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Correlations between energy metabolism, osmotic balance and external smolt indices in smolting young salmon, *Salmo salar* L.

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Body silvering, condition factor, blood haematocrit value, concentrations of blood haemoglobin, glucose and lactate, liver glycogen content, muscle water content and concentrations of plasma protein and ions were determined in young salmon seven successive times from the second summer of the fish brood beyond the normal releasing time of reared smolts. Connections between external smolt indicators, energy metabolism and osmotic balance were estimated by examinining their correlations in individual fishes.

The salmons silvered, their condition factor decreased, liver glycogen was mobilized and the concentrations of blood glucose and plasma protein and ions were radically altered during the course of smoltification in spring. The significant correlations between these changes suggest that an altered ionic and osmotic balance is coupled with changes in energy metabolism in the early stages of smoltification.

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1. Introduction

Altered osmoregulatory mechanisms and energy metabolism are amongst the most important changes that accompany the smolting of migrating salmonids. The preadaptation to hypoosmotic regulation in fresh water, as expressed by elevated Na,K-ATPase activity in gills and better regulation of body water and ions in sea water, are well documented phenomena (for a review, see Folmar & Dickhoff 1980). In fresh water, plasma and tissue chloride concentrations decrease (Fontaine 1960; Houston 1960; Houston & Threadgold 1963) and glomerular filtration rate and urine flow alter (Holmes & Stainer 1966, Eddy & Talbot 1985). The body energy stores, total body lipid and liver glycogen content decrease, and blood glucose concentration increases during smoltification (Wendt & Saunders 1973; Komourdjian et al. 1976; Farmer et al. 1978). These changes indicate that energy reserves are mobilized for the metabolic needs of smoltification. Woo et al. (1978) suggested that the mobilization of lipid and glycogen reserves is required for the development of hypoosmoregulatory capacity.

Although the changes in osmoregulation and energy reserves during smoltification are quite well documented, little is known about the connection between these physiological changes. Smoltification in a salmon population is not a rapid and synchronous phenomenon, but rather a series of metabolic and behavioural changes taking place with individual rhythms. Hence some idea of the connection between different metabolic changes can be obtained by investigating how different physiological properties are associated in individual fishes. The aim of this study was to correlate the changes in osmotic and ionic balance and increasing metabolic activity with external smolt indicators.

From the measured parameters, the blood haematocrit value (Hct) and haemoglobin concentration (Hb), the plasma concentrations of glucose, lactate and protein, and the liver glycogen content, describe the energy metabolism of fish; the muscle water content and the plasma ion concentrations describe the ionic and osmotic status of fish; body silvering and condition factor (CF) are considered as external indicators of smoltification.

