BIMODALITY OF GROWTH AND SMOLTING IN ATLANTIC SALMON, *SALMO SALAR* L.

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ABSTRACT

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  The occurrence, heritability, environmental control, and timing of bimodality of growth
in juvenile Atlantic salmon *Salmo salar* L., is reviewed. Preliminary data on RNA : DNA
ratios show that these provide a valid short term index of growth, which can be used to
determine the time of divergence of the two growth groups more precisely than by size
frequency distributions.
  On evidence from the midsummer divergence in the distributions, published data on
the timing of gametogenesis in juvenile salmonids and comparisons between the patterns
of occurrence of precocity in experimental stocks in Canada, Scotland and Sweden, it is
suggested that bimodality of growth in juvenile Atlantic salmon is related primarily to
sexual maturity, and only secondarily to smolting.

INTRODUCTION

The phenomenon

Bimodality in the frequency distributions of length and weight was apparent by the first autumn of growth among sibling populations of juvenile Atlantic salmon, *Salmo salar* L., reared in radial flow tanks at the Almondbank smolt rearing station, Scotland (Thorpe, 1977). The separation into two modal groups did not correspond to segregation of sexes, or apparently of mature from immature fish. Simpson and Thorpe (1976) reported that the two groups developed into 1-year (S1) and 2-year (S2) smolts respectively. These findings have been repeated many times since then, both in radial and in tangential flow tanks, and have been confirmed in Canadian Atlantic salmon (Bailey et al., 1980).

Its heritability

Thorpe (1977) showed that the proportion of fishes entering the upper modal group was strongly influenced genetically, and in subsequent experi-

ments Thorpe and Morgan (1978) showed that the genetic influence of male and female parents over growth of their progeny differed quantitatively and qualitatively. The male parents appeared to influence rates of development more strongly than did the females, while the latter dominated in influence over absolute body size. By comparing the growth and development of progeny of individual female salmon paired with a range of males of differing maturation rate (mature 1-year-old male parr, to 4-year-old sea-run adult salmon), it was shown (Thorpe and Morgan, 1980) that male parents having an inherently high developmental rate confer such a property on their offspring. Thus the proportion of the population segregating into the upper growth mode by their first autumn was significantly higher in the progeny of mature parr than in those of older sea-run males, and among the lower modal groups of these parr-progeny populations the incidence of maturity was high among males a year later.

Bailey et al. (1980) showed similar influences of parental maturation history on the growth and development of salmon in Canada. Simpson and Thorpe (1976) speculated on the mechanism by which such a segregation into two distinct growth groups could have occurred. They pointed out that differences in growth and maturation rates must have resulted from differences in biochemical rates under endocrine control. A prerequisite of physiological and structural change was that certain threshold levels of circulatory hormones should have been exceeded, and that such response thresholds would themselves be determined genetically at the target and secretory sites. In this case they speculated that, as metabolic rates began to decline during the late summer in response to falling temperatures, these rates may have been partially compensated for by a photoperiod-induced increase in thyroid stimulating hormone, leading to increased plasma thyroxine levels (known for *Pleuronectes platessa* (Osborn and Simpson, 1978) and *Salmo gairdneri* (Osborn et al., 1978)). Fish with a low threshold of response to thyroxine would remain responsive to food particles and continue to grow, while those with a high threshold would cease to feed and would switch to a catabolic state. Growth bimodality would then ensue. The precise levels of environmental variables, range of fish size, and timing at which this physiological decision was taken to continue to grow or not, were not known. However, these critical variables, being genetically determined, would assume different values between families.

Environmental influences

Thorpe and Wankowski (1979) found that the proportion of available cover affected the performance of sub-populations of sibling salmon: small amounts of cover led to local crowding of fish, and relatively low proportions entered the upper modal group, while larger covers permitted the development of sub-populations showing significantly higher proportions in the upper group. Water velocity experienced by the fish also influenced growth performance.

