Available online at www.sciencedirect.com
SCIENCE DIRECT®
Aquaculture 222 (2003) 71–82
Aquaculture
www.elsevier.com/locate/aqua-online

Smolting in anadromous and landlocked strains of Atlantic salmon (*Salmo salar*)

Tom O. Nilsen, Lars O.E. Ebbesson, Sigurd O. Stefansson*

Department of Fisheries and Marine Biology, University of Bergen, Bergen High Technology Centre, Bergen N-5020, Norway

Received 29 October 2002; accepted 15 December 2002

Abstract

Juvenile Atlantic salmon from a landlocked population ('Blege', lake Byglandsfjord, south–central Norway) and an anadromous population (river Vosso, southwestern Norway) were reared in freshwater on simulated natural photoperiod (60°25′N) between December 2000 and June 2001. Fish from the Blege (mean length: 13.4 cm) and Vosso (mean length: 13.9 cm) strains were transferred to seawater tanks in late May for studies of long-term post-smolt performance. Condition factor of fish from the Blege strain increased throughout the study, whereas in the anadromous Vosso strain condition factor increased until April followed by a decrease between April and June. Smolts from the Vosso strain showed all the morphological characteristics of smolting, whereas smolt-sized fish from the landlocked population obtained a lower degree of silvering, and distinct parr-marks and red dots in the skin prevailed. Gill Na^+,K^+-ATPase activity remained low in both strains in January and March, with a significant increase in the Vosso strain in April and May to peak levels of approximately 17 μmol ADP/mg protein/h. In contrast, only a slight increase was seen in the Blege strain in May, with peak level of approximately 8 μmol ADP/mg protein/h. In mid-June Na^+,K^+-ATPase activity was down to parr levels. Improved short-term hypoosmoregulatory ability (seawater challenge tests, 34‰, 96 h) was observed in both strains; however, the Vosso strain showed better seawater tolerance than the Blege strain in March and April. There was no mortality among the smolt-sized fish of the Vosso strain transferred to seawater in late May, whereas high mortalities (40%) were observed in the Blege strain during the 2 weeks of seawater rearing. Our findings show that landlocked Atlantic salmon, represented here by the Blege population, having been isolated from the sea for approximately 9000 years, may have abandoned key elements of the parr–smolt transformation associated with marine life. Our

* Corresponding author. Tel.: +47-55584470; fax: +47-55584450.
E-mail address: Sigurd.Stefansson@ifm.uib.no (S.O. Stefansson).

0044-8486/03/$ - see front matter
doi:10.1016/S0044-8486(03)00103-0

results further emphasize the importance of the gill Na^+,K^+-ATPase for long-term seawater performance.

Keywords: Osmoregulation; Smoltification; Parr–smolt transformation; Na^+,K^+-ATPase

1. Introduction

Anadromous Atlantic salmon display a life cycle with a characteristic migratory pattern and the smolt as the migratory juvenile stage. The smolt migrates downstream, leaves freshwater and enters the marine environment (McCormick et al., 1998). Prior to seawater entry, juvenile anadromous salmon undergo a parr–smolt transformation (smoltification), characterized by behavioral, morphological and physiological changes, which pre-adapts the freshwater parr to a life in seawater (reviews by Folmar and Dickhoff, 1980; Wedemeyer et al., 1980; McCormick and Saunders, 1987; Hoar, 1988; Boeuf, 1993). The hyperosmotic marine environment demands drinking of water and excretion of ions to provide water for the tissues (McCormick and Saunders, 1987; Hoar, 1988). The gill plays a major role in ionic and osmotic regulation through the action of chloride cells (Pisam et al., 1989; Perry, 1997), which are rich in the enzyme Na^+,K^+-ATPase, a protein directly involved in the excretion of monovalent ions (De Renzins and Bornancin, 1984; McCormick, 1995). The enzyme activity peaks prior to seawater entry and is generally further elevated after several days in seawater before stabilizing at a new higher level (McCormick, 1995; Handeland et al., 1998, 2000).

In the ocean, salmon grow rapidly for 1 or more years before returning to their natal river and spawn (Hoar, 1976; McCormick et al., 1998). Although this is the dominating life strategy, several populations of non-anadromous, landlocked salmonids of most species belonging to the genera *Salmo*, *Oncorhynchus* and *Salvelinus* complete their life cycle in freshwater (Rounsefell, 1958; Behnke, 1972; Berg, 1985; McDowall, 1988).

Physiological differences, e.g. development of chloride cells, Na^+,K^+-ATPase activity and seawater tolerance, have been observed between anadromous and landlocked Atlantic salmon. In Newfoundland, non-anadromous salmon have been found to exhibit lower gill Na^+,K^+-ATPase activity, smaller and less abundance of chloride cells than smolting anadromous salmon (Birt et al., 1991; Birt and Green, 1993). In contrast, Staurnes et al. (1992) reported similar levels of gill Na^+,K^+-ATPase activity between juvenile landlocked salmon and smolts of anadromous salmon. Further investigations on the discrepancy in gill Na^+,K^+-ATPase activity and seawater tolerance between non-anadromous and anadromous populations of Atlantic salmon may provide information about the underlying mechanisms of parr–smolt transformation.