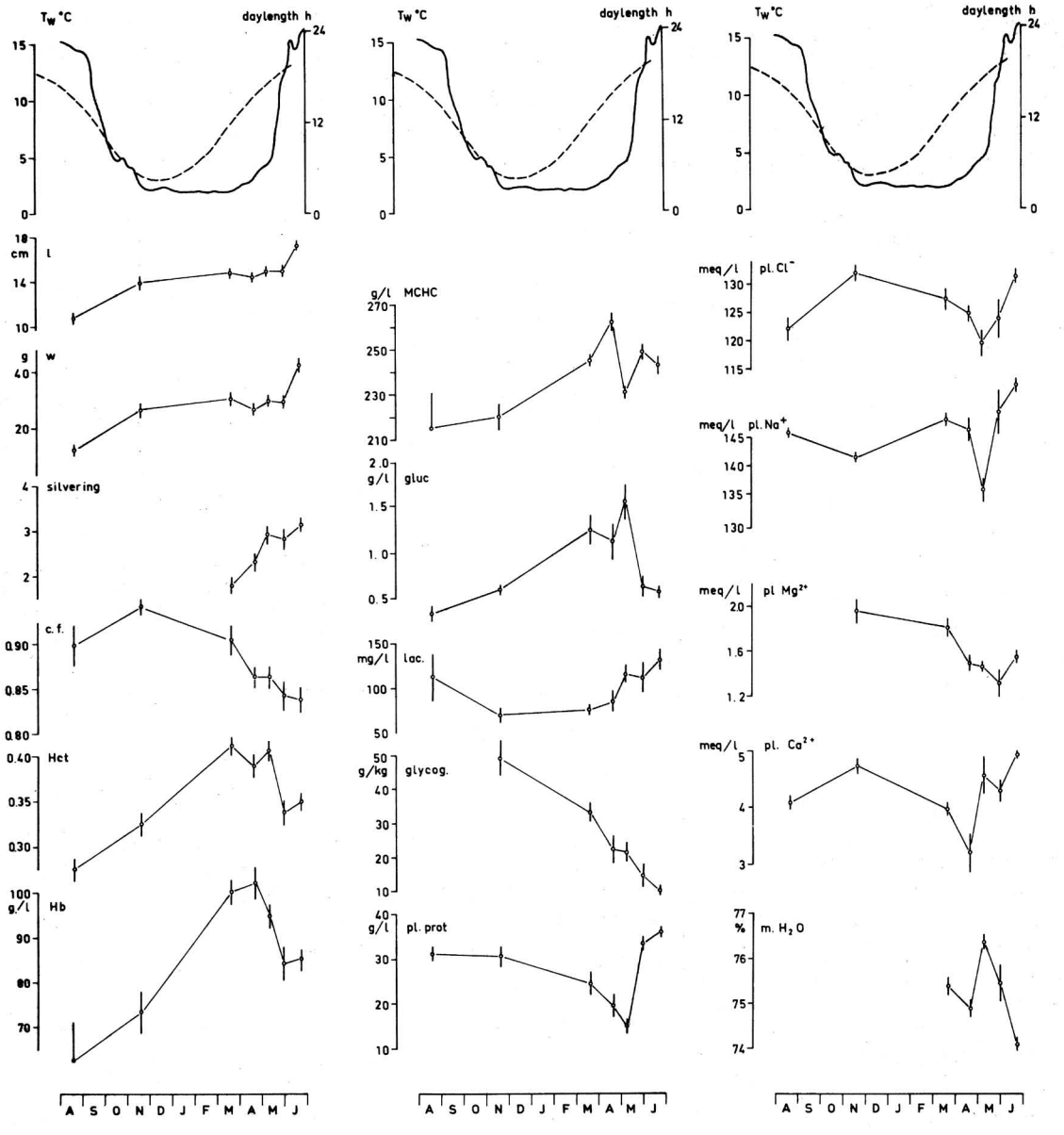

Fig. 1. Changes in some external and physiological parameters of young salmon from their second summer beyond the time of natural smolt migration. l = fish length, w = fish weight, c.f. = condition factor, Hct = blood haematocrit value, Hb = blood haemoglobin concentration, MCHC = mean corpuscular haemoglobin content, gluc = blood glucose concentration, lac = blood lactate c., glycog. = liver glycogen content, pl. prot = plasma protein c., pl. Cl^- to pl. Ca^{2+} = plasma ionic c's, m. H_2O = muscle water content. The bars indicate standard error (*SE*). Water temperature (solid line) and daylength (broken line) are included.

2. Material and methods

Young salmon from the stock of the River Neva were reared indoors in 4-m^2 plastic basins at Laukaa Fish Culture Research Station (LFCRS) in Central Finland. At the beginning of the experiment they were one-year-old individuals being reared for stocking in the Baltic Sea as two-year-old smolts. The water temperature followed the natural variation (Fig. 1) of Lake Peurunkajärvi, the source of the rearing water. The water quality has been reported in Oikari & Soivio

Table 1. Coefficients of linear correlations between the parameters. Parameter pairs with mostly nonsignificant correlations are excluded. S = silvering; BW = body weight; CF = condition factor; LG = liver glycogen; BG = blood glucose; PCl = plasma Cl^-; MW = muscle water. ND = not determined, NS = not significant, ° = significant at 10 % risk level; probability limits indicated by the asterisks: * = 5%, ** = 1%, *** = 0.1% . Sample size is shown in brackets.

