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Standard metabolic rate, growth rate and smolting of the juveniles in three Atlantic salmon stocks

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We examined oxygen consumption and growth rates of juveniles in three Finnish Atlantic salmon (*Salmo salar*) stocks (Neva, Saimaa, Teno) reared at the same fish farm. The measurements were carried out four times: in winter 2005, early spring 2006, autumn 2006 and late spring 2007 using fish hatched in February 2005, and the size and temperature ranges were wide. The salmon stocks differed in their geographical origin and native habitat presumably selecting for differences in physiological parameters. The southernmost Neva stock had higher values of a relative standard metabolic rate (rSMR) at the yolk-sac stage than the Teno stock, and the northernmost Teno stock had a higher growth rate (SGR) values at the smolt stage than the two other stocks. In addition, the stocks differed in physiological parameters characteristic of smolting: the post-smolts in the northernmost Teno stock had significantly higher rSMR and SGR, and lower condition factor values than the ones in the two other stocks.

Introduction

Metabolism is usually the largest part of energy budgets in animals, and it has a central role to play in physiological traits, like growth and energy storage, that vary with behavioural and life history decisions (e.g. Metcalfe *et al*. 1995, Cutts *et al*. 1998, Forseth *et al*. 1999, McCarthy 2001, Wikelski *et al*. 2003, Lindström *et al*. 2005). Metabolic rate is highly variable since it is influenced by environmental factors (e.g. Claireaux and Lagardere 1999, McNab 2002), body size and composition (e.g. Daan *et al*. 1990, Chappel *et al*. 1999), nutritional status and activity. Of the environmental factors, temperature is considered to be a controlling factor, whereas dissolved oxygen concentration a limiting factor for metabolic rate (Fry 1971).

Metabolism in fish may be divided into the metabolic costs of maintaining basic bodily functions, metabolism related to activity, and the metabolic costs associated with digestion, absorption and processing of food (Adams and Breck 1990, Jobling 1994). Standard metabolic rate (SMR) is required for maintaining the critical physiological functions: it is the minimal, or resting, metabolic rate of unfed fish performing no swimming activity (Brett and Groves 1979, Priede 1985, Jobling 1994). Normally, fish live above this resting level having normal activ-

ity such as daily feeding without stress, this is termed routine metabolic rate. The upper limit of aerobic metabolic rate with maximum sustained swimming is known as active metabolic rate (AMR) (Jobling 1994). According to Priede (1985), both the standard and active metabolic rates of healthy fish are mandatory, and their magnitude cannot be regulated. However, SMR can be lowered or raised by starvation or stress, respectively (O'Connor *et al*. 2000, Sloman *et al*. 2000). For fish, metabolic rate has been found to correlate with growth (e.g. Cutts *et al*. 1998, Huuskonen and Karjalainen 1998, Yamamoto *et al*. 1998, Álvarez and Nicieza 2005).

Salmonids have considerable variation in life-history patterns, growth rate, age, and size at sexual maturation as well as at smolting both between and within species (Thorpe 1989). Smolting and sexual maturation are the two major developmental transitions occurring in the life of Atlantic salmon (*Salmo salar*) both processes being circannual, and synchronized by the photoperiod (Thorpe *et al*. 1998, Metcalfe 1998). The direction of the developmental route depends on the individual's responses to prior feeding opportunity, and its current metabolic performance (Thorpe 1989), in other words, certain genetically-determined threshold values in body size and energy stores are involved (Thorpe *et al*. 1998, Metcalfe 1998).

During smolting, Atlantic salmon parr undergo morphological, physiological and behavioural changes which transform freshwater parr to salt water tolerant smolts (e.g. Hoar 1976, 1988, Folmar and Dickhoff 1980, McCormick and Saunders 1987, Boeuf 1993, Kiiskinen *et al*. 2002). Silvery coloration, dark fins and streamlined body shape are the most characteristic external indicators of smolting in salmonids (McCormick and Björnsson 1994). During parr–smolt transformation, total body and muscle lipid contents decrease (Saunders and Henderson 1970, 1978, Kiiskinen *et al*. 2002, 2003, Morgan *et al*. 2002) causing a decrease in condition factor (Farmer *et al*. 1978, Kiiskinen *et al*. 2002). An increase in the activity of respiratory enzymes in the gills is a commonly observed phenomenon as well (e.g. Langdon and Thorpe 1985, McCormick and Saunders 1987, Kiiskinen *et al*. 2002, 2003).

