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FACTORS AFFECTING THE PARR-SMOLT TRANSFORMATION
IN ATLANTIC SALMON

by

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ABSTRACT

Factors affecting the parr-smolt transformation in Atlantic salmon Salmo salar are reviewed. The factors discussed are growth rate, temperature, photoperiod, salinity, food quality and quantity and hormones. Significance of dwarf males is also discussed.

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INTRODUCTION

The intention with this paper is not to give a complete review, of the smoltification process in the Atlantic salmon, Salmo salar, but to stress some of the most important factors affecting smoltification in this species. In some cases where the investigations on Atlantic salmon are more or less insufficient it is referred to studies on other salmonids.

Allan and Ritter (1975) have proposed a definition of a smolt of Atlantic salmon in the following way: "The smolt stage is defined as a fully-silvered juvenile salmon during its first seaward migration, normally in the spring, and is capable of surviving transition from fresh water to fully saline water".

In addition to silvering, seaward migration and an increasing tolerance to sea water other indicators of smoltification has been used in scientific investigations. According to Zaugg and Wagner (1973) there is an increase in an enzyme, Na^+K^+ -activated ATPase, activity in the gill microsomes prior to migration of salmonid smolts. Saunders and Henderson (1977) states that this ATPase activity is a sensitive indicator of the ability of Atlantic salmon to osmoregulate in sea water, but it is of less value as an indicator of smolt preparedness to migrate to sea than lipid-moisture content, tolerance to high salinity and migratory behaviour.

GROWTH IS ONE OF THE MOST IMPORTANT FACTORS DECIDING WHEN A PARR IS GOING TO SMOLTIFY

Fish farmers in Norway have a rule of thumb that says: "if a parr has reached a fork length of at least 10 cm before winter, when growth stop, it will be large enough to smoltify the following spring". The time from hatching and until the parr has reached this minimum size is dependent on what possibilities of growth the parr has got, and is therefore dependent on several

factors of which the most important are inheritance, amount and quality of food and water temperature. In Norway Atlantic salmon smolts migrate during spring at a size of about 12 to 16 cm fork length.

Size is more important than age for sea water tolerance

Refstie et al. (1977) referring to several authors state that size is one of the most important factors determining the age at which salmon smoltify, and parr must reach a certain minimum size before the smoltification process can start. Parr which fail to reach this minimum size in the spring or early summer of one year will remain parr, regardless of growth, until the following spring.

The statement above is supported by the work of Simpson and Thorpe (1976) who say that, populations of juvenile Atlantic salmon develop a bimodality in the frequency distributions of length and of weight during their first year of growth. They furthermore say that, fish in the upper size mode develop into smolts in one year; members of the lower mode remain as parr for a further year.

Hoar (1976) also supports the statement when saying that salinity resistance increases in both Salmo and Oncorhynchus as the young fish increase in size and that for a given age, the larger fish are more resistant.

TEMPERATURE REGULATES SMOLTIFICATION

Temperature regulates smoltification through growth

Temperature is one of the most important factors regulating growth in Atlantic salmon parr (Foda and Henderson, 1977; Knutsson and Grav, 1976; Peterson et al., 1977). We also know that growth is one of the most important factors deciding when the smoltification process starts. It is therefore easy to draw

the conclusion that temperature regulates smoltification in Atlantic salmon.

Foda and Henderson (1977) studied growth at five different temperature regimes in order to find the best one for production of 1-year smolt. At an incubation temperature of 10°C and a rearing temperature of 15°C fish attained a size of 17,7 cm ± 1,7 from full swim-up fry in eight months. This was, however, not achieved without a great loss through death (69%) and deformities. Therefore, Foda and Henderson recommend one of the other experimental temperature regimes, which was less costly and more natural, and under which the fishes attained a size of 15,2 cm ± 1,7 by early May in the second year. In all their experimental groups the upper temperature limit was around 15°C. But they suggest that the growth would have been even better if the temperature had been maintained at 18°C (65F) instead of 15,5°C (60°F) from the latter part of June through September.