Parameter pairs	Sampling months					
	November	March	April	May 6th	May 30th	June
S – BW	ND	0.659 ** (16)	0.282 NS (16)	0.301 NS (17)	0.638 ** (17)	–0.195 NS (15)
S – CF	ND	0.202 NS (17)	–0.531 * (15)	0.092 NS (18)	–0.554 * (16)	–0.206 NS (15)
S – LG	ND	0.465 NS (15)	–0.568 NS (9)	0.176 NS (10)	–0.749 * (8)	–0.247 NS (8)
LG – BW	0.767 *** (18)	0.615 * (11)	–0.614 ° (9)	0.286 NS (10)	–0.754 * (8)	–0.107 NS (8)
LG – CF	0.685 * (11)	0.210 NS (10)	–0.063 NS (9)	–0.284 NS (10)	0.711 * (8)	–0.077 NS (8)
LG – BG	–0.505 * (18)	–0.475 * (19)	–0.316 NS (15)	0.274 NS (19)	–0.196 NS (21)	–0.536 * (17)
BG – CF	0.144 NS (18)	–0.666 ** (17)	–0.799 *** (15)	–0.582 * (17)	–0.390 NS (15)	0.474 ° (14)
PCl – CF	0.094 NS (18)	0.481 ° (17)	0.603 * (15)	0.560 * (18)	–0.076 NS (15)	0.154 NS (13)
PCl – BG	–0.247 NS (18)	–0.191 NS (17)	–0.846 *** (15)	–0.795 *** (18)	–0.550 * (15)	–0.221 NS (13)
PCl – MW	ND	–0.499 * (16)	0.132 NS (15)	–0.436 ° (16)	–0.567 * (13)	–0.195 NS (11)

(1977). The L:D rhythm mainly followed the natural one, but artificial light was also used for working in the rearing hall. The fish were fed with dry salmon pellets (manufacturer Ewos AB, Sweden) with seasonally varying ratios.

Seven successive samples of about twenty fish were taken during the experimental period, starting from the second summer of the fish brood and continuing over the time of natural smolt migration. The last samples were taken from a fish group retained in fresh water at LFCRS a month after stocking time. Two days before sampling, the sampling group was moved to glass aquaria (volume c. 150 l), which were covered with dark plastic in order to avoid disturbance of the fish before and during sampling. The aquaria were supplied with water from the same source as the rearing basins. For sampling, the fishes were netted individually, and stunned with a sharp blow to the head. Blood was drawn from the caudal vessel in heparinized syringes and analyzed for haematocrit value using 3 min centrifugation at 10000 g, haemoglobin concentration by the cyanmethaemoglobin method, and glucose and lactate concentrations using Biochemica Boehringer test kits (GOD-PERID 124 036 and LACTATE UV 124 842 - methods, respectively). The rest of the blood was centrifuged within 3 min, and separated plasma was analyzed for total protein concentration using the Biuret method, chloride (Cl^-) concentration using Radiometer CMT 10 chloride titrator, sodium (Na^+) and potassium (K^+) concentration with an EEL flame photometer, and magnesium (Mg^{2+}) and calcium (Ca^{2+}) concentration using Wako test kits (B 999-83099 and B 997-21809, respectively). For glycogen determination, a piece of liver was taken and stored immediately in liquid nitrogen. The glycogen content was determined according to Harris et al. (1974). To determine the muscle water content, a small piece (c. 500 mg) of white muscle was taken from the lateral muscle beneath the dorsal fin, and dried to constant weight at 105°C.

The mean corpuscular haemoglobin concentration (MCHC) was calculated by dividing the Hb concentration by the Hct value. The condition factor was calculated from the formula $CF = 100w/l^3$ (w = fish weight (g), l = length (cm)). Body silvering was estimated visually on a scale 0–4 (4 = completely silvered, 0 = typical parr colouring). Correlation coefficients were calculated using the least squares method, and the significance of the coefficient is given as the statistical probability (P_c).

3. Results and discussion

Seasonal changes in the parameters are shown in Fig. 1. The correlations between some selected parameter pairs are given in Tabel 1. These pairs especially describe three interesting associations:

1. external smolt indices — osmotic and ionic balance
2. external smolt indices — energy metabolism
3. osmotic and ionic balance — energy metabolism.

