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Smolting of two-year-old lower and upper size class of Saimaa landlocked salmon (*Salmo salar* m. *sebago* Girard) under fish farm conditions

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Smolt development was assessed in two-year-old lower and upper size class of hatchery-reared Saimaa landlocked salmon during January–July and late April–July, respectively. The fish in both size classes showed increased gill Na^+,K^+-ATPase during the spring suggesting smolting of these fish. The fish in the lower size class showed also a smolting-associated decrease in lipid content of muscle as spring progressed whereas the lipid content in upper-size-class fish appeared to increase during late April–May. The differences in lipid content of muscle as well as in gill Na^+,K^+-ATPase activity between the groups may indicate the presence of non-smolting individuals among the fish sampled from upper size class. However, variation in these as well as other parameters was small. Thus, it is suggested that each class of juvenile Atlantic salmon shows a distinct developmental pattern of ionoregulation.

Introduction

Development of bimodal size distribution is commonly observed in cultured Atlantic salmon (*Salmo salar*) (Thorpe 1977, Thorpe *et al*. 1980). Faster-growing upper modal group (UMG) fish will smolt as one-year-olds whereas the smaller, slower-growing lower modal group (LMG) fish remain as a parr for a further year (Thorpe 1977, Bailey *et al*. 1980, Kristinsson *et al*. 1985). Separation into upper and lower modes has also been observed in Saimaa landlocked salmon (*Salmo salar* m. *sebago* Girard) at Saimaa Fisheries and Aquaculture Research unit (J. Piironen and P. Kiiskinen unpubl. data) and the fish belonging to the upper modal group underwent parr–smolt transformation as one-year-olds (Kiiskinen *et al*. 2003). Shrimpton *et al*. (2000) followed a bimodal population of Atlantic salmon over a period of two years and observed that UMG fish can smolt in two consecutive years.

The present stock of endangered Saimaa landlocked salmon is totally dependent on stockings of cultivated juveniles (Pursiainen *et al*. 1998). Under common stocking practise juveniles of Saimaa salmon are released as two-year-olds near the parental broodstock's reproduction areas. However, hatchery practises may lead to separa-

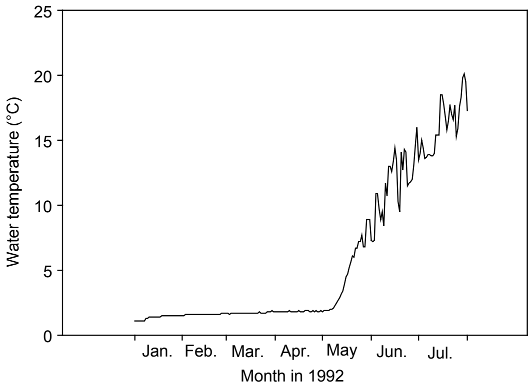

Fig. 1. Rearing water temperature of Lake Ylä-Enonvesi during the experiments.

tion into modal groups and thus different timing of smolting. The present study was undertaken to examine whether upper size class of Saimaa landlocked salmon, which were assumed to undergo parr–smolt transformation as one-year-olds will repeat this process as two-year-olds. The data from one-year-old Saimaa salmon sized identical to the present upper-size-class fish in the beginning of their second growing season showed that these fish indeed smolted as one-year-olds (Kiiskinen *et al*. 2003). Smolt development of the upper-size-class fish was compared with that of the lower-size-class fish that were assumed to complete their smolting first time as two-year-olds. As reported above, juveniles of Saimaa salmon are stocked near the parental broodstock's reproduction areas. This is essential for their subsequent homing as spawners back to the river, where they will be caught for the collection of milt and eggs for cultivation. To ensure the movement of the juvenile fish from the river into larger feeding areas it is essential that the fish used in stockings are smolts.