In the present study, juveniles from two wild populations of Atlantic salmon were used to investigate smolt-related changes of branchial Na^+,K^+-ATPase activity and the ability to adapt to seawater during smoltification. The landlocked 'Blege' strain is a freshwater resident dwarf salmon where the juveniles migrate into lake Byglandsfjord for a pelagic life (Dahl, 1928). Smolts of the anadromous Vosso strains, a multi-seawater salmon (10–15 kg) when returning to the river Vosso after 3–4 years in the ocean, migrate into

seawater in mid-May (Geir Ove Henden, personal communication, Hatchery Manager, Voss Hatchery).

2. Materials and methods

2.1. Fish material and rearing conditions

Atlantic salmon parr from the non-anadromous population 'Blege' originating from lake Byglandsfjord, 200 m above present day sea level (south–central Norway) and from the anadromous population 'Vosso' of the river Vosso (southwestern Norway), were brought to the Aquatic Laboratory of the Bergen High Technology Center in late November 2000. The Blege and Vosso strains had been hatched (hatcheries at Evje and Voss, respectively) from eggs collected from wild broodstock, and first fed late in May 2000. The Blege strain was reared at ambient water temperature (approximately 4 °C in January, 2 °C in February and March, increasing to 12 °C from late April to early June, reaching a peak of 18 °C in August). The pH was between 6.2 and 6.7. The Vosso strain was reared in ambient water temperature (1.5–3.4 °C from January through April increasing to 6 °C in May). From late May, heated water (10 °C) was used until ambient water temperature was >10 °C. The water temperature from June throughout August did not exceed 14 °C. The pH was approximately 6.2. Both strains had been reared under constant light until autumn. Upon arrival in Bergen, mean length (S.E.M.) of the Blege and Vosso fish was 10.4 (0.23) and 9.7 (0.08) cm, respectively. The populations were reared separately in two 1-m^2 indoor tanks supplied with flow-through freshwater (pH: 6.9–7.1) at 8 °C, increasing to 9 °C in May, and exposed to simulated natural photoperiod (60°25′ N) between December 2000 and June 2001. The fish were fed in excess on a commercial dry diet (T. Skretting, Stavanger, Norway) for 8–12 h during the photo-phase. The fish were starved 15 h before sampling.

2.2. Sampling procedures and analysis

Gill tissue for determination of gill Na^+,K^+-ATPase activity (McCormick, 1993) were obtained from 12 fish per group in freshwater on January 22, March 7, April 19, May 21 and June 12, and after seawater challenge (see below) in March, April, May and June. Gill Na^+,K^+-ATPase activity was also determined after 2 weeks in seawater. Potentially smolt-sized fish (>12 cm) were always sampled. In addition, 12 fish from the Blege strain (< 10 cm) were sampled in late May. The fish were quickly dip netted out of the tanks and anaesthetized directly in 100 mg/l MS222 (Finquell, USA). The fish were transferred to a maintenance anaesthetic (30 mg/l), when reaching deep anaesthesia, after approximately 45 s. Seawater challenge tests (natural seawater, 34 ‰, 96 h, six fish from each strain) to determine capacity for seawater adaptation were run from March through June. For Na^+,K^+-ATPase activity, the second gill arch was dissected out and placed in Eppendorf vials containing ice-cold SEI buffer (250 mM sucrose, 10 mM EDTA, 50 mM imidazole, pH 7.3) and stored at − 80 °C until assayed. From all fish sacrificed for determination of gill ATPase, blood was collected from the caudal vessels using heparinized 1-ml syringes and stored on ice before being

centrifuged (600 × *g*, 10 min, 4 °C, BHG Hermle, ZK380). Plasma was aliquoted in vials and stored at − 80 °C until assayed. Only results from the seawater challenges are included here. Fish were also transferred to seawater tanks in late May for studies of long-term post-smolt performance. As high mortalities (40%) were observed in the Blege strain after 2 weeks of seawater rearing (see below), the experiment was discontinued for ethical reasons and the surviving Blege sampled.

Based on changes in mean size of fish sampled for physiological parameters, the Vosso strain showed a higher freshwater growth than the Blege strain (Table 1). No mature males or females were observed among fish from neither the Vosso nor the Blege strain.

The microassay method of McCormick (1993) was used to determine gill Na^+,K^+-ATPase activity. The Ouabain sensitive Na^+,K^+-ATPase activity is expressed as μmol ADP/mg protein/h. Plasma chloride levels (mM) after seawater challenge was analyzed in duplicate 10 μl samples in a Radiometer CMT 10 titrator (Copenhagen, Denmark).