Temperature can have a direct influence on parts of the smoltification process

Salinity tolerance is affected by temperature

The question of a upper temperature limit for smoltification is very important. Adams et al. (1973) showed that the increase in gill ATPase activity and consequent salinity tolerance of steelhead trout is temperature dependent. At their experimental temperatures 6,5 and 10°C they found a twofold increase in ATPase activity and a sharp decrease in coefficient of condition at the beginning of the smolt season in March. At 15 or 20°C there was no increase in ATPase activity nor did the coefficient of condition decrease during the smolt season.

Zaugg and Wagner (1973) showed that gill ATPase activity was decreased and migration reduced in steelhead trout subjected to temperatures of about 13°C or greater. Later investigations by Zaugg and McLain (1976) have revealed temperature dependency of gill ATPase in coho salmon Oncorhynchus kisutch.

Unfortunately there is no similar investigation on Atlantic salmon. Saunders and Henderson (1977) have, however, shown that gill ATPase activity increased during winter-spring in Atlantic salmon held at 10°C. An investigation with the purpose of trying to reveal any temperature dependency of gill ATPase activity in Atlantic salmon would be of great interest to, among others, those smolt farmers who use elevated temperatures in order to produce smolts in one year.

The work of Knutsson and Grav (1976) indicates a detrimental effect of temperature on smoltification at 15°C. Growth and smoltification at different temperature and photoperiod regimes were studied. As a measure of smoltification were used survival rate in sea water (34°/oo). In spite of a better growth at 15 compared to 11°C a tendency of higher survival rate was found at 11 compared to 15°C.

Today we have a rather good knowledge of what are the best temperature regimes in order to promote and get a high proportion of 1-year old smolt. However, there is good reason to be careful in using too high temperatures when the smoltification process has started. Because it is likely that high temperatures will have a detrimental effect on the smoltification process in Atlantic salmon as it has in steelhead trout.

Temperature affects silvering in Atlantic salmon

Johnstone and Eales (1968, 1970) traced changes in the purine content of the skin of Atlantic salmon during parr-smolt transformation. Photoperiods were manipulated in several ways from late December until June. Neither lengthening photoperiod nor rising temperature had any marked effect on the onset of silvering, although increasing temperature during the spring did increase the amount of purine deposited in the skin.

It seems that the parr-smolt transformation can start at very low temperatures. In Norwegian smolt-farms the author has personally observed very silvery fishes below +1°C in the beginning of March.

No clear connection between temperature and migration in Atlantic salmon

For steelhead trout Salmo gairdneri Wagner (1974) found that temperature did not appear to influence the onset of migration, but did affect the duration of it.

Bakshansky et al. (1976) looked upon the effect of water temperature on the dynamics of migration in Atlantic salmon smolts. Their conclusion was that, in a number of cases the dynamics of downstream migration coincides with changes in water temperature and in some other cases there is no relationship between migration and water temperature traced.

PHOTOPERIOD AFFECTS SMOLTIFICATION

Several works have demonstrated that photoperiod does have a regulatory effect on smoltification (Baggerman, 1969; Johnston and Eales, 1970; Saunders and Henderson, 1970; Wagner 1974). The effect is either directly through the influence on biochemical processes involved or indirectly through its effect on growth.

Photoperiod affects growth rate

Photoperiods indirect effect on smoltification through growth may also be either direct or indirect. The direct effect on growth through the production of growth hormones is discussed by Komourdjian et al. (1976). They found that longer daylengths coincided with an increase in number and apparent activity of pituitary somatotrops.

Knutsson and Grav (1976) showed the indirect effect of photoperiod on smoltification through growth. In their experiment underyearling Atlantic salmon were fed by automatic feeders when light was on. The feeding time thus coincided with the photoperiod. Highest growth rate and most seawater adapted

fishes were found at the longest photoperiod, 24 hours of light a day. In a laboratory experiment temperature was found to be more important than photoperiod in promoting growth in Atlantic salmon (Knutsson and Grav, 1976). Furthermore, temperature seemed to influence growth independently of photoperiod, while the effect of photoperiod seemed to be dependent on temperature. Of the three experimental temperatures 7, 11 and 15°C, highest growth rate was found at 15°C.