Materials and methods

Fish and rearing conditions

Two-year-old Saimaa landlocked salmon from a cultivated brood of Saimaa stock reared at the Saimaa Fisheries Research and Aquaculture in south-eastern Finland (62°05´N, 28°55´E) were used in this study. The early development of the fish was accelerated by increasing the water temperature gradually from 4 to 8 °C from about four weeks after the eyed stage of embryos until 'startfeeding' when the ambient water temperature reached 8 °C. The fish were first reared inside in four circular 2.1-m^2 plastic tanks (ca. 250 individuals per tank) supplied with oxygenated water (concentration of oxygen was > 7 mg l^{-1} throughout the year) at a rate of 15–20 l min^{-1}. Then on 26 June 1991 when the fish were one year old they were graded into lower and upper size class groups with a 9-mm bar grader. The mean weights of the fish in lower- and upper-size-class groups were 7.5 g and 26.7 g, respectively. From 26 June 1991 the fish from both groups were reared outside until 28 October 1991 when 400 and 144 individuals of lower- and upper-size-class groups, respectively, were moved inside to circular 3.3-m^2 plastic tanks supplied with oxygenated water at a rate of 50–70 l min^{-1}. On 14 November 1991, length and weight of ca. 100 fish from both groups were measured. The mean length ± S.E. and weight ± S.E. of lower-size-class fish were 16.4 ± 0.1 cm and 51.7 ± 1.3 g, respectively. In the upper-size-class fish, the length was 18.6 ± 0.2 cm and the weight was 70.5 ± 2.5 g. Illumination of the rearing hall was provided by artificial light (intensity of 2 lx at the surface of the rearing tanks) following natural photoperiod. Additional light came also through the windows. Between ca. 7:00 and 16:00, working lights with intensity of 37 lx at the surface of rearing tanks were also used. Rearing temperature followed the natural temperature of lake Ylä-Enonvesi, the source of rearing water (Fig. 1). The fish were fed commercial dry feeds (Ewos) by automatic dispenser (ITUMIC) which adjusted the amount of food according to the water temperature and the size of the fish. Food was delivered throughout daylight hours.

Sampling and analytical procedures

Ten fish from the lower-size-class group were sampled at about one-month intervals in January–July 1992, except in February. Due to the small number of upper-size-class-group fish were sampled in April–June 1992. The fish were not fed for 48 hours before sampling. Fish were killed by a sharp blow on the head, and then blood samples were collected from the caudal vessels into ammonium-heparinized syringes. Plasma was separated immediately by centrifugation. The fish were measured for total length to the nearest 0.1 cm and weighed to the nearest 0.1 g. The external smolt indices, i.e. distinctness of parr marks and percentage of silvered fish were estimated visually. Distinctness of parr marks was estimated on a scale of 0–4, where 0 indicates totally disappeared parr marks. The whole first gill arch and a piece (1–4 g) of great lateral muscle close to the dorsal fin were removed. Gill and plasma samples were frozen in liquid nitrogen (–196 °C) immediately after sampling and then stored for less than a month at –80 °C before they were analysed. Water content of muscle was analysed soon after sampling. Analytical procedures used in determination of muscle water content, gill Na^+,K^+-ATPase activity and plasma ion (Na^+, Cl^-, Mg^{2+}) concentrations are described in detail in Kiiskinen *et al*. (2002). Plasma ion concentrations were not analysed in July because the samples were lost in transportation.

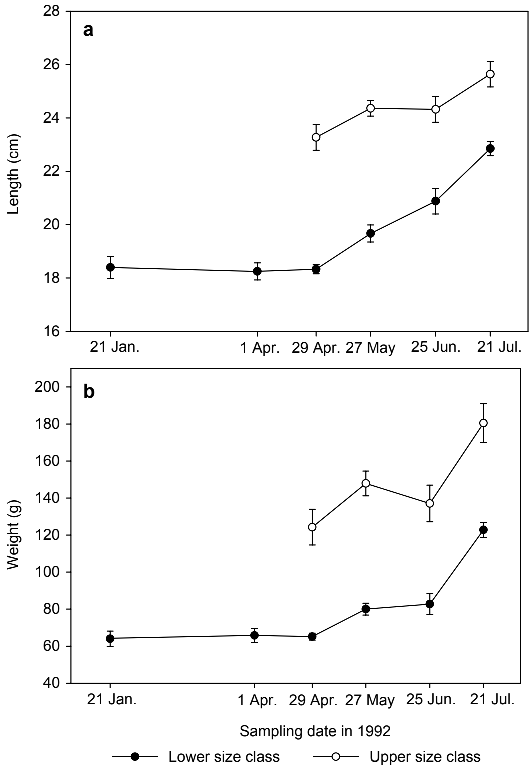

Fig. 2. Length (**a**) and weight (**b**) of two-year-old lower and upper size class of Saimaa landlocked salmon (*Salmo salar* m. *sebago* Girard) reared under hatchery conditions during January–July 1992. Symbols represent the mean values and vertical bars indicate standard error of the mean (S.E.).