At flows maintained at approximately 3,4, 5, and 6 body lengths per second (b.l.s^{-1}) at the fish's head the sub-populations of three separate families showed consistently that the highest proportions segregating into the upper modal group were at 5 b.l.s^{-1} flow. Fontaine and LeLoup (1959) have shown that exposure to high water velocities, inducing high swimming activity, resulted in maintenance of high thyroxine levels in juvenile salmon. Such a mechanism, acting through its general sensitizing role, may account for the higher upper modal group proportions at the relatively high water velocity of 5 b.l.s^{-1}.

Timing of the decision

The development of bimodality in length frequency distributions was recorded for eight families in 25 separate tank populations (Thorpe et al., 1980). Two main conclusions were drawn: the timing of divergence into distinct modal groups differed between families; and the inception of the process must occur earlier in the year probably June—July, rather than September—October as previously supposed. Some data published by Bailey et al. (1980) supported these conclusions. Comparison of these two studies also supported the conclusion that the critical minimal length for the decision varied between families (Thorpe et al., 1980). The lower modal groups among the Canadian fish were longer in November than were the upper groups among the Scottish fish.

Determination of the precise time and conditions under which separation of the growth groups occurs cannot be achieved by study of length frequency distributions, since these only reveal the occurrence of an event weeks or months after it has taken place. A more sensitive short term measure of growth is needed. RNA : DNA ratios, as momentary indices of general protein synthesis, have proved to be closely correlated with change in total size over short intervals in several species of fish (e.g. Bulow, 1970; Haines, 1980).

This paper reports on preliminary measurements of these ratios made on juvenile *Salmo salar*, to evaluate their utility in defining the time of divergence of the modal growth groups.

NUCLEIC ACID MEASUREMENTS

Methods

Approximately 25 fish were sampled from a sibling population of Atlantic salmon every week starting 1 week before first feeding. Freshly killed fish were weighed to the nearest 0.001 g and then dried in an oven at 80°C. The dried tissue was ground to a fine powder for nucleic acid analysis. In pre-feeding fish the yolk sac was removed prior to initial weighing and was not included in the assay for nucleic acids. The specific rate of increase in live weight (G_W % day^{-1}) was calculated during the period between samples from the equation:

$$G_W = \frac{(\log_e W_2 - \log_e W_1)}{t} \times 100$$

where W_1 and W_2 are the sample mean weights at the start and end of a period between samples and t is the number of days in the period.

Similar measurements were also made on approximately ten fish sampled from each modal group of a different sibling population of salmon from November to May. RNA : DNA ratios were measured in 0.3 g of white muscle dissected from below the dorsal fin of freshly killed fish. The RNA—DNA analysis procedure followed the method described by Bulow (1970) as modified in Bulow et al. (1981) with the following exceptions. Neither the dry powder nor the fresh muscle was defatted. The muscle was homogenised in ten volumes of ice cold 0.75% saline. The concentration of nucleic acids was measured in a 2-ml aliquot of the homogenate and in the whole powdered dried fish (approximately 60 mg). Interfering chromogenic substances were extracted from the homogenised muscle and the dry powder using 8 and 6 ml ice cold 10% trichloroacetic acid (TCA) respectively. Nucleic acids were extracted in two 4-ml aliquots of 5% TCA at 90°C for 20 min, and the combined extracts were made up to 10 ml final volume. Aliquots of final extract were mixed 1 : 1 with orcinol reagent and incubated at 90°C for 20 min to determine RNA concentration, and 1 : 2 with diphenylamine reagent followed by incubation at 35°C for 20 h to determine DNA concentration. The concentration of nucleic acids in the extracts and in standards was measured using a Pye Unicam SP spectrophotometer.

RESULTS

First-feeding fish (Fig. 1)

The fish increased in weight from 0.16 g in April to 0.32 g in early June (Fig. 1A). An initial growth rate of 1.8% day^{-1} was observed while yolk was still the source of nutrients. During the transition to exogenous food, the growth rate decreased to 0.16% day^{-1} but subsequently increased to a maximum of 4.7% day^{-1} in late May (Fig. 1B). Changes in RNA : DNA ratio followed changes in growth rate (Fig. 1C) with a significant correlation ($P < 0.05$) between the specific growth rate during a period between samples and the geometric mean of the RNA : DNA ratios for the same period (Fig. 1D). Buckley (1980) found a similar decrease in RNA : DNA ratio in winter flounder larvae between the end of the yolk sac stage and feeding initiation with a subsequent rise after feeding had started.