In the present study, we investigated variation in SMR and specific growth rate (SGR) in three salmon stocks at different life stages, water temperatures and with fish of different size. Our aim was to find out possible population-specific differences as well as associations between SMR, growth rate and smolting. After formation of a bimodal size distribution, only fish belonging to the upper modal group (UMG) were investigated due to temporal limitation of respirometry at certain temperatures. Hence, fish representing the same developmental pathway in different populations were compared. As pointed out by Obedzinski and Letcher (2004), it is important to examine traits over a range of life stages in population comparisons to obtain reliable conclusions of population differentiation.

Materials and methods

Study fish

Three Atlantic salmon stocks that differed in their geographical origin as much as possible and were logistically available were used. The Saimaa stock is a landlocked, non-anadromous population living in Lake Saimaa in eastern Finland (62°N, 28°E), while the River Neva and the River Teno stocks are anadromous, sea-run populations, the former living in Russia (60°N, 27°E) migrating to the Baltic Sea and the latter living in northern Finland (70°N, 25°E) migrating to the Arctic Ocean. The stocks also differ in their native habitats: the Saimaa stock is adapted to freshwater, the River Neva stock to brackish water and the River Teno stock to seawater. The experimental fish populations for comparative physiological and life history studies (P. Kiiskinen unpubl. data) were reared at the Saimaa Fisheries Research and Aquaculture in Enonkoski (Finnish Game and Fisheries Research Institute) in eastern Finland, from where the parent fish of the Saimaa and Neva stocks originated. The parent fish of the Teno stock originated from the Inari Fisheries Research and Aquaculture in northern Finland. All parent fish used for obtaining eggs and milt were from first hatchery generations.

In order to produce genetically representative progeny, random pairwise (1 female × 1

male taken always from different year classes) fertilizations were conducted between 60 pairs of the Saimaa and Teno salmon obtained from three different year classes and between 45 pairs of the Neva salmon from two different year classes on 25 to 29 October 2004. The fish were maintained from egg fertilization onwards in freshwater under identical experimental conditions to control for the environmental variation. The eggs and alevins were held in standard hatchery troughs, two troughs for each stock. Since growth season in Finland is relatively short, we accelerated the early development of fish by increasing the water temperature gradually from 4 °C to 10 °C approximately four weeks after the eyed embryo stage until the ambient water temperature reached 10 °C during the spring. This method has been routinely used at the Saimaa Fisheries Research and Aquaculture. From then on, simulated natural photoperiod and ambient water temperature was used to avoid any disturbance of endogenous rhythms of the fish. After yolk-sac absorption in February–March 2005, 1500 fish per population were transferred to standard circular holding tanks (diameter 80 cm, flow 18 l min^{-1}, five tanks per population). In October 2005, 200 fish per population selected to represent the size distribution, i.e. lower and upper modal groups (LMG and UMG, respectively) of each stock were moved into larger tanks (diameter 160 cm, flow 18 l min^{-1}, three tanks per population). As the size distribution frequencies of the stocks were not equal, limits of the size groups and number of individuals in LMG and UMG were slightly different in the Saimaa (< 95 mm/100 and > 105 mm/100), Neva (< 90 mm/100 and > 100 mm/100) and Teno (< 90 mm/120 and > 100 mm/80) stocks. The test fish represented UMG, and they were taken randomly from the holding tanks. Fish were fed salmon pellets (nutraG EWOS, Florø, Norway, diameter 0.5–2.5 mm) *ad libitum* by automatic dispensers during the whole study period. The pellet size was adjusted according to the size of the fish.