It is assumed that photoperiod may influence sea water tolerance in smoltifying Atlantic salmon

Baggerman (1960) studied salinity preference, thyroid activity and seaward migration of four species of pacific salmon Oncorhynchus. She concluded that in juvenile salmon the length of the daily photoperiod controls the time at which the change in preference from fresh to salt water takes place and that this reflects the induction of migration-disposition. She further says that there is considerable evidence that the day length activates the pituitary-thyroid system, one of the endocrine mechanisms, involved in the induction of migration-disposition.

Through immediate transition experiments, Wagner (1974) found that sea water adaptation was independent of photoperiod in juvenile steelhead trout.

Komourdjian et al. (1976) and Saunders and Henderson (1977) have, however, shown for Atlantic salmon, that gill ATPase activity responds to photoperiod manipulation. Saunders and Henderson showed that gill ATPase activity increased with increasing daylength during spring. They also showed a very close connection between the ability to osmoregulate and gill ATPase activity. It is therefore tempting to assume that photoperiod may have a rather direct influence on sea water tolerance in smoltifying Atlantic salmon.

SALINITY TOLERANCE INCREASE AFTER EXPOSURE TO BRACKISH WATER

Zaugg and McLain (1970) studied seasonal variations and salt water influence on ATPase activity in gills of coho salmon. They suggest that the spring rise in ATPase activity observed in coho salmon is a biochemical manifestation of readiness to accept sea water.

For pre-smolt coho salmon Otto (1971) found that salinity tolerance was clearly increased by exposure to dilute salinities, the increase in tolerance being directly related to the concentration.

Adams et al. (1973) showed a correlation of salt water survival with high gill ATPase activity in steelhead trout.

In Atlantic salmon, Saunders and Henderson (1977) found that gill ATPase activity increased during winter-spring and that exposure to 40⁰/oo salinity for periods up to 14 days gave marked increases in ATPase activity over levels measured in fresh water. They concluded that gill ATPase activity is a sensitive indicator of the ability of Atlantic salmon to osmoregulate in sea water.

Brackish water has no growth promoting effect on Atlantic salmon parr

We have seen that both temperature and photoperiod have an indirect effect on smoltification through its growth promoting effect. The question now is if also salt water may have such a growth promoting effect on juvenile Atlantic salmon.

Canagaratnam (1959) and Otto (1971) found that growth of coho salmon Oncorhynchus kisutch underyearlings was greatest at environmental salinities of 5-12⁰/oo throughout the presmolt period.

Shaw et al. (1975) studied growth of 21 months old Atlantic salmon parr at environmental salinities of 0.1, 10 and 20⁰/oo,

but they did not find any growth promoting effect. So the preliminary conclusion is that brackish water environment does not effect smoltification in Atlantic salmon parr through enhanced growth rate.

Ability to osmoregulate develops during the whole smoltification process in Atlantic salmon

From his investigations of steelhead trout, Wagner (1974) makes the point that salinity tolerance in salmonids develops many months before smoltification and is separate from smolting. Farmer et al. (1978) maintain that sea water acclimation of Atlantic salmon parr is possible. However, Saunders and Henderson (1970) have found that although pre-smolt tolerate high salinity those salmon of comparable size judged to be smolts grew better in sea water. Komourdjian et al. (1976) and Saunders and Henderson (1977) have also shown that there is a degree of salinity tolerance that is undeveloped before smoltification is completed. They showed this by challenging juvenile salmonids to salinities of over 40⁰/oo.

Parry (1961) studied changes in blood concentration in parr and smolt of Atlantic salmon after a direct transfer from fresh water to full strength sea water. She measured the freezing-point depression and found that parr of the 2+ year age group required 150-300 hrs to regulate its blood concentration to the normal levels. Smolts, however, regulated their blood within a 24 hrs period.

FOOD REGULATES GROWTH AND SMOLTIFICATION

Through its growth promoting effect, food is one of the most important factors deciding when a parr is going to smoltify.