Bimodal population (Fig. 2)

Changes in specific growth rate of the two modal groups were mirrored by similar changes in their RNA : DNA ratios. The ratios for the upper modal group were consistently greater than those for the lower group (Fig. 2B).
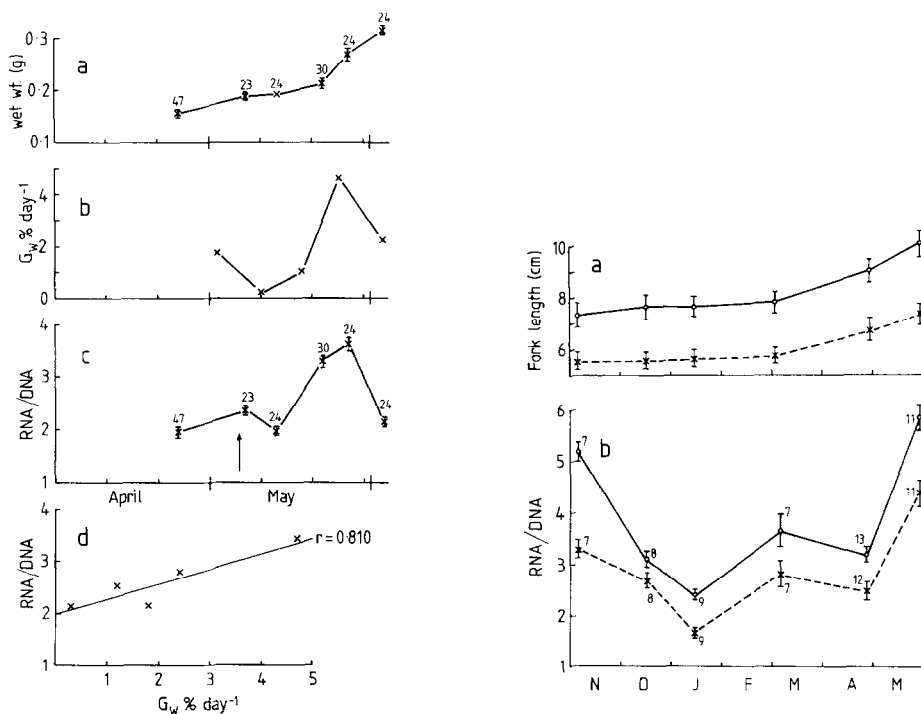
Fig. 1. Growth indices of a 0+ sibling population of Atlantic salmon.
Salmo salar L. A: Mean wet weight ± SE of fish sampled for RNA—DNA analysis. B: Specific
growth rate during each period between samples. C: Mean RNA : DNA ratios ± SE. The
arrow marks the point at which exogenous food was presented. D: The relationship between
specific growth rate and the geometric mean of RNA : DNA ratios for the relevant period.
The numbers at each data point represent sample sizes.
Fig. 2. Growth indices of a bimodally length-distributed sibling population of Atlantic sal-
mon. Solid lines: upper modal group; hatched lines: lower modal group. A: Mean fork length
± SE of the whole population. B: Mean RNA : DNA ratios ± SE: the numbers at each data
point represent sample sizes.

Conclusions

RNA : DNA ratios represent valid indices of specific growth rates of in-
dividual juvenile Atlantic salmon.

These ratios differ between the modal groups of a sibling population.

As momentary indices of growth rate their own frequency distribution
within such a population should provide a sensitive indicator of the timing
of the divergence of the two growth modes. Also, as the nucleic acid analysis
can be carried out on a small fraction of the body mass (e.g. on white muscle)
the remainder of the carcass can be examined later using histological methods
to evaluate the degree of development of selected organs. This facility could
allow a more precise investigation prior to the divergence of the growth modes,
of differences in the ontogeny of fish which, on the basis of RNA : DNA
ratios, are considered to be growing at different rates.