Seawater challenge

Ten fish from each size class were exposed during January–July (except in February) and April–July, respectively, to a seawater challenge test (SW test) for 48 hours at ca. 30‰ using ion-balanced salt (Instant Ocean). The volume of the test water was 320 l per group and the water was oxygenated with aquarium aerators. Tests were done at a constant temperature of 10 °C with a two- to five-day acclimation period (depending on the rearing temperature) before salt was added. The fish were not fed during acclimation or exposure. The mortality, muscle water content and concentrations of plasma ions (Cl^-, Na^+ and Mg^{2+}) were determined from these test fish. Change in muscle water content in seawater was expressed as a difference in water content of muscle between fish in freshwater and exposed to seawater.

Statistical procedures

Effects of time and size of the fish on the different parameters were tested by two-way ANOVA. To normalise the variance, all percentage values were subjected to angular transformation ($TP = \sin^{-1} \sqrt{P}$, where P is percentage value).

Results

Size and external smolt indices

The size difference between lower- and upper-size classes was clear during the whole study period (Fig. 2). The effect of time was statistically significant in length and weight (Table 1). The lower-size-class fish showed no change in size in January–April, but from May onwards they increased in length and weight (Fig. 2a and b). Also the upper-size-class fish showed increased growth rate in July.

All fish sampled from the upper-size-class group were silvered in May and June and the proportion of silvered fish was high also in July (Table 2). In the lower-size class, percentages of silvered fish in May, June and July were 40, 80 and 80, respectively (Table 3). Sex ratios for the upper- and lower-size-class fish are presented in Tables 2 and 3, respectively.

Lipid and water content of muscle in freshwater

In the lower-size-class fish, the muscle lipid content decreased as spring progressed, whereas the upper-size-class fish had a higher muscle lipid content in May than in April and June–July (Fig. 3a). An increasing trend in the muscle water content in freshwater was observed in the lower-size-class fish in January–late April, which was followed by a small decrease in May–June (Fig. 3b). In the upper size class, no large changes were observed (Fig. 3b). The effect of time was statistically significant on the muscle lipid and water contents in freshwater (Table 1). In muscle lipid as well as in water content interactions were found between the fish size and time.

Table 1. Effects of size and time on different parameters of two-year-old lower and upper size class Saimaa landlocked salmon tested with two-way ANOVA.

Source	df	MS	*F*	*p*
Length				
Size	1	575.199	176.721	0.000
Time	5	37.058	11.385	0.000
Size × Time	5	7.451	2.289	0.051
Error	103	3.255		
Weight				
Size	1	148117.223	127.885	0.000
Time	5	7764.988	6.704	0.000
Size × Time	5	2359.184	2.037	0.080
Error	103	1158.210		
Muscle lipids				
Size	1	8.409E–04	3.769	0.055
Time	5	9.599E–04	4.302	0.001
Size × Time	5	7.092E–04	3.178	0.010
Error	103	2.231E–04		
Muscle water in FW				
Size	1	3.297E–05	0.221	0.640
Time	5	3.983E–04	2.666	0.026
Size × Time	5	7.597E–04	5.084	0.000
Error	104	1.494E–04		
Muscle water in SW				
Size	1	2.789E–02	1.869	0.174
Time	5	4.371E–02	2.929	0.016
Size × Time	5	3.835E–02	2.570	0.030
Error	123	1.492E–02		
Na^+,K^+-ATPase				
Size	1	55.200	22.784	0.000
Time	5	46.527	19.205	0.000
Size × Time	5	8.911	3.678	0.004
Error	103	2.423		

Gill Na^+,K^+-ATPase activity and water content of muscle after 48 h exposure to seawater

Gill Na^+,K^+-ATPase activity increased in the lower-size-class fish from January onwards, reaching a peak in May, that was followed by a decrease in June–July (Fig. 3c). Although gill Na^+,K^+-ATPase activity was lower in the upper-size-class fish in late April–May as compared with that in the lower-size-class fish, the activity was higher in May–June than in April and July (Fig. 3c). Gill Na^+,K^+-ATPase activity was significantly affected by the fish size and time, whereas time was the only factor significantly affecting muscle water content of the fish exposed to seawater (Table 1). In both gill Na^+,K^+-ATPase activity and muscle water content in seawater an interaction between the fish size and time was observed.