Foda and Ritter (1977) compared return rate of Atlantic salmon reared to smolt stage on two commercial diets. They found a difference of 41% between the two diets, and the different sea

survival rates were independent of differences in smolt size between the two groups. Their results emphasize the importance of diet in production of Atlantic salmon smolts.

Farmer et al. (1977) found lipid content to be 45% lower at the end of May than at the beginning of March, in the larger reared juvenile Atlantic salmon. This may reflect a greater energy expenditure by the larger individuals during parr-smolt transformation.

Experiments at the Salmon Research Institute in Sweden have shown that Atlantic salmon require a high quality protein, and that fat of an unsaturated type is the best energy source (Bergstrøm, 1967).

Today only dry diets are used at Swedish salmon smolt rearing plants and diets containing as much as 16% of fat have shown to give high growth rate and survival without evidence of lipid accumulation in the livers of juvenile Atlantic salmon (Bergstrøm, 1973). Furthermore, Peterson (1973) found a higher rate of returning adults after feeding the Atlantic salmon smolts a food with 16% marine fat, instead of the usual one of 6%, for the last month before release.

Dietary salt seems to make sea water adaptation easier for Atlantic salmon smolts

The findings of Zaugg and McLain (1969) encouraged Basulto (1976) to study the effects of salt-enriched diets on Atlantic salmon parr. Using survival rates as an indication of resistance to changes from fresh to salt water, he concluded that salmon parr of about 12 cm fork length fed a salt-enriched diet seemed to have an increased tolerance to salt water. Unfortunately Basulto was not able to draw any firm conclusions from his experiment, due to the low number of fishes in the experiment.

Zaugg and McLain (1969) studied the effects of salt enriched diets on growth and osmoregulatory processes in young coho

salmon. They found that excess dietary salt caused reduced growth rates and decreased efficiency of diet utilization. But, they also found that fish fed supplemental salt adopted to full strength sea water with lower mortalities than fish receiving a control diet. The salt ingestion seemed to induce an activation of mechanisms involved in the osmoregulatory process similar to one of the physiological changes reported for euryhaline fishes during natural adaptation to sea water.

Shaw et al. (1975) studied the effect of dietary sodium chloride on growth of Atlantic salmon smolts in fresh and sea water. Large dietary salt loads were almost completely absorbed from the gastrointestinal tracts of fish within 24 hours, and plasma sodium and chloride concentrations were positively affected at this time. Growth and food conversion efficiency were, however, not demonstrably affected by different levels of dietary sodium chloride.

THE THYROID AND ADRENAL GLANDS TAKE PART IN SMOLTIFICATION IN ATLANTIC SALMON

Earlier investigations have shown the thyroid gland to be hyperactive during smoltification in Atlantic salmon (Hoar, 1939; Fontaine et al., 1952; Leloup and Fontaine, 1960).

The thyroid is connected with migration and silvering during smoltification

Thyroid activity increase before and during migration

Hoar and his co-workers (1952; 1955) found a correlation between thyroid activity and locomotion in salmon and considerable evidence has been accumulated which links thyroid with smoltification (Idler, 1973).

Baggerman (1960) found thyroid activity to increase shortly before onset of migration, remain high during the migration season and to decrease towards its end.

Smith (1956) studied the role of the endocrine organs on the salinity tolerance of trout. To him it seemed unlikely that the thyroid should be the main endocrine factor controlling osmotic regulation. Instead it seemed to him more likely that the thyroid was concerned more with the aspect of movement. He referred to Hoar et al. (1952), who had recorded small but definite changes in schooling and swimming behaviour in salmon fry treated with thyroxine.

Godin et al. (1974) found that injections with thyroxine lowered swimming activity, aggressive behaviour, and upstream orientation of yearling Atlantic salmon. Treatments with triiodothyronine caused similar but less pronounced effects.

Similar behavioral modifications accompany smolt migration and are parts of the smoltification process. The hypothesis of Godin et al. (1974) that thyroid hormones may play a role in arousing migratory tendencies in Atlantic salmon, also means that they may affect the smoltification.

