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SELECTION AGAINST PARR MATURATION IN ATLANTIC SALMON

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ABSTRACT

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The feasibility of using scale characteristics to detect maturation as parr of anadromous male Atlantic salmon was examined. Smolt age and growth rate were found to be reliable indicators of prior maturation, whereas scale morphology did not differ between maturation phenotypes. Although determination of prior maturation was not 100% efficient, the resulting selection intensities would allow for effective artificial selection against anadromous males which had matured as parr.

INTRODUCTION

Maturation of males prior to seaward migration is common among populations of Atlantic salmon, *Salmo salar.* These small, "precocious" parr fertilize eggs in competition with large, anadromous males (Jones, 1959), and can stimulate anadromous females to spawn in the absence of anadromous males (Myers and Hutchings, 1986). Maturation of male parr can have major economic consequences. Increased mortality and delayed smoltification associated with parr maturation is responsible for the loss of 60% of the male salmon production in Newfoundland (Myers, 1984). As there is additive genetic variability for parr maturation (Naevdal et al., 1976), it would be advantageous to use anadromous males which had not previously matured as parr for broodstock. Selection could take place in hatcheries or when males ascend fishways if there was a method of determining whether males had previously matured.

Scale characteristics of smolt (salmon undertaking their first seaward migration) were analyzed to assess the feasibility of using the "river" zone of scales from anadromous males to identify individuals which had matured as parr. The usual method of determining prior maturation from scale analysis, by identification of spawning marks, cannot be used for deter-

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mining maturation at the parr stage because of the absence of scale resorption in most populations (Jones, 1959). Age at smoltification, growth rate, and scale morphometry were examined to distinguish males which had previously matured as parr.

Maturation before migration to sea is common among male salmonids (e.g., *Salmo gairdneri*, Schmidt and House, 1979; *Oncorhynchus tshawytscha*, Robertson, 1957; *O. masou*, Utoh, 1976; *O. nerka*, Hanson and Smith, 1967; *Salvelinus fontinalis*, Power, 1980). Techniques for distinguishing such males in Atlantic salmon may be useful for other iteroparous salmonids.

METHODS

Methods of detecting parr maturation by scale examination were tested on smolt whose maturation history had been independently determined by gonadal examination. For this feasibility study, male smolt were assumed to be representative of returning anadromous males. This is an approximation because mortality at sea may depend upon smolt age and size.

Scales of smolt (n = 1052) collected by A.R. Murray from the Little Codroy River, Newfoundland, Canada, were used in the analyses (Murray, 1968a,b; Myers, 1984). The Little Codroy River is close to the centre of the Atlantic salmon's range in North America. Approximately 70% of 1-year-old male parr mature in this stock (Myers, 1984). Surviving mature parr either smoltify (approximately 7%), or remain in the river and mature the following year. Approximately 10% of the males mature for the first time as age 2 parr. Smolt age is predominantly 2, 3, or 4 years.

Yearly growth was inferred from scale annuli as determined by standard criteria (Berg and Grimaldi, 1967). Annulus radii were measured from the focus along the longest oral radius (Tesch, 1968). Scale width was measured as the distance from the focus to the first, second, or third annulus along the 45° angle from the principal scale axis. This measurement was repeated along the 315° angle.

The amount of selection applied to a population can be measured by the selection intensity, the difference in the mean of a trait before and after selection divided by the phenotypic standard deviation of the trait before selection (Falconer, 1981). A modification of the notion of selection intensity is required for a trait such as sexual maturation because it is discontinuous, i.e., a male either matures or it does not, although the trait is controlled by more than one gene. Selection intensity for non-maturation as parr is therefore defined assuming parr maturation to be a threshold character having an underlying normal distribution for "liability" (Falconer, 1981, chapter 18). The mean liability of a group is the deviation of the threshold from the group mean in standard deviation units of liability (calculated from Appendix Table A in Falconer, 1981). The selection intensity is thus defined as the difference in liability for non-precocious maturation from the selected stock, divided by the standard deviation for liability (assumed to be the same before and after selection).

