<td>186</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>82 X 59†‡</td>
<td>10.6 ± 0.8</td>
<td>65.6 ± 8.4</td>
<td>6.62 ± 0.34</td>
<td>0.0000</td>
<td>+0.001</td>
<td>165</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>82 X 98 a</td>
<td>9.8 ± 0.7</td>
<td>54.6 ± 5.9</td>
<td>7.50 ± 0.40</td>
<td>-0.0077</td>
<td>-0.088</td>
<td>28</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>82 X 98 b</td>
<td>12.1 ± 1.4</td>
<td>39.3 ± 3.8</td>
<td>7.72 ± 0.36</td>
<td>-0.0130</td>
<td>-0.135</td>
<td>173</td>
<td>&lt;0.10</td>
</tr>
<tr>
<td>a and b</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td>60† X 59†‡</td>
<td>9.6 ± 1.1</td>
<td>58.9 ± 7.7</td>
<td>7.26 ± 0.37</td>
<td>+0.0058</td>
<td>+0.122</td>
<td>90</td>
<td>&gt;0.10</td>
</tr>
<tr>
<td>60† X 62‡</td>
<td>9.8 ± 1.4</td>
<td>65.9 ± 10.9</td>
<td>7.12 ± 0.46</td>
<td>+0.0008</td>
<td>+0.007</td>
<td>56</td>
<td>&gt;0.10</td>
</tr>
</tbody>
</table>

* Means given ± standard deviation.
† SL = standard length.
‡ Indicates fish from Japan.

as they are developmentally able to do so. If conditions are still stable, but with less abundant food, then it should be advantageous for a fish to grow slowly and delay maturation. Under very poor conditions, or strongly fluctuating, unpredictable conditions, such as may be found in a body of water that might not be permanent, a fish that matures at a small size is better off genetically than one that waits for the attainment of a larger size that may never be reached. According to this line of reasoning, the distribution of maturation genotypes should be predictable on an environmental basis. Furthermore, I would expect maturation to be age determined in rich or unpredictable conditions, and size determined otherwise.

The metamorphosis of flounders appears to depend on size. It involves the exchange of a pelagic life for a benthic one, and thus entails a change in diet. It is likely that predation rates and the size of potential food items are fairly constant within both pelagic and benthic habitats, and different between the two. One thus expects size to be the important trigger for metamorphosis, and that there is little genetic variability. In other words, there is nothing to be gained by metamorphosing at a small size if the newly metamorphosed juvenile cannot eat the available food.

My first general point is that if the environment is stable in time and space, then there is no difference between age- and size-triggered changes. This is because in such an environment there will be little variation in growth rate for a given genotype, and age and size will be closely correlated.

In some cases changes appear to depend on the organism's finding a favorable environment. For example, females of the dermestid beetle Troglodera glabrum (Herbst) require the presence of a granular substrate and a male of the species for pupation (Beck, 1971). In the echiuran, Boscilla viridis Rolando, larvae landing on the proboscis of a female develop into very small males, while most other larvae grow into much larger females (Bacci, 1965). Many other marine invertebrate larvae metamorphose only upon finding a suitable substrate, at varying sizes and ages (Thorson, 1957; Jackson and Strathmann, 1981; Pechenik, personal communication).

This may be merely a complication of the same basic issue. In spite of the environmental trigger, there is still a requirement for physiological competence to change stage, and it is of interest to know what factors influence the attainment of this competence. In some cases this complication becomes serious. For example, in polychaetes there is a great variety of physiological mechanisms and environmental cues involved in reproduction (Clark, 1979). This variety will undoubtedly make it harder to understand the physiological correlates of competence to become sexually mature.

If there is some important environment-
factor that influences two stages very differently, such as different food types being available to the different stages, or the existence of different predators on the different stages, then the change should be triggered by size. The metamorphosis of starry flounders probably represents an example of this. It may be the case that in order to successfully function at a particular stage, a certain minimum amount of energy is required, and this would also lead to a size-triggered change. There is danger of circularity here, though, because the judgement that there is a minimum energy requirement for a given stage may rest on having found a size-dependent transition to that stage.

If reproduction when small costs a lot, both in terms of survival and later reproduction, and if reproductive success increases quickly with increased size, then size should be the trigger at least in conditions that favor rapid growth. In other words, if less is lost by waiting until large size is reached, in terms of mortality, than is gained by reproducing at large size, then size should be the trigger. Maturation in fast-growing platyfish seems to be an example of this, as well as the size-related occurrence of flowering in mayapples (*Podophyllum peltatum* L., Sohn and Policansky, 1977).

Sex change is usually considered to be a size-related phenomenon (Ghiselin, 1969; Warner, 1975; Charnov, 1982), and it may thus be included in this class of changes. For example, sex change in jack-in-the-pulpit (*Arisaema triphyllum* L. Schott) appears to be size determined (Policansky, 1981). In pandalid shrimp, which change sex, first breeding is related to size, and sex change appears to be also (Rasmussen, 1953), but sex change may also be related to the population sex ratio (Charnov, 1979, 1982). On the other hand, if reproductive success does not increase much with increased size, and mortality of reproducitives of all sizes is high, then the transition should be triggered by age. The platyfish in our experiments that grew slowly because of poor environmental conditions probably represent this case. A good test of these ideas would be provided by comparing males and females of a species in which the relationship of reproductive success or reproductive cost differs for the two sexes.

One case of age-determined maturation, that of the pink salmon, remains puzzling. These fish have the most strongly age-determined maturation I know of, yet it is not clear how their mortality, growth and reproductive success differ from those of other salmonids, none of which have such strongly age-determined maturation. In at least one of them (*Salmo salar* L.) size seems to be an important factor, since there is a strong positive correlation between the size of returning (*i.e.*, recently matured) fish with the length of the spawning river (Schaffer and Elson, 1975).

Perhaps this case is unclear because of insufficient information; perhaps it is irrelevant, because some other selective factor or constraint is operating. A rigidly size-determined maturation would not be easy to explain in this case either. In spite of this difficult case, however, it does appear that there are patterns to be found, and that careful studies of the ecological and physiological correlates of transitions between life stages are important for an understanding of demography.

**Acknowledgments**


**References**