Thyroid extracts induces silvering

Landgrebe (1941) and LaRoche et al. (1949, 1950) induced silvering respectively a decrease in the pigmentation of Atlantic salmon parr with injections of mammalian thyroid extracts.

The idea that the whole of smoltification might be directly dependent on the thyroid was brought forward on a histological basis by Hoar (1939) but had later to be abandoned. Thyroid feeding admittedly promotes silvering, but it is unable to prevent the depression of the hyposmotic regulation capacity during desmoltification, although it keeps the animals quite silvery (Quoted: Koch, 1968).

Robertson (1949) injected mammalian thyroid extract and thyrotropic hormone into two-year old rainbow trout. After 6 weeks of fri-weekly injections the treated trout resembled closely the naturally occurring silvery rainbow smolts.

A direct connection between thyroid and salinity tolerance is not shown in Atlantic salmon

Baggerman (1963) demonstrated an increased thyroid activity and salinity preference in TSH(thyroid stimulating hormone)-treated underyearling coho salmon. Baggerman (1960) further found that the level of thyroid hormone in the blood influences salinity tolerance and preference.

Smith (1956) attempted to correlate thyroid activity with salinity tolerance of brown trout without success. Furthermore he did not find thyroxin effective in increasing salinity tolerance at what he considered to be physiological doses.

Smith (1956) followed thyroid activity of brown trout through the year concurrently with salinity tolerance and found no evident correlation between them. He also found that trout subjected to increasing salinity showed a fall in thyroid activity.

Smith (1956) found growth hormone to be effective in promoting salinity tolerance in rainbow trout at a level that he believed to be physiological and Enomoto (1967) demonstrated that the intraperitoneal injection of bovine growth hormone produced a considerable excretion of chloride in the urine of rainbow trout (Quoted: Idler, 1973).

After injections with thyroxine Smith (1956) found a general raise in salinity tolerance of trout, but the doses required seemed to him to be above the physiological level. He discussed the effect of thyroxine on salinity tolerance and suggested that its effect could be indirect by stimulating the secretion of growth hormone.

Barrington et al. (1961) found acceleration of growth in yearling rainbow trout after thyroid treatment. Growth in length as well as weight was affected.

The adrenal gland is active during smoltification

Fontaine and Oliverau (1959) present histological evidence for an increased activity of the adrenal gland during smoltification of Atlantic salmon. This conclusion is consistent with the finding of Leloup-Hatey (1964) that smolts have elevated levels of cortisols and cortisone in the plasma. It seems therefore not unreasonable to suggest that corticosteroids assist Atlantic salmon to absorb and conserve water when they migrate to the sea (Quoted: Idler, 1973).

It has been established that an enzyme, Na^+K^+ -dependent ATPase, plays an important role in salt transport and sea water adaptation in salmonids (Kamiya and Utida, 1969; Zaugg and McLain, 1970; Adams et al., 1973; Saunders and Henderson, 1977).

However, we do not know what hormone or hormones that control the Na^+K^+ -dependent ATPase in the gills of salmonids. But Idler (1973) suggests that the high enzyme activity is due to the action of adrenal-corticosteroids. As support for his presumption he shows to the findings of Pickford et al. (1970) that cortisol restores normal Na^+K^+ -dependent ATPase activity in the gills of hypophysectomised killifish maintained in sea water.

FORMATION OF DWARF MALES AFFECTS THE PRODUCTION OF SMOLTS

One of the interesting biological characteristics of salmonids is that, in addition to anadromous males, there are so-called dwarf males which do not migrate to the sea, but mature and take part in spawning in the parr stage (Leyzerovich, 1973). The incidence of dwarf males varies among stocks of Atlantic salmon (Schiefer, 1971; Schaffer and Elson, 1975; Nævdal, 1978; Saunders and Sreedharan, 1977).

Dwarf males have a higher growth rate than immature juvenils

I have not been successful in finding any literature that shows a triggering effect of photoperiod or temperature on maturation

of parr. But two authors (Flo, 1965; Leyzerovich, 1973) clearly show a correlation between growth and formation of dwarf males in Atlantic salmon.