2.3. Statistics

Student's *t*-tests were used to compare means between the Vosso and Blege strains at each time point. Levene's *F*-test was used to test for homogeneity of variances. One-way ANOVA followed by Tukey HSD post-hoc tests were used to determine statistical significance between time points within each strain.

3. Results

3.1. Mortality

Mortality was negligible during the freshwater phase. Mortality among fish challenged with seawater (96 h) was low; only one fish from the Blege strain died in March. There was no mortality among the smolt-sized fish (>12 cm) of the Vosso strain transferred to

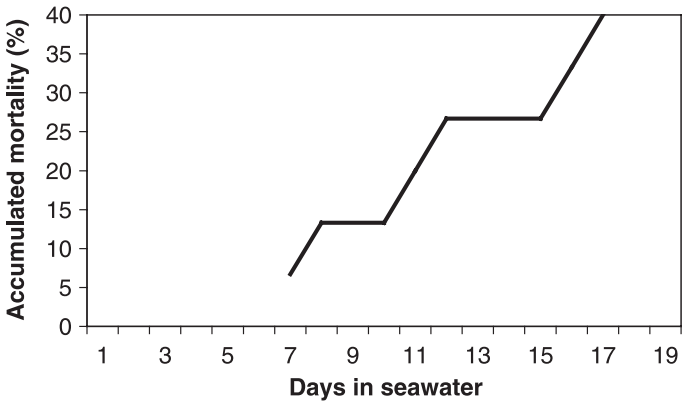

Fig. 1. Cumulative mortality (%) among smolt-sized fish (>12 cm) of landlocked Blege strain of Atlantic salmon transferred to seawater. No mortality was observed among the anadromous Vosso strain.

seawater in late May, whereas high mortalities (40%) were observed in similar sized fish of the Blege strain during the 2 weeks of seawater rearing (Fig. 1). At this time, the experiment was discontinued for ethical reasons.

3.2. Condition factor and morphology

Changes in condition factor differed between strains, with the Blege strain showing an increase in condition factor throughout the study, whereas in the anadromous Vosso strain an increase until April followed by a significant ($P<0.01$) decrease between April through June was observed (Table 1). Smolts from the Vosso strain showed all the morphological characteristics of smolting, whereas smolt-sized fish from the landlocked population retained distinct parr-marks and red dots, although a slight increase in silvering was observed.

3.3. Gill Na^+,K^+-ATPase activity and hypoosmoregulatory ability

Freshwater gill Na^+,K^+-ATPase activity remained low (3–4 μmol ADP/mg protein/h) in both strains until early March (Fig. 2), with a significant ($P<0.001$) increase in the Vosso strain in April resulting in a four-fold increase between March and May when a peak mean level of 17 μmol ADP/mg protein/h was attained. In contrast, enzyme activity for the Blege strain remained low until a significant ($P<0.001$) 2.5-fold increase occurred in May, with a peak level of 8 μmol ADP/mg protein/h. The activity dropped rapidly to parr levels in both strains (3–4 μmol ADP/mg protein/h) in mid-June. Na^+,K^+-ATPase activity remained at parr levels among small-sized (<10 cm) Blege strain in late May.

Short-term seawater exposure consistently increased gill Na^+,K^+-ATPase activity in Vosso parr and smolts (Fig. 3). Levels of approximately 20 μmol ADP/mg protein/h in May and June were higher than corresponding freshwater levels, with a five-fold difference in June. In contrast, no consistent increase in enzyme activity was observed after

Table 1
Mean weight, length and condition factor (CF) for landlocked Blege and anadromous Vosso strains of Atlantic salmon

Date	Mean weight (g S.E.M.)		Mean length (cm S.E.M.)		Mean CF (S.E.M.)	
	Blege	Vosso	Blege	Vosso	Blege	Vosso
22 January	20.4 (1.4)	12.7 (0.6)	12.9 (0.3)	10.6 (0.2)	$0.94\ (0.01)^{A}$	$1.06\ (0.01)^{a,B}$
7 March	21.1 (0.8)	17.9 (0.4)	12.8 (0.2)	11.7 (0.1)	$0.99\ (0.02)^{a,A}$	$1.13\ (0.01)^{b,B}$
19 April	21.4 (0.6)	24.9 (0.5)	12.8 (0.1)	13.0 (0.1)	$1.01\ (0.02)^{b,A}$	$1.15\ (0.01)^{B}$
21 May	24.8 (1.1)	29.5 (0.9)	13.4 (0.2)	13.9 (0.1)	$1.03\ (0.02)^{A}$	$1.09\ (0.01)^{c,B}$
12 June	30.3 (1.1)	31.1 (1.0)	14.2 (0.2)	14.2 (0.2)	$1.06\ (0.01)^{c}$	$1.08\ (0.01)^{d}$
12 June (SW)	22.8 (1.4)	28.6 (1.1)	13.2 (0.2)	14.0 (0.2)	0.98 (0.04)	1.03 (0.01)

$n=12$, except for the Blege strain in seawater (SW) on 12 June ($n=6$). Condition factor was significantly lower for the Blege strain from 22 January through 21 May. On 12 June, there was no significant difference in condition between the Vosso and Blege strains, neither in freshwater nor seawater. Small and capital letters indicate significant differences in condition factor within and between strains, respectively.