To recognize the fish individually during the trials, the fish were tagged with passive integrated transponders (EURO-ID-tags, Trovan®, Köln, Germany). The ID-tag (length 12 mm and diameter of 2 mm) was inserted into the body cavity of fish. The fish were anaesthetized with sodiumbicarbonate ($NaHCO_3$) buffered MS-222 (tricaine methane sulphonate, Finquel®, Argent Chemical Laboratories, Redmond, Washington, USA) solution before tagging and measuring operations.

Respirometry

Oxygen consumption of the experimental fish was measured four times: in winter 2005 (Trial 1), in early spring 2006 (Trial 2), in autumn 2006 (Trial 3) and in late spring 2007 (Trial 4). Measurement temperature (mean ± SD) in each period was 4.6 ± 0.2 °C, 2.7 ± 0.1 °C, 13.9 ± 0.2 °C and 10.0 ± 0.1 °C, respectively. The test fish in oxygen consumption measurements were alevins at yolk-sac stage in trial 1 and individually marked juveniles in trials 2, 3 and 4 (Table 1).

Oxygen consumption was measured with an automated three-chamber intermittent-flow respirometer equipped with YSI 5750 polarographic oxygen sensor (Forstner 1983, Wieser *et al.* 1988). The respirometer system included three parallel transparent acrylic measuring chambers and the flow rate was about 200 ml min^{-1}. The experimental design enabled chambers of different sizes, depending on the fish body mass, to be used. This allowed the ratio of fish volume to water volume to be approximately constant. Chamber volumes used were 158–167 ml and 884–897 ml for the measurements of smaller and larger fish, respectively. In trial 1, oxygen consumption of 95 alevins from each stock was measured in eight groups per population (one group consisted of 10–15 individuals).

Before experiments began, the fish fasted for 24 hours in the aquaria, as well as simultaneously acclimated to the experimental temperature; the change from rearing temperature to the experimental temperature was 0.5–0.8 °C. Measurements were started immediately after introducing the fish into the chambers, a common practice that has been used in numerous studies (e.g. Forstner 1983, Holopainen *et al.* 1997, Huuskonen and Karjalainen 1998, Lahti *et al.* 2002). Each experiment lasted for 24 hours, of which 16 hours were in the light and 8 hours in the dark. The measurement period was long enough for the fish to recover from handling

Table 1. Mean (± SD) length (*L*), mass (*M*) and condition factor (*K*) and mass-specific SMR of the Saimaa, Neva and Teno stocks in March 2005, March 2006, September 2006 and May 2007.

Stock	Saimaa				Neva				Teno			
	March 2005	March 2006	September 2006	May 2007	March 2005	March 2006	September 2006	May 2007	March 2005	March 2006	September 2006	May 2007
Number	8	18	11	9	8	18	10	8	8	18	9	7
L (mm)		126.3 (± 7.2)	176.1 (± 10.7)	219.3 (± 15.0)		110.4 (± 4.9)	166.3 (± 10.4)	209.9 (± 17.7)		127.6 (± 6.9)	187.0 (± 13.2)	242.9 (± 26.8)
M (g)	0.2 (± 0.1)	18.2 (± 3.3)	51.4 (± 10.5)	110.4 (± 28.4)	0.2 (± 0.1)	12.5 (± 1.6)	42.8 (± 6.5)	95.1 (± 28.0)	0.1 (± 0.0)	18.3 (± 2.9)	51.5 (± 11.1)	134.7 (± 47.6)
K		0.89 (± 0.03)	0.93 (± 0.09)	1.00 (± 0.09)		0.92 (± 0.06)	0.93 (± 0.05)	1.01 (± 0.11)		0.87 (± 0.03)	0.79 (± 0.14)	0.91 (± 0.07)
SMR (μmol g^{-1} h^{-1})	1.58 (± 0.60)	1.08 (± 0.23)	3.19 (± 0.59)	2.66 (± 0.34)	2.07 (± 0.40)	1.06 (± 0.32)	3.30 (± 0.66)	2.83 (± 0.53)	1.36 (± 0.49)	1.09 (± 0.26)	3.96 (± 0.99)	2.74 (± 0.34)