All fish survived from 48 h exposure to seawater, except in July when there was 20% mortality in the lower-size-class fish (Tables 2 and 3). Both the lower- and the upper-size-class fish showed good ability to regulate their muscle water content in seawater in May–June, as opposed to late April and July when the loss of muscle water in seawater was higher (Fig. 3d).

Plasma ion concentrations in freshwater

Decreases in plasma sodium, chloride and magnesium concentrations were observed in the lower-size-class fish as spring progressed (Fig. 4a, b and c) and also in the upper-size-class fish the trends were similar (Fig. 4d, e and f). The concentrations of plasma sodium and chloride in freshwater were significantly affected by time (Table 4).

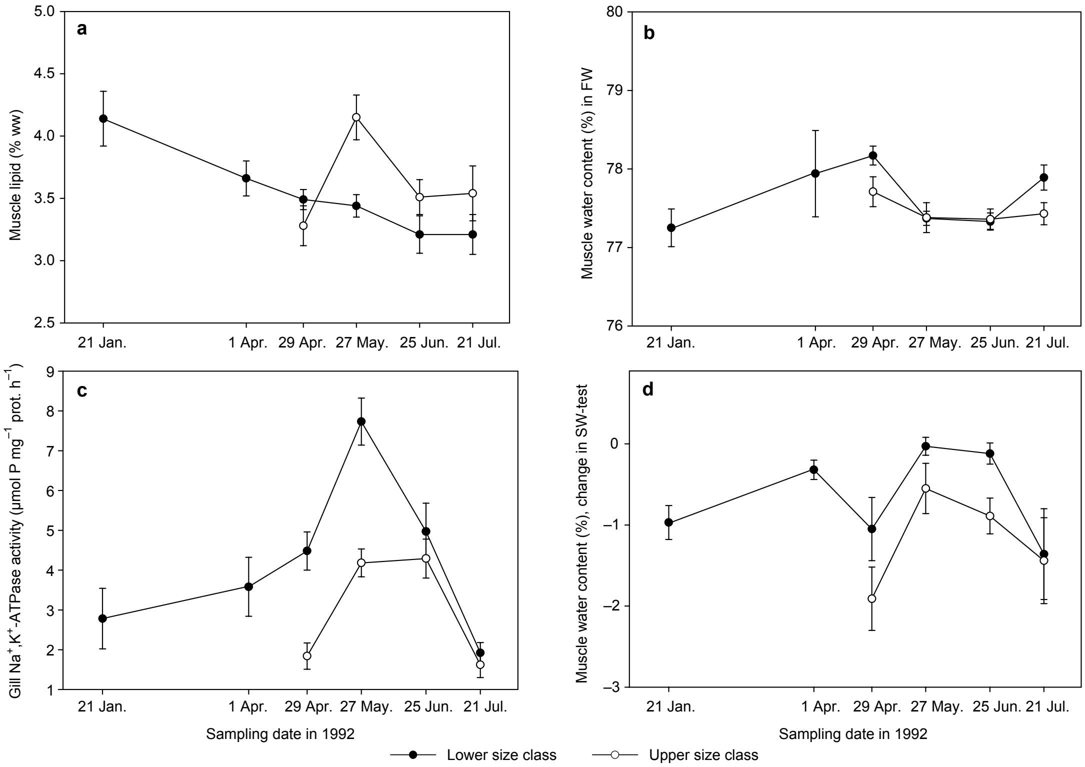

Fig. 3. Lipid content in muscle (**a**), water content in muscle (**b**), gill Na^{+},K^{+}-ATPase activity (**c**) and the change in muscle water content after 48 h seawater exposure (**d**) in two-year-old lower and upper size class of Saimaa landlocked salmon (*Salmo salar* m. *sebago* Girard) reared under hatchery conditions during January–July 1992. Symbols represent the mean values and vertical bars indicate standard error of the mean (S.E.).

Table 2. External smolt indices (means ± S.E.), sex ratio and mortality following 48 h exposure to seawater at ca. 30‰ salinity for two-year-old upper size class of Saimaa landlocked salmon (*Salmo salar* m. *sebago* Girard) under hatchery conditions during January–July 1992.