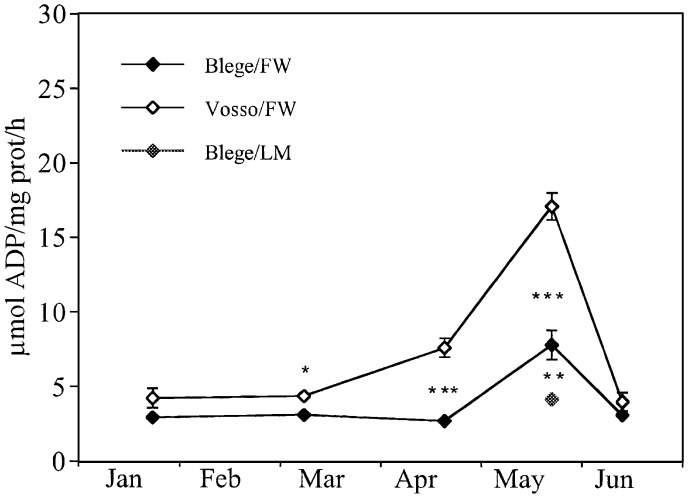

Fig. 2. Gill Na^+,K^+-ATPase activity in landlocked Blege and anadromous Vosso strains of Atlantic salmon in freshwater (FW) during the period between January 22 and June 12, and lower mode Blege (LM) on May 21. Values are given as means ± S.E.M. ($n=12$). The asterisks indicate *$P<0.05$, **$P<0.01$ and ***$P<0.001$.

seawater exposure among fish from the Blege strain through May, whereas in mid-June seawater exposure increased levels to approximately 16 µmol ADP/mg protein/h as compared to freshwater levels of 3 µmol ADP/mg protein/h.

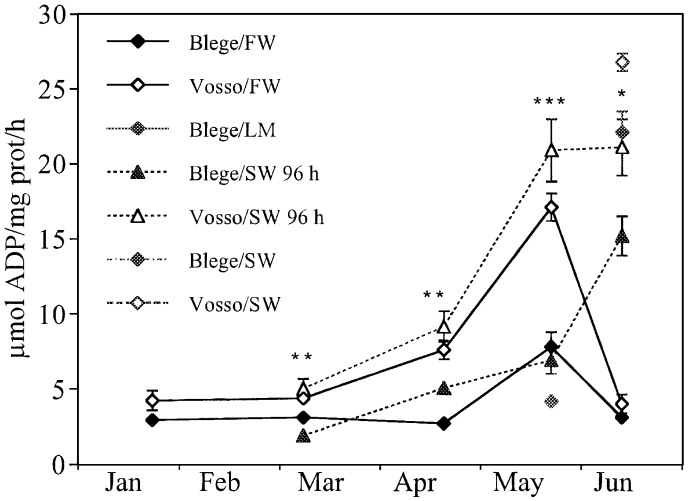

Fig. 3. Gill Na^+,K^+-ATPase activity of landlocked Blege and anadromous Vosso strains of Atlantic salmon after 96 h seawater exposure (SW 96 h) during the period between March 7 and June 12. Values are given as means ± S.E.M. ($n=6$), except Blege on March 7 ($n=5$). Gill Na^+,K^+-ATPase activity for Blege/SW ($n=6$) and Vosso/SW ($n=12$) exposed to seawater from May 25 through June 12. The asterisks indicate **$P<0.01$ and ***$P<0.001$. Gill Na^+,K^+-ATPase activity for Blege and Vosso in freshwater are also presented (see also Fig. 2).