stress and acclimate to the chambers. During this period the oxygen consumption of each chamber was recorded for 15 min every hour, of which the average rate was extrapolated to an hourly value. The signals from the polarographic oxygen sensor were fed on-line into the computer and integrated each minute. The oxygen electrode chamber and the fish chambers were flushed after each measurement with aerated water. Microbial oxygen consumption in the respirometer was measured at the beginning and at the end of the experiments: it was subtracted from the total decline in the oxygen content. The respirometer system was cleaned and disinfected every week. After the experiments, the fish were anaesthetized, weighed and measured for the total length. In order to keep the stress level of the fish at a minimum, the fish were not disturbed during respirometry measurements. SMR was defined as a mean of the two lowest oxygen consumption values recorded during the experiment. Relative SMR (rSMR) was calculated according to Metcalfe *et al*. (1995) to control for the differences of the fish body mass in statistical comparisons. The rSMR for each fish was calculated as the residual from linear regression of $\log_{10}$-transformed SMR (μmol O_2 h^{-1}) and body mass (g) data. Using this procedure, fish with higher SMR than expected for their mass had positive values whereas those with SMR lower than expected had a negative rSMR (Metcalfe *et al*. 1995).

Condition factor and growth

The total length and fresh mass of each fish was measured; in addition, existence of the most characteristic external indicators of smolting (silvery coloration and dark fins, McCormick and Björnsson 1994) were noted in March 2006, in September 2006 and in May 2007. Fulton's condition factor (*K*) was calculated as follows:

$$K = W \times L^{-3} \times 100$$

where *W* is the fresh mass (g) and *L* (cm) is the total length, determined individually for each fish.

Growth rates for the three populations were monitored in a group of individually tagged fish

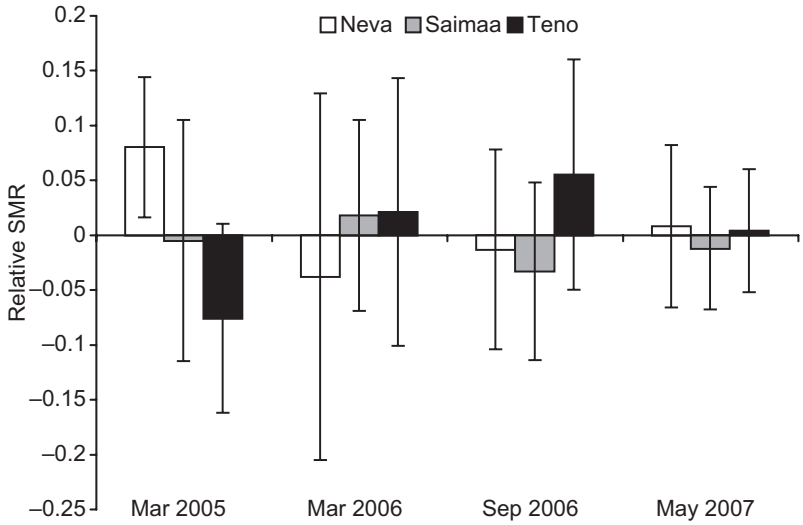

Fig. 1. Mean (± SD) relative SMR of the three Atlantic salmon stocks: Neva, Saimaa and Teno in March 2005, March 2006, September 2006 and May 2007.

two times, in autumn 2006 (n = 30) and in spring 2007 (n = 24). The specific growth rate (SGR, the percentage growth per day) for individually known fish was calculated according to Jobling (1994) as follows:

$$SGR = 100 \times [(\ln W_2 - \ln W_1)/T]$$

where W_1 is the mass (g) at the start of the measurement period, W_2 is the mass (g) in the end of the measurement period, and T is the length of the growing period in days, determined individually for each fish. Between the measurements, the fish were kept in the same standard holding tanks (200 fish/tank and five tanks per population) as mentioned above.

Ethical note

All the experiments were carried out following the principles of animal treatment and welfare for scientific experimentation according to the permission given by the ethical committee of the Finnish Game and Fisheries Research Institute (Permission No. 18/05).

