

Parental influence on growth rate, smolting rate and survival in hatchery reared juvenile Atlantic salmon, *Salmo salar*

J. E. THORPE AND R. I. G. MORGAN

Freshwater Fisheries Laboratory, Pitlochry, Perthshire PH16 5LB, Scotland

(Accepted 27 February 1978)

The proportion of potential 1-year smolts, their mean length, the mean length of potential 2-year smolts, and the mortality rate in four half-sib families of Atlantic salmon, reared under four contrasted conditions of overhead cover, is shown to be influenced primarily by genetic factors (89.9%, 86.1%, 82.7% and 80.2% of total variance respectively). Variation between families in smolting rate and mortality rate is influenced by both parents, but more by the male than the female. Variation in mean length is influenced almost entirely by the female parent. These results are discussed in relation to previous findings on bimodality of size distribution and inheritance of growth and mortality characteristics in Atlantic salmon.

I. INTRODUCTION

In a review of the bimodal distribution of size of juvenile Atlantic salmon, *Salmo salar* L., within 52 unrelated family groups reared at the Almondbank smolt rearing station, Thorpe (1977) found a significant correlation between the proportion of progeny in the upper mode of their length distributions and the fork length of the female parent, but no such correlation with the male parent. It was concluded tentatively that the progeny of females of high growth capacity show a higher growth capacity themselves than do those of females of lower growth capacity. This paper reports on a subsequent experiment, using half-sib family groups, designed to examine this hypothesis more closely.

II. MATERIALS AND METHODS

The age and growth histories of a group of mature adult salmon, caught in October 1975 from the spawning migration in the River Almond, Perthshire, were determined by scale-reading. Two male and two female fishes of two stream years plus two sea winters (2.2+) were selected, and each female's eggs divided into two batches. For each female one batch of eggs was fertilized with milt from one male. The four sets of half-sib juveniles (Table I) were reared in a 4 × 4 latin square array of 2 m diameter radial flow fibreglass tanks (Minaur, 1973) as in the 1975 experiments (Thorpe, 1977), each tank having an initial stocking density of 800 alevins. The effects of four conditions of overhead cover (Table II) were also examined in this experiment, but specific effects of cover will not be considered in this paper. The fish were fed on a standard commercial dry diet, growth in length and weight was monitored by measuring every individual in each tank after 171–174 days feeding. Separation of the modes in the bimodal distributions of lengths was achieved by Cassie's (1954) method. Survival from first feeding to monitoring averaged 85.3%.

III. RESULTS

PROPORTION IN UPPER LENGTH MODE (TABLE III)

The four families showed consistent differences in their length distributions under all four conditions of cover (Fig. 1). Since mortality also varied between families

TABLE I. Mating scheme for half-sib families

Family No.	Male	Parents		Length (cm)
		Length (cm)	Female	
1	A	91.1	C	88.0
2	B	89.0	C	88.0
3	A	91.1	D	79.7
4	B	89.0	D	79.7

TABLE II. Layout of tanks

	Column			
	1	2	3	4
Row 1	1WR	3W	2NR	4N
2	4NR	2N	3WR	1W
3	2W	4WR	1N	3NR
4	3N	1NR	4W	2WR

Top covers: N, Net; W, Wire mesh and black polythene ring.

Inner cover: R, Aluminium ring.

Families: 1-4.

TABLE III. Percentage of populations in upper length mode 25-29.10.76

Tanks	Column			
	1	2	3	4
Row 1	68.0	31.0	30.0	15.0
2	9.0	31.0	31.0	65.0
3	28.0	7.0	76.0	37.0
4	24.0	83.5	8.0	6.5

Mean values: Family: (1) 73.1%, (2) 23.9%, (3) 30.8%, (4) 9.8%.
Progeny of ♂A: 51.9%, B: 16.8%, ♀C: 48.5%, D: 20.3%.

(Table IX), the proportion data of Table III are based on differing numbers of fish between tanks, and therefore the analysis of variance (Table IV) has been made on angular transformations of these data. The individual parents of both sexes show large and statistically significant differences in their influence on the proportions of their progeny in the upper length mode: the family interaction and environmental effects do not.