DISCUSSION

The growth change

Thorpe (1977) found that the upper modal group continued to grow throughout the winter, while the lower group did not. Wankowski and Thorpe (1979) showed that the rate of increase of weight with length was significantly less for the upper modal group than for the lower. The comparable regression relationship for upper group fish diverged progressively further from that of the lower group through the winter. Such a change implies reallocation of resources within the fish enhancing skeletal relative to muscular growth at this time. Evropeizeva (1959) noted differences between smolts and parr in several morphological indices in stocks from Russian rivers. Nikolskii et al. (1947) recorded that post-anal length of smolts was proportionately greater than in parr, and interpreted the shorter stockier build of parr as an adaptation to life in a high velocity current. Riddell and Leggett (1981) compared body proportions of stream phase salmon from two different natural flow regimes, and concluded that longer slimmer proportions were correlated with higher flows: however, they did not report on proportion changes at smolting. They found a positive correlation between paired fin size and flow in salmon from several different habitats. Nikolskii et al. (1947) showed that the proportionate size of the pectoral fins was reduced at smolting. It would appear that the lengthening and streamlining, accompanied by reduced fin-size implying reduced hydrofoil braking capacity, represented the abandonment at smolting of morphological adaptations to life in a riverine habitat. This is in conformity with the argument presented recently (Thorpe, 1982) that changes at smolting consisted of relinquishment of behavioral and physiological adaptations of a marine animal to a freshwater riverine environment. This envisages smolting chiefly as a complex of passive consequences of loss of adaptation, rather than of active prospective changes pre-adapting the animal to a change of environment. It is pertinent to examine growth bimodality in this same context.

Smolting and maturation

Reproduction is the ultimate index of biological success for the individual. Many salmonid species have achieved reproduction without passing through a smolt phase at all. Evropeizeva (1959) suggested that smolting and sexual maturation were biologically incompatible processes, since they depended on the same lipid stores as their energy source, and that these were inadequate to meet both needs. Her data were from smolts held back from migration in May, and she showed that spermatogenesis was initiated in June and July. The timing of divergence of the modal growth groups (Thorpe et al., 1980) has shown that individual fishes take a physiological decision whether or not to smoltify 9—10 months before they emigrate. The decisions about

smoltification versus sexual maturation cannot then depend primarily on the extent of tissue energy stores in the spring of the emigration year.

In Canadian experiments Bailey et al. (1980) found high proportions of mature male parr among the lower modal length group in November of their first year, and a few individual mature fish in the upper modal groups at the same time. In Scottish experiments Thorpe and Morgan (1980) reported the occurrence of such mature parr only in the lower modal groups, and then only at the end of their second summer. In Swedish experiments, Eriksson et al. (1979) found parr maturing at the end of their second summer in a population which was unimodal and which had yet to produce smolts. The growth rates of these three stocks decline from west to east.

Among salmonid species the first individuals to mature are usually the fastest growers (e.g. Alm, 1959). This has also been found among caged populations of Atlantic salmon in the sea (Simpson and Thorpe, 1976). It seems likely that such a positive correlation between developmental processes should also apply at the freshwater stage (cf. Saunders et al., 1982), in which case, the lower modal length groups should represent those fish whose initial growth was most rapid, and in which maturation has been triggered and somatic growth retarded as a consequence of gonadal development. In the fastest growing populations the degree of "precocity" should be greatest and evident soonest, and the size separation of the modal groups most pronounced conversely, in the slowest growing groups these developments should appear more slowly, and the divergence of the populations should be least. The comparisons of experimental data from Canada, Scotland and Sweden support this hypothesis (Fig. 3). Histological data in its support are lacking, but should be obtainable when the short-term growth indices have been developed which will provide the necessary evidence relating somatic and gonadal growth at this very early stage. Glebe (in Bailey et al., 1980) has detected maturation of male parr in June of their first year. As precocity is only apparent in males, the argument depends heavily on evidence from one sex. However, Thorpe (1977) and Bailey et al. (1980) have shown that the lower modal groups contain female fish also. Since the energetic cost of production of ovaries is much greater than that of production of testes, it is possible that the riverine environmental resources are inadequate to permit the female salmon to build sufficient ovarian tissue, and therefore even in those individuals which have been triggered to mature, emigration may occur before maturation has been completed.