Statistical analyses

Length, mass and condition factor were, if necessary, $\log_{10}$-transformed to normalise the distributions and to correct for the heteroscedasticity of variances. Specific growth rate (SGR) was arcsine-transformed prior to statistical testing. rSMR, length, mass, condition factor and growth rate were tested with ANOVAs using stock as a fixed effect. Pairwise comparisons were made with a Tukey *post hoc* test. The relationships between different parameters were examined with Pearson's product–moment correlation. Differences between post-smolts and non-smolts were determined using a Bonferroni adjusted two-sample *t*-test.

Results

Mass-specific SMR values in each trial are given in Table 1.

In trial 1, rSMR values differed significantly among the populations (Fig. 1 and Table 2), the Neva stock having higher rSMR values than the Teno stock (ANOVA, Tukey test: $p < 0.05$). The difference was not significant between the Neva and Saimaa stocks. There was no difference in the mass of the yolk-sac alevins among the stocks (Tables 1 and 2).

A bimodal size-frequency distribution during the first year of growth was observed in each stock but the size distribution frequencies of the stocks were not equal (P. Kiiskinen unpubl. data). Hence, the number of individuals in LMG and UMG in the Teno stock (120 and 80) was

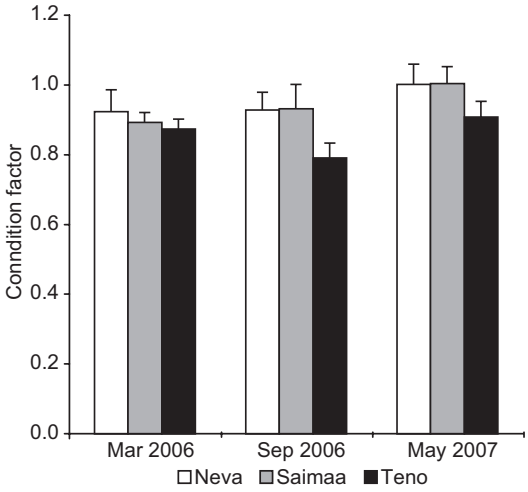

Fig. 2. Mean (+ SD) condition factor of the three Atlantic salmon stocks: Neva, Saimaa and Teno in March 2006, September 2006 and May 2007.

Table 2. ANOVA table for the effects of stock on relative SMR (rSMR), length (*L*), mass (*M*), condition factor (*K*) and specific growth rate (SGR) in March 2005, March 2006, September 2006 and May 2007. *L*, *M*, and *K* were $\log_{10}$-transformed if the assumptions of normality and homogeneity of variance were not met. SGR was arcsine-transformed prior to analysis.

	Source	df	*F*	*p*
Mar. 2005	rSMR	2, 17	5.207	0.017
	M	2, 17	1.105	0.354
Mar. 2006	rSMR	2, 51	1.184	0.314
	L	2, 51	40.317	< 0.001
	M	2, 51	34.421	< 0.001
	K	2	14.520*	0.001
Sep. 2006	rSMR	2, 27	2.408	0.109
	L	2, 27	7.809	0.002
	M	2, 27	2.705	0.085
	K	2, 27	6.220	0.006
	SGR	2, 27	3.943	0.031
May 2007	rSMR	2, 24	0.282	0.757
	L	2, 21	5.393	0.013
	M	2, 21	2.419	0.113
	K	2, 21	3.467	0.048
	SGR	2, 21	7.407	0.004

* Due to unmet assumptions even after transformation differences in the condition factor were tested with a Kruskal-Wallis test.

different from that in the Saimaa and Neva stocks (100 and 100).

In trial 2, there was no difference in rSMR between the stocks (Fig. 1 and Table 2). Instead, length (*L*), mass (*M*) as well as condition factor (*K*) (Fig. 2 and Table 2) differed significantly between the stocks: the fish in the Neva stock were smaller than those in the Teno and Saimaa stocks (ANOVA, Tukey test: $p < 0.001$), whereas *K* of the Neva fish was higher than that of the Saimaa fish (Kruskal-Wallis, PC test: $p < 0.05$) and Teno fish (Kruskal-Wallis, PC test: $p < 0.01$). Furthermore, rSMR did not correlate with *L*, *K* or SGR (p always > 0.05). None of the fish showed indicators of smolting in their external appearance.