Variable	21 January	1 April	29 April	27 May	25 June	21 July
Visibility of parr marks[1] (0–4)	–	–	2.1 ± 0.10	1.0 ± 0.00	1.0 ± 0.00	1.3 ± 0.15
Visibility of parr marks[2] (0–4)	–	–	2.8 ± 0.13	1.7 ± 0.15	1.5 ± 0.17	1.6 ± 0.16
Silvered (%)	–	–	0	100	100	70
Sex (♂/♀)	–		2/8	7/3	5/5	4/6
Mortality in SW-test (%)	–	–	0	0	0	0

[1] Visibility of parr marks on the surface of scales; [2] Visibility of parr marks on the surface of skin.

Table 3. External smolt indices (means ± S.E.), sex ratio and mortality following 48 h exposure to seawater at ca. 30‰ salinity for two-year-old lower size class of Saimaa landlocked salmon (*Salmo salar* m. *sebago* Girard) under hatchery conditions during January–July 1992.

Variable	21 January	1 April	29 April	27 May	25 June	21 July
Visibility of parr marks[1] (0–4)	2.3 ± 0.16	3.6 ± 0.22	2.9 ± 0.10	1.6 ± 0.20	1.6 ± 0.16	1.2 ± 0.13
Visibility of parr marks[2](0–4)	4.0 ± 0.00	4.0 ± 0.00	3.9 ± 0.10	3.1 ± 0.18	2.3 ± 0.21	2.0 ± 0.00
Silvered (%)	0	0	0	40	80	80
Sex (♂/♀)	6/2	5/5	4/6	6/4	7/3	5/5
Mortality in SW-test (%)	0	0	0	0	0	20

[1] Visibility of parr marks on the surface of scales; [2] Visibility of parr marks on the surface of skin.