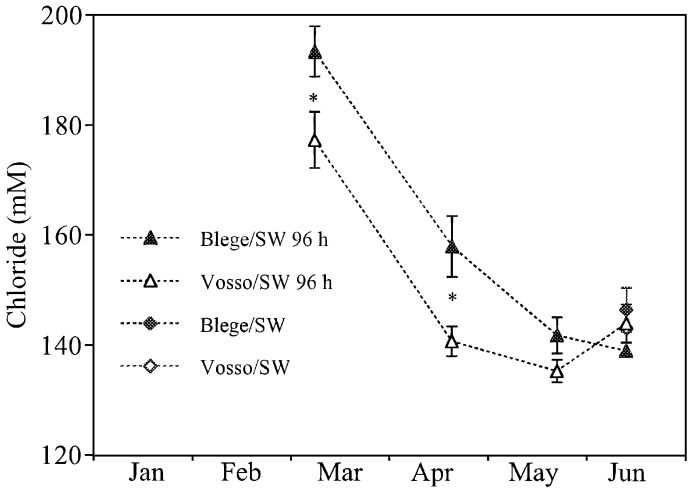

Fig. 4. Plasma chloride levels (mM) of landlocked Blege and anadromous Vosso strains of Atlantic salmon after 96 h seawater exposure (SW 96 h) during the period between March 7 and June 12. Values are given as means ± S.E.M. ($n=6$), except Blege on March 7 ($n=5$) and Vosso on June 12 ($n=3$). Plasma chloride levels (mM) for Blege/SW ($n=6$) and Vosso/SW ($n=12$) exposed to seawater from May 25 through June 12. The asterisks indicate $*P<0.05$.

After 2 weeks in seawater, gill Na^+,K^+-ATPase activity was highest in the Vosso strain, >27 μmol ADP/mg protein/h. Elevated levels (>22 μmol ADP/mg protein/h) were also observed in the surviving Blege strain at this time.

Improved short-term hypoosmoregulatory ability, measured as ability to maintain hydromineral balance after 96 h in 34 ‰ seawater, was observed in both strains (Fig. 4). Ion levels were, however, consistently lower among the Vosso strain than for the Blege strain through late May. Ion levels increased in the Vosso strain in June, while a continued decrease was observed in the Blege strain; hence, levels were not significantly different in June.

4. Discussion

Our findings show that landlocked Atlantic salmon, represented by the Blege population from lake Byglandsfjord, having been isolated from the sea for more than 9000 years (Berg, 1985), may have abandoned key elements of the parr–smolt transformation associated with marine life. Although the Blege are still capable of short-term seawater adaptation, our findings show that this strain of Atlantic salmon experiences high mortality when exposed to full strength seawater for several days.

It is generally accepted that landlocked forms of Atlantic salmon are derived independently from various anadromous founder populations, which were later prevented from reaching the previously accessible upper reaches of watersheds with the elevation of the land post-glaciation (Power, 1958; Behnke, 1972). In the case of Blege, anadromous salmon are presently prevented from reaching lake Byglandsfjord by the Vigelandsfossen

waterfall between the sea and the lake (Dahl, 1928; Berg, 1985). Studies of landlocked Atlantic salmon from North America and Europe have shown differences in the capacity of these strains to adapt to seawater (Barbour and Garside, 1983; Chernitsky and Loenko, 1983; Burton and Idler, 1984; Birt et al., 1991; Birt and Green, 1986, 1993; Staurnes et al., 1992; Schmitz, 1995). In contrast with our findings, Staurnes et al. (1992) reported similar levels of gill Na^+,K^+-ATPase activity in juvenile Blege as those found in smolts of anadromous Atlantic salmon. This conclusion, however, was based on one time point only (May) for the Blege and no assessment of hypoosmoregulatory ability was done. In line with our present findings, landlocked 'Gullspång' Atlantic salmon from lake Vänern in south–central Sweden are reported to show a gradual increase in hypoosmoregulatory ability during spring (Schmitz, 1995), although no information is available on changes in gill Na^+,K^+-ATPase activity nor long-term seawater adaptability. Studies of landlocked strains of Atlantic salmon in eastern North America have yielded somewhat contrasting results. The general pattern seems to be a gradual improvement in seawater tolerance during spring, despite lower levels of gill Na^+,K^+-ATPase activity than those found in anadromous populations (see Birt and Green, 1986, 1993; Birt et al., 1991). Parr–smolt transformation is an energetically demanding process (Hoar, 1976, 1988) during which the juvenile salmon abandons its freshwater adaptations and acquires morphological, physiological and behavioral adaptations preparing the smolt for marine growth and survival (McCormick and Saunders, 1987). In the case of landlocked populations, however, aspects of smoltification associated with hypoosmoregulation can be considered maladaptive, as energy is wasted in a process, which reduces the individual's physiological capacity and overall fitness. Hence, a gradual, secondary adaptation to freshwater would be expected. Given the relatively short time since landlocked salmon populations became isolated, a partial and variable re-adaptation to a fully freshwater existence among populations would be expected.