Small percentage values in the upper mode in October are difficult to distinguish accurately by the Cassie method. Therefore values for all families were checked again in February 1977, when separations of modes were clear, due to continued length growth of the upper mode fish during the winter (Thorpe & Morgan, in preparation *a*). The percentage values in February did not differ from those in October (χ^2 values for the comparisons of families as follows: (1) 0.25, (2) 0.06, (3) 0.73, and (4) 1.16.)

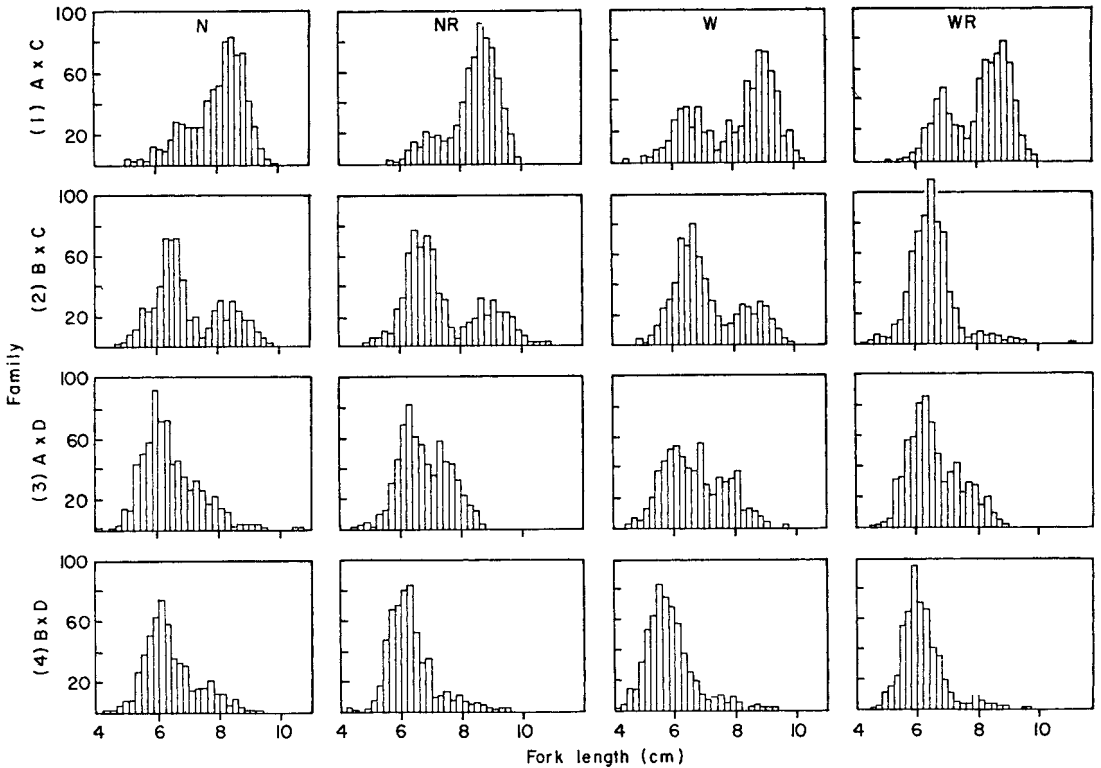


FIG. 1. Fork length frequency distributions in October for four half-sib families (males A, B; females C, D) of O+ Atlantic salmon (*Salmo salar*), reared under four conditions of cover (N, top net; W, top wire-mesh+polythene; R, 15 cm-wide aluminium ring suspended inside tank).

TABLE IV. Analysis of variance of angular transformation of data of Table II

Source of variation	Sum of squares	Degrees of freedom	Mean square	<i>F</i>	<i>t</i>	<i>P</i>
Male parents	2130.98	1	2130.98		7.47	<0.01
Female parents	1282.89	1	1282.89		5.80	<0.01
Family	223.43	1	223.43		2.42	n.s.
Top cover	128.54	1	128.54		1.84	n.s.
Inner cover	4.96	1	4.96		0.36	n.s.
Rows	59.17	3	19.72	0.517		n.s.
Columns	63.56	3	21.19	0.555		n.s.
Error	152.66	4	38.16			
Total	4046.19	15				

MEAN LENGTHS

(a) Upper Mode (Table V)

The female parents show significant differences in their influence on the size of their upper mode progeny, whereas the males do not (Table VI). There are no significant effects attributable to family interactions or to environmental constraints.