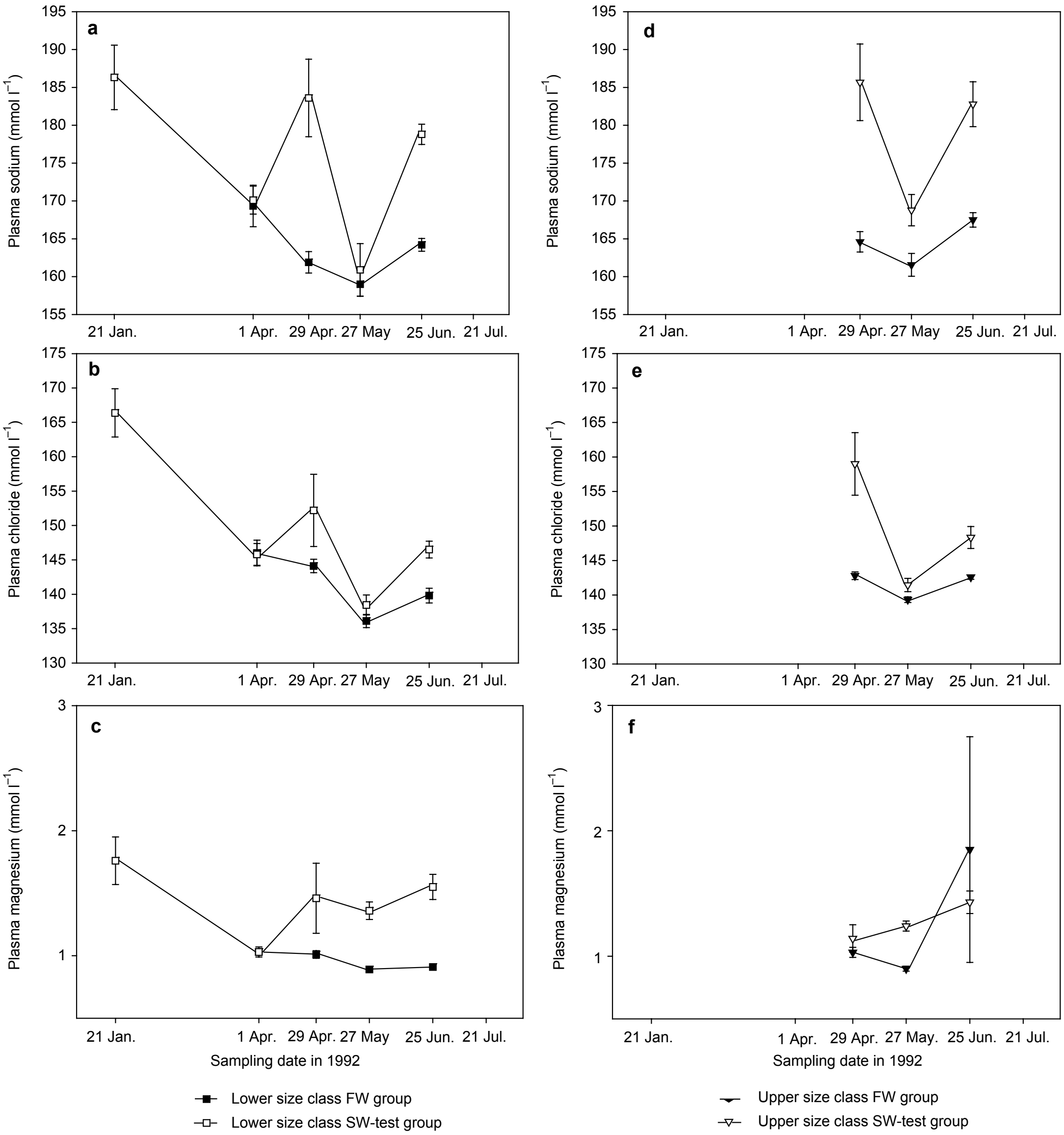

Fig. 4. Plasma sodium (**a** and **d**), chloride (**b** and **e**) and magnesium (**c** and **f**) concentrations in freshwater and following 48 h exposure to sea water in two-year-old lower and upper size class of Saimaa landlocked salmon (*Salmo salar* m. *sebago* Girard) reared under hatchery conditions during January–July 1992. Symbols represent the mean values and vertical bars indicate standard error of the mean (S.E.).

Plasma ion concentrations after 48 h exposure to seawater

Plasma sodium and chloride concentrations in seawater were high in the lower-size-class fish in all months sampled except in early April and in May when there were no differences between the fish exposed to seawater and those reared in freshwater (Fig. 4a and b). Also the fish in the upper-size-class group showed lower levels of plasma sodium and chloride concentrations in May (Fig. 3d and e). In the lower-size-class fish the plasma magnesium concentration was lower in April–June than it was in January (Fig. 4c), whereas in the upper size class no large changes were observed in late April–June (Fig. 4f). A clear increase in plasma sodium concentration was observed in both groups in June. The effect of time was statistically significant in plasma sodium and chloride concentrations following exposure to seawater (Table 4).

Discussion

The spring increase in the concentration of the gill Na^+,K^+-ATPase has been used as an indicator of smolting and in previous studies we found it to reliably describe smolt development of hatchery-reared Saimaa landlocked salmon (Kiiskinen *et al*. 2002, 2003). In the present study, both the lower- and the upper-size-class fish showed elevated activity of gill Na^+,K^+-ATPase indicating smolting of these fish.

Gill Na^+,K^+-ATPase is known to play a central role in the salt-secretory function of the chloride cell (McCormick 1995). Traditionally the increase of this enzyme activity has been associated with "preparing the fish for life at sea". However, the increase of this enzyme activity occurs some weeks before the fish would reach the sea (Thorpe and Moore 1997), and it occurs in salmon that never encounter the sea as showed by the present as well as the earlier results from Saimaa landlocked salmon (Kiiskinen *et al*. 2002, 2003). It has been suggested that the increase of gill Na^+,K^+-ATPase activity would be a response to seasonal osmoregulatory difficulties in maintaining hydromineral balance in freshwater (Langdon and Thorpe 1985, Simpson 1985, Primmett *et al*. 1988, Reis-Henriques *et al*. 1996, Thorpe and Moore 1997). Data from the present experiments as well as those of earlier ones (Kiiskinen *et al*. 2002, 2003) are consistent with this since lower levels of plasma Na^+ and Cl^- concentrations were observed in fish of the freshwater groups at the time of elevated gill Na^+,K^+-ATPase activity. An increase in muscle water content in freshwater observed in the lower-size-class fish in January–late April and decrease in plasma Mg^{2+} concentration during the spring suggest osmoregulatory difficulties as well. Since plasma Mg^{2+} is mainly or entirely excreted through kidneys (Hickmann and Trump 1969) the decrease in plasma Mg^{2+} may indicate increased urine output. Eddy and Talbot (1985) reported that smolting Atlantic salmon produced greater quantities of urine. This has been regarded as an attempt to restore water balance in freshwater (Thorpe and Moore 1997).