In trial 3, the stocks did not differ in rSMR (Fig. 1 and Table 2) but there was a significant difference in *L*, *K* and SGR among the stocks (Fig. 3 and Table 3), the Teno stock fish were longer than the Neva stock fish (ANOVA, Tukey test: $p < 0.01$), while the *K* in the Teno stock was lower than that in the two other stocks (ANOVA, Tukey test: $p < 0.05$). Regarding SGR, the Neva stock had higher values than the Saimaa stock (ANOVA, Tukey test: $p < 0.05$). In addition, there was a significant correlation between rSMR and SGR over the period of eight months after the oxygen consumption measurement ($r = 0.595$, $n = 24$, $p = 0.002$), whereas rSMR did not correlate with *L* or *K* (p always > 0.05). Within stocks, rSMR and SGR did not correlate (p always > 0.05). Although the trial was carried out in autumn, many of the experimental fish showed external indicators of smolting (silvery coloration, streamlined body shape and dark fins). Obviously these fish had smolted in spring between trials 2 (age-1 fish) and 3 (age-1+ fish), and hence they represented post-smolts at the time of measurements in autumn. The prevalence of post-smolts among the SMR-measured fish was 60.0%, 63.6%, and 66.7% in the Neva, Saimaa and Teno stocks, respectively. The ratios between females and males among post-smolts and the non-smoltified fish were 4:3 and 4:5, respectively. Post-smolts had significantly higher rSMR than non-smoltified fish ($t_{28} = -6.856$, $p < 0.001$; Fig. 4) but they did not differ in *L*, *M*, *K* or SGR (p always > 0.05). Post-smolts in the Teno stock were longer than the smolts in the

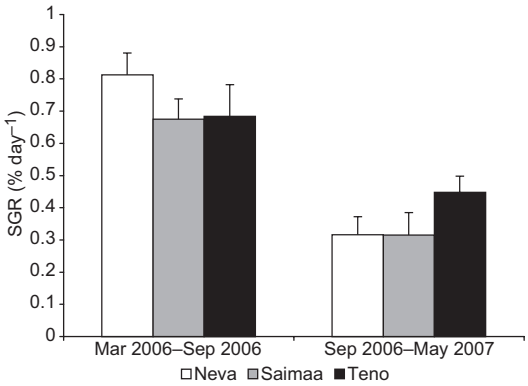

Fig. 3. Mean (+ SD) specific growth rate (SGR) of the three Atlantic salmon stocks: Neva, Saimaa and Teno from March 2006 to September 2006 and from September 2006 to May 2007.

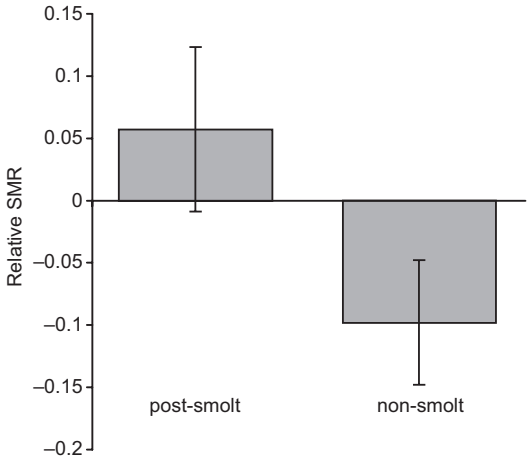

Fig. 4. Mean (± SD) relative SMR of the post-smolts and non-smolts among the three Atlantic salmon stocks in September 2006.

two other stocks (ANOVA, Tukey test: $p < 0.05$; Table 3); in addition, they had higher rSMR values as compared with those in the Neva and Saimaa stocks (ANOVA, Tukey test: $p < 0.05$; Table 4). However, there was no difference among the stocks in *K* and SGR (Table 3).

In trial 4 (age-2 fish), all except one fish showed obvious external indicators of smolting at the time of the measurement in spring 2007. There were no significant differences between the stocks in rSMR (Fig. 1 and Table 2) and *M* but in *L* (Table 2), *K* (Fig. 2 nd Table 2) and SGR (Fig. 3 and Table 2) the stocks differed; the fish in the Teno stock were longer than those in the Neva stock (ANOVA, Tukey test: $p < 0.05$) and had lower *K* (ANOVA, Tukey test; $p < 0.05$) and higher SGR values than the fish in the two other stocks (ANOVA, Tukey test: $p < 0.01$). Furthermore, rSMR did not correlate with other parameters (p always > 0.05).

