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**Influence of Variations in Freshwater Growth on Yield of Atlantic Salmon**

**by**

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### Abstract

Recent work suggests that freshwater growth and sex ratio of parr is related to density. In this paper, a simple model is used to examine variations in growth rate on smolt age and yield. The model suggests that slower growth rates will produce more older smolts, but, because of the extra years of mortality, not all that many more: the smolt age structure does not change much with changes in growth rate, although the number of smolts does. Secondly, if sex ratio responds to density-dependent growth, changes in sex ratio will have only a small influence on yield.

### Résumé

De récents travaux donnent à penser que la croissance en eau douce et la proportion des sexes des tacons sont reliées à la densité. Dans l'article qui suit, nous utilisons un modèle simple dans l'analyse des variations du taux de croissance en fonction de l'âge et du rendement des smolts. Le modèle suggère que des taux de croissance lents produiront un nombre beaucoup plus grand de smolts âgés mais que, à cause d'années supplémentaires de mortalité, ce nombre ne sera pas tellement plus élevé: la structure par âge des smolts ne change pas beaucoup en fonction de changements du taux de croissance, bien que le nombre de smolts change. En outre, si la proportion des sexes est influencée par une croissance dépendante de la densité, les changements de cette proportion n'auront qu'une faible influence sur le rendement.

## Introduction

Recent work suggests that the mean age of Atlantic salmon smolts may be influenced by the density of parr (Gibson 1978; Naiman 1982; Chadwick 1982). A likely mechanism is density-dependent reduction in growth (Ferno *et al.* 1976; Refstie and Kittelsen 1976; Prouzet 1978), which delays the time when parr will attain a size sufficient to become smolts. Whatever the mechanism, an increase in the length of time parr spend in the river will decrease egg-to-smolt survival and therefore salmon yield.

There is also evidence that density-dependent growth can influence sex ratio. Chadwick (1982) found that the sex ratio of smolts was more unbalanced for younger smolts and smaller year-classes on Little Codroy River. Unbalanced sex ratios of smolts are a result of male parr becoming sexually mature and not going to sea. Many authors have linked this early maturity of males to faster growth rates (Evropeytseva 1960; Glebe *et al.* 1978; Lundquist 1980); some authors have linked it to density-dependent growth (Bailey *et al.* 1980). Thus it appears that density-dependent growth could be an important component of yield.

This paper is aimed at exploring the influence of variation in growth of parr on the yield of Atlantic salmon. Western Arm Brook is used as a case study. For pedagogic purposes (i.e. to assure the authors that they understand what they are doing), a model is being developed in a series of small elaborations, the first of which is described here.

First, a brief description of the life of a parr. Eggs are laid in November, hatch the following May, and fry emerge from the gravel into the stream in late June to become 0+ parr. In June-July, the stream is full of insects and the parr do most of their feeding and growing for the year. The following May a distinct ring is laid down in the scale, and parr which have this ring are now called 1+. The cycle repeats until the parr become smolts. Smolting can occur at all times of year, but almost all smolts go to sea in June (at least, all that are going). Note that an  $n+$  parr may have had either  $n$  or  $n+1$  feeding seasons, depending on when in the year it is taken. However, an  $n+$  sea-run smolt will always have had  $n$  feeds.

The model deals with the variable growth rate of parr in a stream, and how this influences the size and age distribution of smolts. The model is an oversimplification in many ways: a more realistic, detailed formulation would obscure the point we wish to make, to no particular purpose. We assume that conditions in the stream are constant from year to year, so that the distribution of smolts within a year is the same as within a year-class. We assume that everything about a parr is fixed except its growth rate. In particular, we assume that there is some fixed length which parr must attain in order to become smolts: a parr will become a smolt following the feeding season in which it attains or exceeds this length. Attaining the required length, or becoming a smolt, does not alter the growth rate during that feeding season. The length of a parr at emergence is fixed at 28 mm. For purposes of illustration we take the length required for smolting to be 160 mm. For each parr, we assume that the growth rate is fixed for life during the first season

after emergence; the distribution of growth rates of parr is given in Table 1. This table is derived from observations of smolts, using the formula

$$\text{growth rate} = \frac{\text{length} - 28}{\text{age}} \text{ mm/yr.}$$

and adjusting numbers at age to take account of mortality.

In order to become an  $n+$  smolt, a parr must gain  $160-28 = 132$  mm of length in  $n$  growing seasons. Table 2 presents the minimum growth rate necessary in order to become an  $n+$  smolt. (The growth rate which divides between, say a 4+ and 5+ smolt, 33 mm/year, does not fall on a class boundary in Table 1. Table 2 was constructed from the original data which had smaller class intervals.) Notice that if the growth rates are distributed symmetrically the distribution of times to smolt length will be skewed, with a preponderance of small times which include a larger range of growth rates.