3.1. Growth, condition factor and body silvering

The average growth rate of the salmon during their second summer from June to the beginning of November was about 1.3%/d. In November, the water temperature decreased to the winter level of about 2°C, and no weight increment took place at that temperature. Higgins (1985) reported that the "upper mode" of the fish brood, which smoltified the following spring, had a higher growth rate than the "lower mode" in autumn and winter. Unfortunately, no growth comparisons between the lower and upper mode were made in this study. The poor weight increment is possibly due to the low feeding rates in winter. However, the length of the fishes increased

during the winter by one cm (7%). Thus CF, which rapidly increased during the growth period in summer, gradually decreased in the winter and spring. In spring, the growth was not accelerated until the end of May at a temperature of about 10°C. The body silvering was not estimated until March, when the parr marks had already partially disappeared. Subsequently, the silvering proceeded rapidly, and maximum silvering was reached in early May. The changes in body silvering and condition factor were synchronous and rather similar to those reported by Farmer et al. (1978).

During this time (March–May), the body silvering correlated positively with body weight, indicating that the bigger parr tend to silver earlier, and the silvering is more intense at the releasing time than in the smaller ones. The relation between the size of fish and body silvering was similar to the one reported e.g. by Johnston & Eagles (1970). According to Wedemeyer et al. (1980), the size threshold for smolting in Atlantic salmon is 12–13 cm, and most of the smolts are in the 14–17 cm range. The connection between body silvering and the condition factor was more complicated: a significant negative correlation was not seen until the releasing time. This is apparently due to the fact that larger parrs, which tend to silver first, originally have a higher condition factor than the smaller ones (Table 1, Farmer et al. 1978).

3.2. Blood haematocrit value, haemoglobin concentration and mean corpuscular haemoglobin concentration

The blood Hct value and Hb concentration of salmonids are dependent on water temperature and season (Lane 1979, Nikinmaa et al. 1980, Härdig & Höglund 1984, Virtanen & Oikari 1984). In this study, the lowest values were observed in summer at 15°C and the highest in winter and early spring at 2-4°C. In spring the Hct and Hb values decreased rapidly with increasing temperature. However, during the winter at fairly constant temperatures, the Hct and Hb values increased, so that they were highest at early stages of smoltification. Changes in MCHC were partly concomitant with those of Hb. The high oxygen carrying capacity in smolting salmon can be related to the increased oxygen need, as reported by Barduc & Fontaine (1956). At the individual level, however, the Hb concentration correlated positively with body weight (in April and June significantly), but not with such smolt indices as silvering or CF. This indicates that the variation in blood Hct and Hb are more related to seasonal and temperature changes than to smoltification.

3.3. Blood glucose and lactate concentration, liver glycogen content

The concentration of blood glucose exhibited almost the same seasonal variation as the blood Hct value, with an even greater (about fivefold) increase during the autumn and winter. The fish sampled in November (at 3°C) had a markedly lower blood glucose level than those sampled in March-May at similar temperatures. Concomitant with the temperature rise in spring, the blood glucose concentration decreased by over 50 %. The blood lactate concentration was lowest in winter and increased in spring about 75 % above the winter level.

The liver glycogen content was not analyzed until November. In winter, the glycogen reserves were significantly lowered, and the decrease was further accelerated in spring.

In November, the body weight and condition factor correlated positively with liver glycogen content, indicating that large, fat fish had high glycogen stores at the end of the growth period. This situation was reversed during smoltification: at the releasing time, the liver glycogen content correlated negatively with fish weight. Apparently the bigger parr, which tend to silver first, start to lose their energy reserves earlier and/or at a higher rate than the smaller ones. One of the most marked differences between the smolts of this study and a group of smaller young salmon was the change in the liver glycogen content during the spring (Virtanen, unpublished). This indicates that in smolts the energy demand greatly exceeds that assimilated from food, whereas parr start to increase their energy reserves with increasing food consumption in spring. Sheridan et al. (1985) have reported an increase in glycolytic activity of smolting coho salmon (*Oncorhynchus kisutch*). The activity of some respiratory enzymes in liver increase, and this is possibly associated with the activation of the thyroid gland (Blake et al. 1984). Also, the body silvering is regulated by thyroid hormones (Robertson 1949). Hence the negative correlation between body silvering and liver glycogen, as well as between silvering and CF, observed in this study may be based on the fact that both silvering and an increased