Smolting anadromous Atlantic salmon exhibit a seasonal increase in freshwater gill Na^+,K^+-ATPase activity, with peak levels in spring, coinciding with the development of seawater tolerance (Saunders and Henderson, 1978; McCormick and Saunders, 1987; McCormick et al., 1987, 1999). Further, high gill Na^+,K^+-ATPase activity has been found in wild stocks of seaward migrating smolts (Birt et al., 1990; Whitesel, 1993; McCormick and Björnsson, 1994). Both the anadromous Vosso and the non-anadromous Blege showed peak freshwater Na^+,K^+-ATPase levels in late May; hence, transfer of both strains to seawater for studies of long-term post-smolt performance, coincided with the time of peak enzyme levels. Further, peak gill Na^+,K^+-ATPase activity of the Blege strain, being only 50% of levels observed in the Vosso strain, suggests that these fish did not obtain true smolt status. Elevated levels of freshwater Na^+,K^+-ATPase activity among smolt-sized Blege strain, compared to those found in small Blege (<10 cm) in late May, indicate, however, that some euryhaline capacity is still present in the Blege strain, as further indicated by the improved ion-regulatory capacity and ability to induce enzyme levels in June. However, the 'pre-adaptation' unique for smolts may no longer be present. Further, the modest increase in freshwater gill Na^+,K^+-ATPase activity may also be a consequence of endocrine changes preparing the juveniles for downstream migration and a pelagic life in the lake. Further analysis of the endocrine system will likely reveal the underlying mechanisms of these changes.

The high mortality observed among the Blege strain, transferred for long-term seawater performance in May, is consistent with the lower peak levels in freshwater Na^+,K^+-ATPase activity. Still, the Blege strain exhibited improved short-term hypoosmoregulatory ability, measured as plasma Cl^- levels, when exposed to seawater for 96 h. Seawater exposure has been found to increase gill Na^+,K^+-ATPase activity in anadromous salmon parr (Bjerknes et al., 1992) and smolts (Berge et al., 1995; Handeland et al., 2000). In the present study, no induction of Na^+,K^+-ATPase activity was found in Blege strain after 96 h of seawater exposure, except in June, coinciding with best hypoosmoregulatory ability, although freshwater gill Na^+,K^+-ATPase activity was down to parr levels. Despite these contrasting observations, our results further emphasize the importance of the gill Na^+,K^+-ATPase activity for long-term seawater performance in Atlantic salmon. In line with our findings, Birt and Green (1993) found no smolt-related increase in freshwater gill Na^+,K^+-ATPase activity in non-anadromous salmon from Five Mile Pond East stock (Avalon Peninsula, Newfoundland); however, long-term exposure to seawater increased enzyme levels, although mortality was almost 100%. Additionally, Burton and Idler (1984) found that fish from the same strain were unable to maintain normal hydro-mineral balance when challenged with seawater. Birt et al. (1991) reported that non-anadromous salmon (Gambo River, Newfoundland) were able to withstand seawater challenge, although no distinct increase in freshwater gill Na^+,K^+-ATPase was observed. However, the authors suggested this may have been due to low challenge salinity (32‰).

Anadromous Vosso smolts showed all the morphological characteristics associated with smolting in Atlantic salmon (Hoar, 1976, 1988; Folmar and Dickhoff, 1980), whereas the Blege strain retained distinct parr-marks and red dots, and only exhibited a slight degree of silvering in late May. In the case of the Blege strain, our findings are in line with those of Dahl (1928). In contrast, Staurnes et al. (1992) reported that the Blege strain attained a typical smolt colouration. Although less pronounced than in anadromous salmon, populations of landlocked salmon in North America (Birt and Green, 1986) and Europe (Dahl, 1928; Berg, 1953) seem to have retained a certain degree of silvering enabling them to adapt for a pelagic life when migrating into lakes.

Although both strains were cultured under the same conditions, one should not overstate the differences in growth observed in the present study. In general, parr–smolt transformation in anadromous Atlantic salmon results in reduced condition factor, probably related to changes in metabolism, e.g. higher catabolism of fat, protein and carbohydrate (Wedemeyer et al., 1980; Hoar, 1988; Sheridan, 1989). Both the Vosso and the Blege strains increased in weight and length throughout the study, whereas only the Vosso strain showed a significant decline in condition factor from April onwards, clearly indicating smolting. Both strains were fed in excess, appeared to be well adapted to rearing conditions, and feeding well, hence the lower freshwater growth and steady increase of condition in the Blege strain, compared to the Vosso strain, indicate no smolt-related metabolic changes. The reduction in condition factor in both strains following 2 weeks of seawater exposure is consistent with studies of anadromous salmon (Solbakken et al., 1994; Handeland et al., 2000). Our findings are consistent with what seems to be the general trend of higher condition, or the absence of a smolt-related reduction in condition factor among several populations of non-anadromous salmon (Birt and Green, 1986; Birt et al., 1991). Our results, however, contrast those reported by Rottiers (1993), where

presumably landlocked Atlantic salmon (Lake George, New York) showed a sharp decrease in condition factor. Dahl (1928) reported that the juvenile Blege strain remain in the rivers for 2–4 years, until they reach a length of 12 cm, before migration into the Byglandsfjord, an oligotrophic lake with a poor invertebrate population and no forage fish. In the lake, the Blege strain exhibit enhanced growth rates, while max size generally does not exceed 30 cm and 250 g (Dahl, 1928). After having been landlocked for thousands of years, an adaptation to the poor growing conditions may explain the differences in growth observed between the Blege and Vosso strains in this experiment. However, the Blege strain are able to exhibit enhanced growth when transferred to lakes with ample forage fish available (Jensen, 1984).