Inverse relationships between age at smolt migration and years at sea before spawning have been shown for many Atlantic salmon stocks [see Thorpe and Mitchell (1981) for references]. Such a relationship is entirely consistent with the present hypothesis, since the early fish to leave the river would be immature, and the later, maturing or mature: hence the late fish would be expected to return after only a short period at sea.

The fish may return to spawn after one or more winters at sea. Simpson and Thorpe (1976) considered this a second, analogous physiological decision,
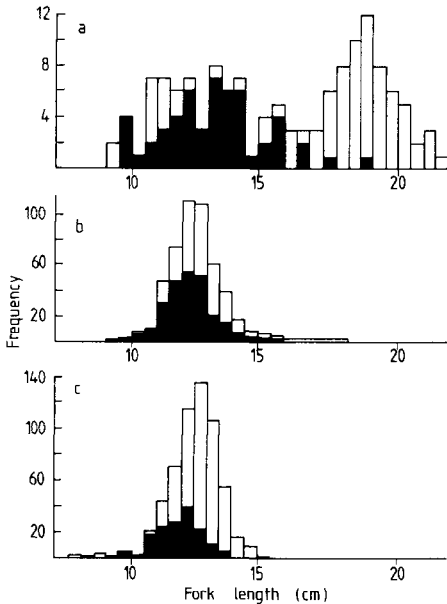
Fig. 3. Occurrence of mature male Atlantic salmon parr in hatchery populations in Canada, Scotland, and Sweden. Open columns: immature fish; hatched columns: mature males. A (from Bailey et al., 1980): 1975 year class, age 0+, November 1976: Big Salmon River ♂ × Saint John River ♀: Canada. B: 1971 year class, age 1+, lower modal group only: November 1973 (upper modal group released as smolts in April 1973) R. Almond stock: Scotland. C (from Eriksson et al., 1979): 1975 year class, age 1+. October 1977: Ume River × hatchery stock: Sweden.

which led to a further bimodal separation in size distribution of a population. On the present argument these decisions are seen as the same one taken on at least two occasions.

Schaffer and Elson (1975) showed that variations in age at maturation in Atlantic salmon populations were adaptive phenomena. They considered that the decisions whether or not to return to spawn after one or more years at sea were trade-offs between the probability of mortality before the next spawning season, and the probability of growth and enhanced reproductive output. Since such a mechanism must operate through the responses of individual fish to environmental conditions it may be supposed that a fish would continue to feed and grow while conditions were good for it, and only concentrate on gonad production when such conditions deteriorated. Brown (1972) recorded that alewives (*Alosa pseudoharengus*) matured a year later than usual when intraspecific competition was eased after the massive reduction of population numbers in 1967 in Lake Michigan. Conversely, T.H. Simpson (personal communication, 1979) has induced maturation in cage-cultured Atlantic salmon by food deprivation.

A similar mechanism may be postulated for young fish in fresh water. If conditions ceased to be favourable for somatic growth for an individual at a

season when gonadal development is susceptible to triggering, then the fish would switch resources toward gonad growth at the expense of somatic tissue. Since each individual in a sibling population would perceive its environment differently, only those in the population whose response threshold was exceeded would switch to a maturing phase.

The separation of modes in the length frequency distribution has been shown to have occurred by late summer, which implies that the divergence probably began in midsummer. Simpson and Thorpe's (1976) original hypothesis related to a divergence occurring in the autumn. It cannot therefore account for the primary cause of segregation, but may serve to maintain that segregation once it has developed. Gametogenesis in salmonids occurs from midsummer onwards (Evropeizeva, 1959; Billard and Breton, 1978; Dodd et al., 1978). As mature male fish are present in the lower modal group before any appear in the upper group, it is suggested that this lower group represents the most rapidly developing element of the population, and that bimodality of growth is related primarily to sexual maturity and only incidentally to smolting. Bimodality of growth characteristics would then represent retention of freshwater adaptations by maturing fish, and their abandonment (and hence smolting) by those which are not maturing. Experimental tests of the hypothesis are in progress.

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