energy requirement are caused by the increase in thyroid hormone concentration. This hypothesis is also supported by the synchrony of silvering and rise in plasma thyroxine in Baltic salmon (Virtanen & Soivio 1985). On the other hand, increased interrenal activity and elevated corticosteroid levels in smolting salmon may also play an important role as catabolic affectors (Specker 1982, Virtanen & Soivio 1985).

Elevated individual blood glucose levels were associated with depleted liver glycogen stores in November, March and June, but not in April-May, when the metabolic changes in smoltification are at their most distinct. During this time hyperglycemia was associated with low CF and hypochloremia, but not with body silvering. The lack of correlations between blood glucose and liver glycogen and between blood glucose and body silvering is probably based on the following factors:

– the blood glucose concentration is strongly dependent on water temperature, and hence decreased due to the temperature rise in May. Virtanen & Oikari (1984) have reported a 62 % decrease in the blood glucose of presmolt salmon when raising the water temperature from 1.5 to 10°C. This may mask the effects of smoltification on blood glucose.

– hyperglycemia accompanied by low CF and ionic changes was observed at early stages of smoltification, when the parr marks were still to some extent visible.

Elevated blood glucose levels are often associated with increased mobilization of liver glycogen. Inui (1969) reports that in hepatectomized *Anguilla japonica,* no glucose elevation takes place during stress. The lack of correlation between blood glucose and liver glycogen during smoltification in this study may be due to the fact that larger fish with originally larger glycogen reserves, mobilize glycogen at a higher rate than smaller ones.

Another possibility is that elevated blood glucose levels at this time are partly achieved by gluconeogenesis using proteins and amino acids. In *Oncorhynchus*, 60 % of the body protein is catabolized during the migration-spawning phase, and this is associated with an elevation of liver glycogen (Chester Jones et al. 1974). Increased corticosteroid levels observed in smolts accelerate the gluconeogenesis (Specker 1982). It is unclear what role plasma proteins have as a source of gluconeogenesis. In this study, a marked decrease in plasma protein concentration took place at the time of elevated blood glucose levels. Additionally, during smoltification there was a negative correlation between plasma protein and blood glucose concentration and a positive correlation between plasma protein concentration and condition factor.

3.4. Plasma protein and ionic concentrations, muscle water content

The plasma protein concentration decreased during the winter and early spring, and the lowest values were observed in early May. After that the concentration increased rapidly, and the "normal" level of 30–35 g/l was achieved at the end of May (the releasing time). Concomitant with the marked drop in plasma protein during March-April, there was also a decrease of plasma ionic concentrations, although this was less pronounced. However, the concentrations of plasma Ca^{2+} and Mg^{2+} did not return to the original levels synchronously with plasma protein, Na^{+} and Cl^{-}. The water content of muscle was at its highest in early May and decreased significantly in May and June. Thus the evident loss in osmoregulatory capacity in early spring (water temperature 2–4°C) was not observed either at or after the migration time (water temperature 10–15°C).

At the time when plasma protein and ionic levels were low, plasma Cl^{-} correlated positively with CF and negatively with blood glucose concentration. However, plasma Cl^{-} did not correlate significantly with body silvering. Additionally, plasma Cl^{-} correlated negatively with muscle water content in March and late May, but not at the time when the lowest values of plasma protein and ions were observed. This was also the case between plasma protein and the condition factor: significant correlations were observed before and after the low levels of plasma protein and ions.