In conclusion, the present study shows differences between the anadromous Vosso and the landlocked Blege strains in growth, condition factor, gill Na^+,K^+-ATPase activity, hypoosmoregulatory ability and long-term survival in seawater. Further analyses of the endocrine system and osmoregulatory machinery in these two strains may further our understanding of the underlying mechanisms of smolt-related changes in Atlantic salmon.

Acknowledgements

Thanks to Håvard Christensen at Setesdal Settefisk for providing fish of the Blege strain and Geir Ove Henden at the hatchery in Voss for providing fish of the Vosso strain. We thank Bjørn Sveinsbø and Siri Brønlund for their assistance during this experiment. The Research Council of Norway funded this study (Project no. 136260/140).

References

Barbour, S.E., Garside, E.T., 1983. Some physiologic distinctions between freshwater and diadromous forms of the Atlantic salmon, *Salmo salar L.* Can. J. Zool. 61, 1165–1170.

Behnke, R.J., 1972. The systematics of salmonid fishes of recently glaciated lakes. J. Fish. Res. Board Can. 29, 639–671.

Berg, M., 1953. A relict salmon, *Salmo salar L.*, called "småblank" from the river Namsen, North Tröndelag. Acta Boreal., A, Sci. 6, 1–19.

Berg, O.K., 1985. The formation of non-anadromous populations of Atlantic salmon, *Salmo salar L.*, in Europe. J. Fish. Biol. 27, 805–815.

Berge, Å.I., Berg, A., Fyhn, H.J., Barnung, T., Stefansson, S.O., 1995. Development of salinity tolerance in underyearling smolts of Atlantic salmon (*Salmo salar*) reared under different photoperiods. Can. J. Fish. Sci. 52, 243–251.

Birt, T.P., Green, J.M., 1986. Parr–smolt transformation in female and sexually mature male anadromous and nonanadromous Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. 43, 680–686.

Birt, T.P., Green, J.M., 1993. Acclimation to seawater of dwarf nonanadromous Atlantic salmon, *Salmo salar*. Can. J. Zool. 71, 1912–1916.

Birt, T.P., Green, J.M., Davidson, W.S., 1990. Smolting status of downstream migration Atlantic salmon (*Salmo salar*) parr. Can. J. Fish. Aquat. Sci. 47, 1136–1139.

Birt, T.P., Green, J.M., Davidson, W.S., 1991. Contrasts in development and smolting of genetically distinct sympatric anadromous and nonanadromous Atlantic salmon, *Salmo salar*. Can. J. Zool. 69, 2075–2084.

Bjerknes, V., Duston, J., Knox, D., Harmon, P., 1992. Importance of body size for acclimation of underyearling Atlantic salmon parr (*Salmo salar L.*) to seawater. Aquaculture 104, 357–366.

Boeuf, G., 1993. Salmonid smolting: a pre-adaptation to the oceanic environment. In: Ranking, J.C., Jensen, F.B. (Eds.), Fish Ecophysiology, vol. 9. Chapman and Hall, London, pp. 105–125.

Burton, M.P., Idler, D.R., 1984. Can Newfoundland landlocked salmon, *Salmo salar L.*, adapt to sea water? J. Fish. Biol. 24, 59–64.

Chernitsky, A.G., Loenko, A.A., 1983. The osmoregulatory system and possible ways of differentiation in ecological forms of Atlantic salmon, *Salmo salar* (Salmonidae). J. Ichthyol. 23, 84–94.

Dahl, K., 1928. The Blege or dwarf-salmon. Skr. Utg. Av Det Norske Videnskabsakad, 1927, Oslo.

De Renzins, G., Bornancin, M., 1984. Ion transport and gill ATPases. In: Hoar, W.S., Randall, D.J. (Eds.), Fish Physiology, vol. 10B. Academic Press, London, pp. 65–104.

Folmar, L.C., Dickhoff, W.W., 1980. The parr–smolt transformation (smoltification) and sea water adaptation in salmonids: a review. Aquaculture 21, 1–38.

Handeland, S.O., Berge, Å., Björnsson, B.Th., Stefansson, S.O., 1998. Effects of temperature and salinity on osmoregulation and growth of Atlantic salmon (*Salmo salar L.*) smolts in seawater. Aquaculture 168, 289–302.

Handeland, S.O., Berge, Å., Björnsson, B.Th., Lie, Ø., Stefansson, S.O., 2000. Seawater adaptation by out-off-season Atlantic salmon (*Salmo salar L.*) smolts at different temperatures. Aquaculture 181, 377–396.