(b) Lower Mode (Table VII)

Both male and female parents influence the size of their lower mode progeny significantly (Table VIII), but the variation attributable to the female parents (72%

TABLE V. Mean lengths (cm) of fish in upper mode of length distribution, 25-29 October 1976

	Column			
	1	2	3	4
Row 1	8.52	7.74	8.93	7.72
2	7.96	8.29	7.39	8.79
3	8.52	7.94	8.31	7.45
4	7.53	8.59	7.60	8.38

Mean values: Families: (1) 8.55 cm, (2) 8.53 cm, (3) 7.53 cm, (4) 7.81 cm. Progeny of ♂A, 8.04 cm; ♂B, 8.17 cm; ♀C, 8.54 cm; ♀D, 7.67 cm.

TABLE VI. Analysis of variance of mean length data of Table V

Source of variation	Sum of squares	Degrees of freedom	Mean square	<i>F</i>	<i>t</i>	<i>P</i>
Male parents	0.065025	1	0.065205		< 1	n.s.
Female parents	3.0625	1	3.0625		5.697	< 0.01
Family	0.09	1	0.09		< 1	n.s.
Top cover	0.000625	1	0.000625		< 1	n.s.
Inner cover	0.027225	1	0.027225		< 1	n.s.
Rows	0.095625	3	0.031875	0.338		n.s.
Columns	0.018525	3	0.006175	0.065		n.s.
Error	0.37745	4	0.0943625			
Total	3.736975	15				

TABLE VII. Mean lengths (cm) of fish in the lower mode of length distribution, 25-29 October 1976

	Column			
	1	2	3	4
Row 1	6.69	6.04	6.52	5.94
2	5.98	6.23	5.95	6.40
3	6.39	5.85	6.57	6.12
4	5.84	6.73	5.51	6.22

Mean values: Families: (1) 6.60 cm, (2) 6.34 cm, (3) 5.99 cm, (4) 5.82 cm. Progeny of ♂A, 6.29 cm; ♂B, 6.08 cm; ♀C, 6.47 cm; ♀D, 5.90 cm.

of the total variation) is seven times that attributable to the males. There are no other significant sources of variation, but the cover constraints and some uncontrolled environmental factors appear to have influenced the size of these smaller fish more than they have those of the upper mode.

(c) Mortalities (Table IX)

Individual parents of both sexes show statistically significant differences in their influence on the mortality of their progeny (Table X). The family interaction has an added significant influence, as also does some uncontrolled environmental factor evident in the column variance.

TABLE VIII. Analysis of variance of mean length data of Table VII

Source of variation	Sum of squares	Degrees of freedom	Mean square	<i>F</i>	<i>t</i>	<i>P</i>
Male parents	0.180625	1	0.180625		4.115	<0.02
Female parents	1.2769	1	1.2769		10.94	<0.001
Family	0.0081	1	0.0081		0.87	n.s.
Top cover	0.0484	1	0.0484		2.13	n.s.
Inner cover	0.081225	1	0.081225		2.76	n.s.
Rows	0.116125	3	0.038708	3.628		n.s.
Columns	0.019325	3	0.006442	0.604		n.s.
Error	0.042675	4	0.010669			
Total	1.773375	15				

TABLE IX. Total deaths from first feeding (7 May) to monitoring (25-29 October 1976)

	Column			
	1	2	3	4
Row 1	52	132	75	236
2	169	146	72	71
3	106	224	63	106
4	48	53	169	116

Means: Families: (1) 60 (i.e. 7.5% mortality), (2) 111, (3) 90, (4) 200. Progeny of ♂A, 75; ♂B, 155; ♀C, 85; ♀D, 145.