TABLE 1

Age-specific abundance and selection intensity

		Cohort (year of hatching)			
		1956	1957	1958	1959
Smolt abundance estimate					
Age 2	immature	520	482	304	716
	mature	320	231	76	179
Age 3	immature	1137	895	447	489
	mature	1927	934	652	688
Age 4	immature	19	13	13	0
	mature	29	153	26	60
Selection intensity if only river age 2 males breed		0.49	0.42	0.83	0.68
Proportion of males of river age 2		0.21	0.26	0.25	0.42

RESULTS

Discrimination by age

The delay that maturation imparts upon the parr—smolt transformation (Myers, 1984) makes age at smoltification an appropriate variable to use in identifying males which had previously matured. The selection intensity for non-precocious maturation was computed assuming only those anadromous males which smoltified early in life were allowed to reproduce. If the age at smoltification of broodstock salmon could be determined by scale analysis, then it would be possible to select only those males which had smoltified at ages 2 or 3. Yearly variation in age at smoltification necessitates the calculation of selection intensity on an annual basis (Table 1).

If only salmon which smoltified at age 2 were allowed to breed then a significant selection intensity would result. The proportion of eggs fertilized by anadromous males which had not previously matured would approximately double (Table 1).

Discrimination by scale growth

The mean growth rate of mature male parr during maturation is less than the mean growth rate of individuals which do not mature as parr (Leyzerovich, 1973; Saunders et al., 1982). It is therefore reasonable to attempt to identify males which had matured as parr by determining the reduction in scale growth beyond the first year of life. For 2-year-old smolts, this is estimated as the distance between the second and first annulus. Similarly, for 3-year-old smolt, this is the distance between the third and first annulus.

Note that no attempt is made to distinguish between males which mature for the first time at 1 or 2 years, because approximately 70% of the population mature for the first time at age 1 while only about 10% mature for the first time at age 2 (Myers, 1984).

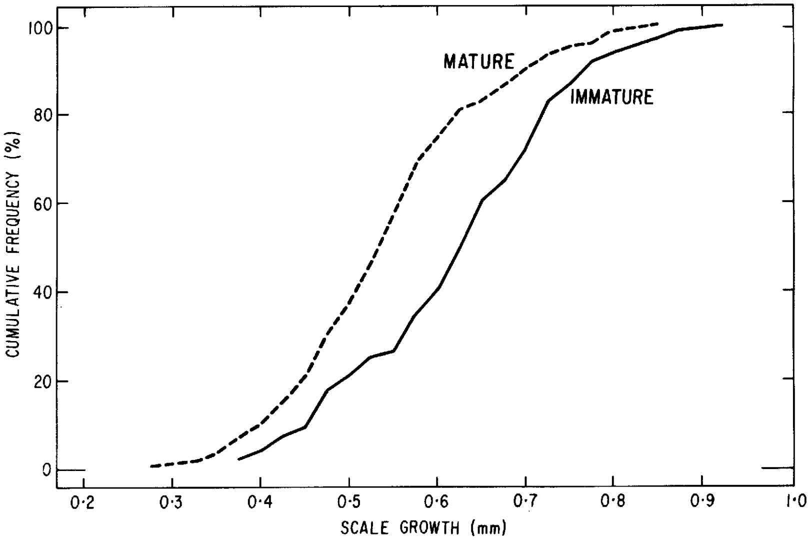

Fig. 1. Cumulative frequency distribution for 96 age 3 male smolts that had matured as parr (······) and 164 that had not (———) plotted against scale growth between ages 2 and 3. Data for 1958 and 1959 smolt classes.

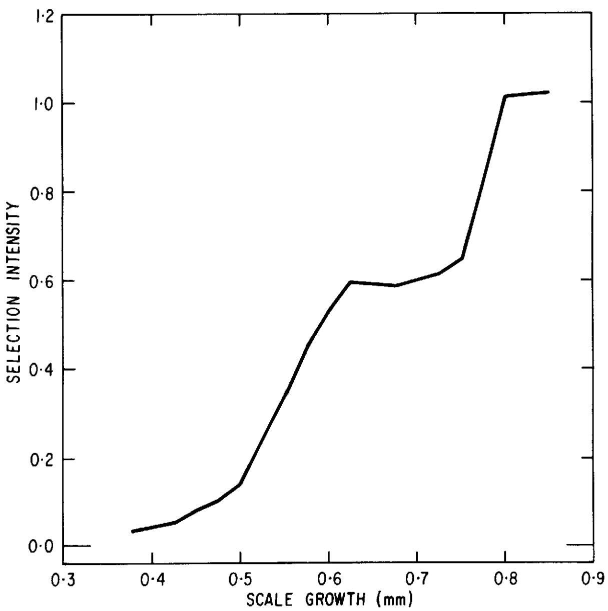

Fig. 2. Selection intensity for age 3 smolts if only those with second and third year scale growth greater than the given level are allowed to breed.