Hoar, W.C., 1976. Smolt transformation: evolution, behavior, and physiology. J. Fish. Res. Board Can. 33, 1234–1252.

Hoar, W.C., 1988. The physiology of smolting salmonids. In: Hoar, W.S., Randall, D.J. (Eds.), Fish Physiology, vol. 11B. Academic Press, London, pp. 275–343.

Jensen, K.W., 1984. Reliktlaks. In: Jensen, K.W. (Ed.), Sportsfiskerens leksikon. Kunnskapsforlaget, Oslo, Norway. ISBN 82-573-0214-7, in Norwegian.

McCormick, S.D., 1993. Methods for non-lethal gill biopsy and measurement of Na^+,K^+-ATPase activity. Can. J. Fish. Aquat. Sci. 50, 656–658.

McCormick, S.D., 1995. Hormonal control of gill Na^+,K^+-ATPase and chloride cell function. In: Wood, C.M., Shuffleworth, T.J. (Eds.), Fish Physiology, Cellular and Molecular Approaches to Fish Ionic Regulation, vol. 14, pp. 285–316.

McCormick, S.D., Saunders, R.L., 1987. Preparatory physiological adaptations for marine life of salmonids: osmoregulation, growth, and metabolism. Am. Fish. Soc. Symp. 1, 211–229.

McCormick, S.D., Björnsson, B.Th., 1994. Physiological and hormonal differences among salmon parr and smolts reared in the wild, and hatchery reared smolts. Aquaculture 121, 244–253.

McCormick, S.D., Saunders, R.L., Henderson, E.B., Harmon, P.R., 1987. Photoperiod control of parr–smolt transformation in Atlantic salmon (*Salmo salar*): changes in salinity tolerance, gill Na^+,K^+-ATPase activity, and thyroid hormones. Can. J. Fish. Aquat. Sci. 44, 1462–1468.

McCormick, S.D., Hansen, L.P., Quinn, T.P., Saunders, R.L., 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 55, 77–92.

McCormick, S.D., Cunjak, R.A., Dempson, B., O'Dea, M.F., Carey, J.B., 1999. Temperature-related loss of smolt characteristics in Atlantic salmon (*Salmo salar*) in the Wild. Can. J. Fish. Aquat. Sci. 56, 1649–1658.

McDowall, R.M., 1988. Life history deviation and landlocking. Diadromy in Fishes, Migrations between Freshwater and Marine Environments. Chapman and Hall, London, pp. 171–185.

Perry, S.F., 1997. The chloride cell: structure and function in the gills of freshwater fishes. Annu. Rev. Physiol. 59, 325–347.

Pisam, M., Prunet, P., Boeuf, G., Rambourg, A., 1989. Ultrastructure features of chloride cells in the gill epithelium of the Atlantic salmon, *Salmo salar*, and their modifications during smoltification. Am. J. Anat. 183, 235–244.

Power, G., 1958. The evolution of the freshwater races of the Atlantic salmon (*Salmo salar L.*). Arctic 11, 86–92.

Rottiers, D.V., 1993. Elemental composition of a migratory and a land-locked strain of Atlantic salmon, *Salmo salar*. Comp. Biochem. Physiol. 104A (1), 93–100.

Rounsefell, G.A., 1958. Anadromy in North American Salmonidae. US Fish. Wildl. Serv. Bull. 58, 171–185.

Saunders, R.L., Henderson, E.B., 1978. Changes in gill ATPase activity and smolt status of Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 27, 1542–1546.

Schmitz, M., 1995. Seasonal changes in hypoosmoregulatory ability in landlocked and anadromous populations of Arctic charr, *Salvelinus alpinus*, and Atlantic salmon, *Salmo salar*. Environ. Biol. Fish. 42, 401–412.

Sheridan, M.A., 1989. Alteration in lipid metabolism accompanying smoltification and seawater adaptation of salmonid fish. Aquaculture 82, 191–203.

Solbakken, V.A., Hansen, T., Stefansson, S.O., 1994. Effects of photoperiod and temperature on growth and parr–smolt transformation in Atlantic salmon (*Salmo salar L.*) and subsequent performance in seawater. Aquaculture 121, 13–27.

Staurnes, M., Lysfjord, G., Berg, O.K., 1992. Parr–smolt transformation of a nonanadromous population of Atlantic salmon (*Salmo salar*) in Norway. Can. J. Zool. 70, 197–199.

Wedemeyer, A.H., Saunders, R.L., Clarke, M.N., 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish. Rev. 42, 97–109.

Whitesel, T.A., 1993. Comparison of juvenile Atlantic salmon (*Salmo salar*) reared in hatchery and introduced into a stream: a two size-threshold model of smoltification. Can. Spec. Publ. Fish. Aquat. Sci. 118, 239–247.