TABLE X. Analysis of variance of mortality data of Table IX

Source of variation	Sum of squares	Degrees of freedom	Mean square	<i>F</i>	<i>t</i>	<i>P</i>
Male parents	25921.0	1	25921.0		10.41	<0.001
Female parents	14042.25	1	14042.25		7.66	<0.01
Family	3481.0	1	3481.0		3.82	<0.02
Top cover	132.25	1	132.25		0.74	n.s.
Inner cover	676.0	1	676.0		1.68	n.s.
Row	2056.25	3	685.42	2.87		n.s.
Column	6892.75	3	2297.58	9.61		<0.05
Error	956.25	4	239.0625			
Total	54157.75	15				

IV. DISCUSSION

Under the present experimental conditions genetic factors outweigh environmental ones in their influence over developmental rate, length, and mortality (Table XI). In the case of length, variation is attributable almost entirely to maternal and hardly at all to paternal influence. This finding supports Thorpe's (1977) hypothesis that growth capacity of salmon progeny is dependent upon that of the female parent and not the male. However, this hypothesis was derived from a correlation between the proportion of progeny in the upper length mode and the length of their female parent, among families derived from parents whose interrelationships were unknown. It was

TABLE XI. Proportionate contribution of genetic and environmental factors to variation in smolting rate,* length, and mortality. (Expressed as % of total variation)

Sources of variation	Smolting rate (% in upper mode)	Mean length (cm)		Mortality
		Upper mode	Lower mode	
(a) Genetic				
Male parent	52.7	1.7	10.2	47.9
Female parent	31.7	82.0	72.0	25.9
Family	5.5	2.4	0.5	6.4
Total	89.9	86.1	82.7	80.2
(b) Environmental				
Cover	3.3	0.7	7.3	1.5
Other	6.8	13.2	10.0	18.3
Total	10.1	13.9	17.3	19.8

* The upper length mode consists of that part of the population which will become smolts in the following spring (Simpson & Thorpe, 1976; Thorpe, 1977).

assumed that this upper mode represented fish which would smolt in the following spring (an assumption verified later (Simpson & Thorpe, 1976)), and that smolting occurred as a consequence of exceeding some critical length (Elson, 1957). Thus by implication, high upper mode proportions indicated high growth rate of parr. But it would now appear that both parents can have a strong influence on the smolting rate, and the male more than the female (Table XI).

It is not yet possible to define the critical length (or confirm its reality) at which the physiological 'decision' is taken to smoltify. Simpson & Thorpe (1976) postulated that a prerequisite for physiological and structural change at smolting was that certain levels of plasma thyroxine should be exceeded, and that these threshold levels were genetically determined at a sub-cellular level of response at the target and secretory sites. During late summer, as metabolic rates start to decline in response to falling water temperature, but are partially compensated by a photo-period induced increase in thyroid stimulating hormone, plasma thyroxine levels would rise (Osborn & Simpson, 1973; Osborn *et al.*, 1978). Parr with a low response threshold to thyroxine would maintain food searching, grow and begin their smolt transformation. Those with a high response threshold would decrease food searching, their plasma cortisol levels would increase, and they would become catabolic. Such a hypothetical model would account for the development of bimodality within a sibling population, but the precise levels of environmental variables, circulating hormones, range of fish size and timing at which the smolting process can be initiated have yet to be determined. Furthermore, the model would also imply that these critical variables, being genetically determined will assume different values between families, and evidence for variation in respect of timing is given in a separate paper (Thorpe & Morgan, in prep. *a*). Hence the physiological decision to smolt may occur over a range of length, albeit small, and over an interval of weeks, between family groups. Thus one family of genetically influenced small length, possessing a low response threshold to thyroxine, timed to occur early, may show a high proportion of parr entering an upper mode at a low mean length: conversely, another family of genetically influenced large length, with high and late response thresholds, would show a small proportion of

parr in the upper mode, at a large mean length. Whilst those lengths may be under maternal genetic influence, we suggest that, from the present data, genetic control over the hypothetical threshold levels and responses is exerted by both parents, and that further experiments are necessary to explore the degree and mechanisms of control.