Flo (1965) studied age, growth and sexual maturity in 200 parr and 27 smolts of Atlantic salmon in the Oselva river in Norway and found that sexually mature males grow faster than the females, and the females grow faster than the immature males.

Leyzerovich (1973) concluded his investigations on dwarf males in rearing tanks with that the mechanisms controlling the formation of dwarf males are connected with characteristics of the growth process which form the external appearance of the young. The growth rate of dwarf males is higher and the condition factor of dwarf males is invariably higher than in sexually immature juveniles of the same age.

According to Yevropeytseva (1962), the quantity of dwarf males obtained in the pond rearing of Baltic salmon is dependent on growth rate in the period preceeding spermatogenesis (Quoted: Mitans, 1973).

Most dwarf males smoltify after breeding

Mitans (1973) studied dwarf males and the sex structure of two Baltic salmon populations, the Salatsa and Daugave rivers. He concluded that most of the male parr in the river mature as dwarfs which have a higher mortality before the downstream migration, but almost all of the survivors migrate to the sea, from where they may return as large spawners.

According to Mitans (1973) only a few of the surviving dwarf males did not become smolts the following spring, but remained in the river and spawned again. Mitans drew his conclusion from the fact that he did not discover any spawning marks on the dwarf males of neither parr nor smolts.

In the scales of 7 of the males, of the 200 parr and 27 smolts, that Flo (1965) studied in the Oselva river he found erosions that he interpreted as spawning marks, 5 fishes had one mark and 2 fishes two marks. All were again sexually mature and ready to spawn for the 2nd and 3rd time respectively.

Leyzerovich (1973) studied the development of dwarf males under hatchery conditions and found that the overwhelming majority of dwarf males which had matured in their second year of life, matured again in their third year.

Modern smolt-production may increase the amount of males in a population

Whatever the truth is about dwarf males, the fact remains that the development of them affects the number of smolts in a year class. It is therefore interesting to know if there are other factors than inheritance that regulates the amount of dwarf males in a population.

Schiefer (1971) suggests that rapid growth rates in juvenile, stream dwelling Atlantic salmon leads to production of dwarf males and that these, in turn, mature and return from the sea as grilse (Quoted: Saunders and Sreedharan, 1977).

We know from the works of Flo (1965) and Leyzerovich (1973) that dwarf males have a higher growth rate than sexually immature juveniles in their first part of life. We also know from work of Mitans (1973) that the amount of dwarf males in a smolt population increases with increasing age of the smolts (see Table 1).

Table 1. Dynamics of the sexual structure of a juvenile salmon population (Mitans, 1973).

Age group	Sex ratio, %		Ratio of males, %		n
	females	males	dwarf	juvenile	
	Smolts				
1	60.6	39.4	0	100.0	155
2	58.1	41.9	63.4	36.6	222
3	31.4	68.6	79.2	20.8	35
4	0	100.0	100.0	0	1

In nature there is a high mortality of especially dwarf males. This high mortality of dwarf males is probably associated with emaciation consequent upon maturation and the more active mode of life in the autumn and winter. It is characteristic that dwarf males which have survived to the smolt state have practically no fat deposits on their viscera, whereas juvenile males retain more appreciable fat reserves throughout the time of overwintering and smoltification (Mitans, 1973). In one case he estimated the total survival of dwarf males in the Salatsa river relative to juvenile males to be 57.1%. Similarly he calculated the relative survival of maturing males throughout the river period of life to be 55.5% on average of the survival of all the remaining non-mature parr (males and females) of the corresponding age classes.

In a modern Norwegian smolt farm the aim is to produce as many 1-year old smolts as possible. To succeed with this one accelerates the growth rate through use of elevated temperatures and intense feeding. The result of the accelerated growth is that the smolt farmers produce smolts in one year compared to about four years in Nature (compare Table 1). Furthermore, in a smolt farm the dwarf males are living in a protected environment, fed food with a high content of fat, and are therefore exposed to less mortalities than in Nature.

As a consequence of higher growth rate and better survival of dwarf males in a smolt farm compared to in Nature, I suggest that modern smolt production may increase the amount of males in a population.

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