The development of hypoosmoregulatory capacity in smoltification is known to accompany osmoregulatory changes in fresh water. The "preadaptation" of gill Na,K-ATPase activity is a well documented indication of smoltification (for a review, see Folmar & Dickhoff 1980). On the other hand, there exist discrepancies between different studies with respect to the hypothesis that a loss of hyperosmoregulatory capacity takes place during smoltification in fresh water. Houston (1960) and Houston & Threadgold (1963) found that in Atlantic salmon, large nonsilvered parr had a lower concentration of plasma and tissue Cl^{-} than silvered parr and smolt. They argued that juvenile salmon lose their ability to regulate body Cl^{-} at early stages of smoltification,

still without visible smolt characteristics. The early results of Koch et al. (1959) and Fontaine (1960) also support this hypothesis. In contrast, Parry (1961) and Saunders & Henderson (1970) observed no decrease in plasma osmotic pressure of Atlantic salmon at smoltification. Accordigly, Conte et al. (1966) and Miles & Smith (1968) found no clear osmotic or ionic changes during the smoltification of coho salmon (*Oncorhynchus kisutch*).

Our results partially support the hypothesis of Houston and Threadgold. Plasma protein and ionic concentrations decreased in early spring before maximal silvering, and increased again to the original levels at the migration time. The correlation of low plasma Cl^- with reduced CF and elevated blood glucose, but not with silvering, indicates that changes in osmotic and ionic balance are associated with early stages of smoltification. However, in a group of smaller young, in which the parr marks partially remained, a somewhat similar reduction also took place (Virtanen, unpublished). Reduced ionic concentrations were earlier restored in this group.

Thorpe (1984) suggests that "maladaptation" based on the breakdown of territorial behaviour and hyperosmotic regulation may play an important role in the onset of smolt migration. Primmet et al. (cit. Thorpe et al. 1987) have recently observed a marked increase in sodium efflux at early stages of smoltification. The faster "recovery" of the ionic balance in the smaller parr may hence indicate that, although the osmoregulatory change of smoltification also starts in these fish, it is not completed and the regulatory capacity of parr is restored before it leads to downstream displacement.

In contrast to Na^+ and Cl^-, the excretion of Ca^{2+} and Mg^{2+} mainly takes place in the kidney, which explains the different patterns of plasma concentrations of these ions. In addition to the renal Mg^{2+} output of smolts increasing markedly with rising temperature (Oikari & Virtanen 1984), there also seem to be other machanisms increasing Mg^{2+} efflux in smoltification. Active renal excretion of Mg^{2+} is a necessary component of ionic regulation in sea water.

3.5. Osmotic and ionic regulation vs. energy metabolism

A strong correlation of blood glucose and plasma chloride indicates that increased activity of the energy metabolism in early spring — when the water temperature is still very low — is associated with osmoregulatory changes in smoltification. Accordingly, Wendt & Saunders (1973) suppose that hyperglycemia in hatchery-reared pre-smolts is related to osmotic or ionic imbalance in fresh water and may be a consequence of the hatchery environment which promotes "premature smoltification". By contrast, Thorpe (1984, 1985 personal communication) suggests that the loss of body ions also takes place in the wild, and that it plays an essential role among the changes which lead to downstream displacement. Also in this model, hyperglycemia can be explained as a consequense of stress caused by the osmoregulatory "maladaptation". However, the activation of glycolytic enzymes in the liver, possibly regulated by the thyroid (Blake et al. 1984; Sheridan et al. 1985), indicates that the hyperglycemia of smolting fish is not only a consequence of osmotic imbalance, but also the result of a change in energy metabolism.

Attention should be paid to the fact that most of the studies dealing with the smoltification process — including this one — are carried out on hatchery-reared salmon. Smoltification in hatchery conditions may differ greatly from that in a natural environment — e.g. because of different fish densities, food, water velocity and illumination. Virtanen et al. (1983) have reported significant differences in the physiological status of wild and reared smolts. Virtanen & Soivio (1985) found that the synchronization of some physiological changes is affected by the rearing conditions. Thus the characteristic and time course of the changes observed in this study can be expected to vary in relation to the environmental conditions.

In conclusion, of the many observed changes commonly associated with smoltification and interpreted to be phenomena induced by smoltification, only some appear in synchrony. Some of the changes, e.g. those in the blood Hb concentration, may be related to other seasonal rhythms and temperature fluctuation.

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