Refstie *et al.* (1977) reported that both environmental and genetic factors affected the smolting rate of Atlantic salmon in tanks at Sunndalsøra, Norway, and they considered that variance between strains in the proportion of 1-year smolts produced was probably principally genetic. They also found significant maternal and paternal influence over smolting rate, but maternal influence was the greater. It is likely that direct comparison between their results and ours is not possible as their measure of smolting rate was based on a definition of a smolt as 'a young salmon not passing a 10-mm grader by March 15th'. We doubt the accuracy of separation of smolts from non-smolts by current mechanical grading methods (Thorpe & Morgan, in prep. *b*), for three main reasons. Firstly, as discussed above, different families may smoltify at slightly different lengths, so that the efficiency of accurate separation using an arbitrary width criterion will differ between families. Secondly, from measurement of a tank stock of some 7000 parr shortly after mechanical grading in late summer, the overlap of size (length) between the larger and smaller fish amounted to 68% of the population, indicating that the method is highly inefficient as a means of separating fish into the two length groups which we have shown represent smolts and non-smolts at this time (Thorpe, 1977; Thorpe & Morgan, in prep. *a*). Thirdly, at smolting the parr undergo morphological change, during which condition factor decreases dramatically (Hoar, 1939), and the length-weight exponent also decreases (Simpson, pers. comm.), implying a reduction in width. Thus grading by width will not be a certain means of separating long thin smolts from short fat parr.

Mortality during the parr stage also appears to be influenced by parental factors. Although these effects are statistically significant, their meaning is not clear at the present time. Kanis *et al.* (1976) also found genetic influence over mortality among juvenile salmon, but in general their mortalities were substantially higher than in the current experiments. Refstie *et al.* (1977) concluded that 'family' selection would be required to improve the percentage of 1-year smolts: our experiments endorse this conclusion but more experimental work is needed to distinguish the most desirable traits in male and female parents which may lead to this goal.

We are grateful to M. S. Miles and his staff at the Almondbank smolt rearing station for their efficient and careful conduct of these experiments: to Dr T. H. Simpson, for much useful discussion and criticism of the paper, and to A. V. Holden and B. B. Parrish for help in its preparation.

References

- Cassie, R. M. (1954). Some uses of probability paper in the analysis of size frequency distributions. *Austr. J. Mar. Fw. Res.* **5**, 513-522.
- Elson, P. F. (1957). The importance of size in the change from parr to smolt in Atlantic Salmon. *Can. Fish. Cult.* **21**, 1-6.
- Hoar, W. S. (1939). The weight-length relationship of the Atlantic Salmon. *J. Fish. Res. Bd Can.* **4**, 441-460.

- Kanis, E., Refstie, T. & Gjedrem, T. (1976). A genetic analysis of egg, alevin and fry mortality in salmon (*Salmo salar*), sea trout (*Salmo trutta*) and rainbow trout (*Salmo gairdneri*). *Aquaculture* **8**, 259–268.
- Minaur, J. (1973). Smolt rearing at Almondbank, Perthshire. *J. Inst. Fish Mgmt* **4**, 65–68.
- Osborn, R. H. & Simpson, T. H. (1973). A possible relationship between thyroidal status and the ease of capture of fish. *I.C.E.S. CM* 1973/B.23.
- Osborn, R. H., Simpson, T. H. & Youngson, A. F. (1978). Seasonal and diurnal rhythms of thyroidal status in the Rainbow trout, *Salmo gairdneri* Richardson. *J. Fish Biol.* **12**, 531–540.
- Refstie, T., Steine, T. A. & Gjedrem, T. (1977). Selection experiments with salmon. II. Proportion of Atlantic Salmon smoltifying at 1 year of age. *Aquaculture* **10**, 231–242.
- Simpson, T. H. & Thorpe, J. E. (1976). Growth bimodality in the Atlantic salmon. *I.C.E.S. CM* 1976/M.22.
- Thorpe, J. E. (1977). Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. *J. Fish Biol.* **11**, 175–184.
- Thorpe, J. E. & Morgan, R. I. G. (in preparation a). Time of divergence of growth groups between potential 1+ and 2+ smolts among sibling Atlantic salmon.
- Thorpe, J. E. & Morgan, R. I. G. (in preparation b). The efficacy of mechanical grading of Atlantic salmon parr, to separate potential 1+ and 2+ smolts.