A reasonable approach to select in a breeding program would be to allow only those males within any river-age class with an inter-annulus distance above a pre-determined level to breed. By plotting the cumulative frequencies against inter-annulus distance, the effect of any selection criterion on immature and mature males can be computed (Fig. 1). For example, if only males with an inter-annulus distance of 0.6 mm were used as broodstock, then 56% of the previously immature males would breed while only 25% of the males which had matured as parr would breed. The resulting selection intensity (calculated for the population of river-age 3 males) is sufficient to be useful in a breeding program even if only one river-age class is present (Fig. 2). The selection intensity is greater than 0.50 for the upper half of the growth range (extreme values are highly variable because of small sample size). The use of inter-annulus distance is slightly less effective for river-age 2 males; there is less separation between the cumulative distributions because the males had been mature for only 1 year.

Discrimination by scale morphometry

The abdomens of mature male parr are distended due to enlargement of their gonads (Jones, 1959). If this increase in body circumference is recorded on the scales it might serve to identify males which had matured as parr. Unfortunately, the increase in scale width during ages 2 and 3 did not discriminate males which had matured as parr from those which had not. There were no significant differences between mature and immature males in (i) width of the third annulus, (ii) width of the second annulus, (iii) scale growth in width during the second year of life (the difference in width of the second and first year annulus), and (iv) scale growth in width during the second and third year of life (the difference in width between the third and first annulus) (t tests, $P > 0.05$, $n = 50$).

DISCUSSION

Biological considerations

The age and growth of salmon, as recorded on the scales, can serve to distinguish males which did mature as parr from those which did not with sufficient accuracy for a broodstock selection program. Significant selection intensities against parr maturation can be obtained by selecting broodstock on the basis of age at smoltification only. In the Little Codroy population, if only salmon which smoltified at age 2 were allowed to breed, then the proportion of eggs fertilized by anadromous males which had not previously matured would approximately double (Table 1).

Selection intensity against parr maturation can be increased by discriminating broodstock on the basis of scale growth. This would be particularly useful if there was little variation in the age at smoltification. Selection intensities greater than 0.5 can be achieved using only the growth data of age 3 smolt during the second and third year of life (Fig. 2).

There was no detectable reduction in the width of scales associated with parr maturation. Similarly little evidence of spawning marks (erosion along the edge of scales associated with spawning) for the Little Codroy population was found. In a study of another Newfoundland population, Dalley (1978) found that only 15% of the smolt known to mature showed signs of spawning marks. However, in populations from the American massif, France, Bagliniere and Maisse (1985) found that nine of the 14 smolt examined known to have matured as parr showed spawning marks. Bagliniere and Maisse (1985) attributed the clarity of the spawning marks in their sample to the excellent conditions for growth of Atlantic salmon in their region. Thus, in areas with good growth rates, discrimination of males through identification of spawning marks may serve as an alternative method to those described herein.

In a broodstock selection program designed to reduce the incidence of mature male parr, it is desirable to avoid selecting against other desirable traits (Doyle and Myers, 1982). For example, although males which mature at age 1+ grow faster on average during their first year of life, selecting for males which grow slowly during the first year of life has an obvious disadvantage; one also selects for slower growth. Thus, only selection on growth rate past the first year was considered in the present work.

Economic considerations

Although it is feasible to select against males which mature as parr using scale analysis, the decision to implement such a scheme would depend in part upon whether selection was carried out in a hatchery or under natural conditions. If salmon are reared to the smolt stage or beyond in a hatchery, then selection against maturation as parr may be unnecessary because maturation can be environmentally controlled (Saunders et al., 1982). If salmon are reared only to the fry stage, as is common in enhancement projects, then selection would probably be profitable if the scale analysis was inexpensive. The cost of the analysis could be partially offset by selling those males not allowed to breed. The principal limit in such a scheme would be the necessity of avoiding inbreeding depression, i.e., selection intensity could not be too great.

Selection could also be carried out in natural populations as males pass through a fishway or counting fence. There are, however, dangers to such a scheme. If early- and late-maturing males are maintained as an evolutionarily-stable mixture of maturation phenotypes, then any unnatural alteration in the phenotype ratio could result in a compensatory response by the population to re-establish a stable equilibrium. That is, instead of selecting against maturation as parr, the realized selection might be for males to forgo smoltification altogether and mature only in the river. Such a selection scheme could not be recommended unless more is known about the evolution of parr maturation (Myers, 1986).

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