In order to calculate the distribution of smolt ages, we must also consider the mortality of parr, taken to be constant at 46% per year (i.e. the survival fraction from one year to the next is 0.54). 3+ smolts will have had one year's mortality more than 2+, and 4+ smolts two. Thus, given the distribution of requisite growth rates from Table 2, the distribution of smolt ages from 2+ to 6+ will have the proportions

$$0.001 : 0.135 \times 0.54 : 0.596 \times (0.54)^2 : 0.237 \times (0.54)^3 : 0.032 \times (0.54)^4$$

or

$$0.00 : 0.25 : 0.60 : 0.13 : 0.01$$

The mean age is 3.86 yr.

All we have done so far is restate what is observed in Western Arm Brook. Now, however, having established a general description, we can ask what would happen if the pattern changed? (That is, what would be the steady-state consequences? We haven't looked at the dynamics, including possible cycles.) We postulate a reduction in the average growth rate, but not in the maximum. The fastest growing class will still be  $>52$  mm/year, and the fractions of population in various classes will stay the same, but the class interval will increase to 3 mm/year (Table 3).

The rationale for Table 3 is that in a population in which individuals differ, the most fit will always get enough to eat, and competition will be expressed as the less fit individuals doing comparatively worse. Similar ideas are found in the work of Lomnicki (1978) and Jones (1979). All the computations above can be repeated for the numbers in Table 3. Clearly there will be more older smolts, but, because of the extra years of mortality, not all that many more: the smolt age structure does not change much with changes in growth rate, although the number of smolts does. The proportions of smolt ages from 3+ to 7+ are:

0.26 : 0.42 : 0.22 : 0.08 : 0.02

The mean age is 4.18 yr.

We now turn to the influence of changes in sex ratio on yield. Male salmon can either go to sea, in which case they are a loss to the spawning stock but not to the fishery, or remain in the stream (mature without becoming smolts), in which case they are a loss to the fishery as well. If, at low growth rates, more males go to sea, then the loss due to additional stream mortality is somewhat offset (although this effect cannot be large). Thus changes in sex ratio will have only a small influence on yield, assuming of course that sex ratio responds to density-dependent growth.

We can also compute the number of smolts that one freshly emerged parr is expected to produce using the data from Table 4. Combining this with other survival rates (egg-emergence:0.18; adults at sea:0.15), the sex ratio (0.7 female) and the number of eggs laid (3000 per female), we calculate that one egg can produce  $0.18 \times 0.084 \times 0.7 \times 0.15 \times 3000 = 5$  eggs. Assuming that one egg only actually produces one egg, we assume that four out of five adults are captured as they return to the stream. For other patterns of growth rate we can similarly calculate surplus production. For example, using the table of lower growth rates (Table 3), one egg would produce three eggs. This illustrates the effect on yield of shifts in smolt age structure. If it were possible to relate growth rate to density of parr in the stream, we could estimate a maximum sustainable yield, but data on this are lacking.

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Table 1. Growth rates of parr taken from all smolts sampled in Western Arm Brook (1971-81).

Growth rate (mm/yr)	Fraction of population
>26	.023
26 - 28	.020
28 - 30	.062
30 - 32	.090
32 - 34	.097
34 - 36	.148
36 - 38	.134
38 - 40	.120
40 - 42	.093
42 - 44	.058
44 - 46	.047
46 - 48	.035
48 - 50	.027
50 - 52	.021
>52	.025

Table 2. Growth rates required for parr to become smolts.

Age at smolting	Required Growth rate (mm/year)	Fraction of population
2+	66	.001
3+	44-66	.135
4+	33-44	.596
5+	26.4-33	.237
6+	22-26.4	.032
7+	18.9-22	.000

Table 3. Hypothesized lower growth rates

Growth rate (mm/yr)	Fraction of population	Age at smolting
13	.023	10
13 - 16	.020	9 - 10
16 - 19	.062	8
19 - 22	.090	7
22 - 25	.097	6
25 - 28	.148	5 - 6
28 - 31	.134	5
31 - 34	.120	4 - 5
34 - 37	.093	4
37 - 40	.058	4
40 - 43	.047	4
43 - 46	.035	3 - 4
46 - 49	.027	3
49 - 52	.021	3
52	.025	3

Table 4. Smolt production by one parr at emergence.

Smolt age	Growth rate fraction	Survival from emergence	Number of smolts
3	.135	.157	.021
4	.596	.085	.051
5	.237	.046	.011
6	.032	.025	.001
			$\Sigma = .084$