Although elevated activity of gill Na^+,K^+-ATPase may be seen as a consequence of loss of freshwater osmoregulatory capacity, overall increase of this enzyme activity is also linked up with increased sodium efflux potential capable of activation in seawater (Primmett *et al*. 1988). In the present study, elevated ability to hypoosmoregulate was observed at the time of increased gill Na^+,K^+-ATPase activity. The fact that the lower-size-class fish showed good ability to hypoosmoregulate in early April but not in late April may be due to general osmoregulatory difficulties; a decrease in plasma Na^+ concentration was found in fish of the freshwater group in late April. However, the decrease in plasma Na^+

Table 4. Effects of size and time on plasma ion concentrations of two-year-old lower and upper size class Saimaa landlocked salmon in freshwater and after 48 h exposure to seawater tested with two-way ANOVA.

Source	df	MS	*F*	*p*
Plasma Na^+ in FW				
Size	1	105.209	4.368	0.040
Time	4	238.371	9.897	0.000
Size × Time	3	3.730	0.155	0.926
Error	74	24.084		
Plasma Cl^- in FW				
Size	1	100.122	2.247	0.138
Time	4	269.145	6.040	0.000
Size × Time	3	29.916	0.671	0.572
Error	74	44.557		
Plasma Mg^{2+} in FW				
Size	1	1.093	1.104	0.297
Time	4	0.646	0.652	0.627
Size × Time	3	1.038	1.048	0.377
Error	74	0.990		
Plasma Na^+ in SW				
Size	1	7.852	0.050	0.824
Time	4	1737.028	11.038	0.000
Size × Time	4	209.256	1.330	0.264
Error	100	157.364		
Plasma Cl^- in SW				
Size	1	9.983	0.088	0.767
Time	4	1820.323	16.033	0.000
Size × Time	4	298.998	2.634	0.039
Error	100	113.536		
Plasma Mg^{2+} in SW				
Size	1	390.382	1.422	0.236
Time	4	374.047	1.362	0.252
Size × Time	4	364.797	1.329	0.265
Error	100	274.550		

and Cl^- concentrations in freshwater was even more severe in May than it was in late April, but despite this the fish in the lower size class were able to regulate their plasma ion concentrations in seawater. This may be explained by a marked increase of gill Na^+,K^+-ATPase activity.

A decrease in gill Na^+,K^+-ATPase, reduced ability to regulate plasma ion concentrations and muscle water content in seawater as well as increasing trend in plasma ion concentrations in freshwater observed in both groups during June–July may be seen as an indication of re-establishment of freshwater type osmoregulation. Also growth rate appeared to increase at that time, especially in the lower-size-class-group fish. Despite these changes associated with loss of smolt characteristics, 80% and 70% of the lower- and the upper-size-class fish, respectively, were silvered in July. This suggests that silvering dynamics may be strongly affected by background coloration or light conditions (Kato 1972, Kazakov and Kozlov 1985, Kiiskinen *et al*. 2003) and thus is not a reliable indicator of the smolt status. Also the ability to survive from short-term exposure to seawater, if used as a single indicator, may be insufficient for estimation of smolt development. This is based on the fact that all fish from lower-size-class group survived 48-h exposure to seawater in January and in late April, but showed no ability to regulate their plasma ion concentrations.

Although developmental changes of smolting were generally similar in the lower- and the upper-size-class fish there were, however, some differences between the groups. The lower-size-class fish showed smolting-associated decrease in their muscle lipid content as spring progressed whereas the muscle lipid content in the upper-size-class fish appeared to increase in late April–May. The differences in the muscle lipid content as well as in gill Na^+,K^+-ATPase activity between the groups may indicate that there were non-smolting individuals among the fish sampled from the upper size class. However, variation in these as well as other parameters was small. Thus, it is suggested that each class of juvenile Atlantic salmon show a distinct developmental pattern of ionoregulation as reported by Langdon and Thorpe (1985). However, considering the differences of smolting-associated changes, further research would be valuable in translating the present physiological findings into migratory behaviour of two-year-old lower- and upper-modal fish. Finally, if hatchery practises lead to separation of fish into modal groups and if upper-modal-group fish undergo parr–smolt transformation as one-year-olds, there is no reason why these fish should not be stocked as one-year-olds. In view of maintenance of genetic variation, it is important that also lower modal group fish as two-year-olds are used in stockings.

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