The populations differed in their response of SMR to temperature; the northernmost Teno stock had low SMR at low temperatures but highest SMR at highest temperature (Fig. 5). This resulted in significantly higher slope in the regression between SMR and temperature in the Teno stock as compared with that for the Neva and Saimaa stocks (ANOVA, Tukey test: $p < 0.05$).

Discussion

Our SMR results did not agree with those reported in several earlier studies (Cossins and Bowler 1987, Garland and Adolph 1991, Spicer and Gaston 1999) suggesting that SMR tends to be higher in populations from higher latitudes/altitudes, reflecting adaptation to a more seasonal climate. This phenomenon is known as countergradient variation. Latitudinal and altitudinal variation in climate is an important environmental factor producing variation in physiological and life history traits in ectotherms (Conover and Schultz 1995, Arendt 1997). In many studies, variation in standard metabolic rates of organisms both within and between species has been suggested to reflect adaptations to specific environmental conditions (e.g. Lahti *et al*. 2002, Broggi *et al*. 2004, Álvarez *et al*. 2006). Salmon

Table 3. ANOVA table for the effects of stock on relative SMR (rSMR), length (*L*), mass (*M*), condition factor (*K*) and specific growth rate (SGR) in post-smolts in September 2006. *L*, *M*, and *K* were $\log_{10}$-transformed if the assumptions of normality and homogeneity of variance were not met. SGR was arcsine-transformed prior to analysis.

Source	df	*F*	*p*
rSMR	2, 16	5.406	0.016
L	2, 16	4.886	0.022
M	2, 16	2.215	0.142
K	2, 16	1.891	0.183
SGR	2, 16	1.511	0.251

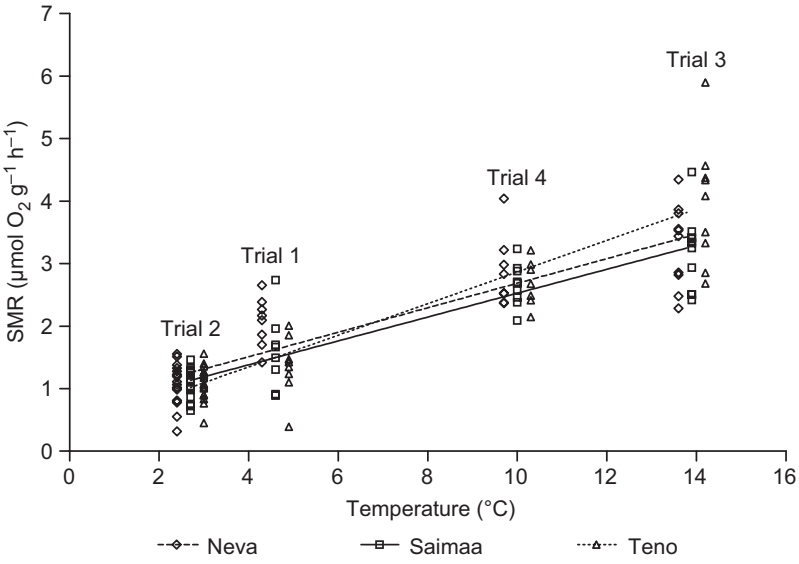

Fig. 5. Temperature-dependent response of SMR in the Neva, Saimaa and Teno stocks: $y = 0.196x + 0.724$, $y = 0.191x + 0.618$ and $y = 0.253x + 0.336$, respectively. The points in Neva and Teno stocks were nudged in order to clarify the figure. Oxygen consumption was measured in March 2005 (Trial 1), March 2006 (Trial 2), September 2006 (Trial 3) and May 2007 (Trial 4).

populations used in this study represented the same species but stocks differed from each other in addition to geographical location and length of incubation period also in the habitat of adult stage (fresh water, brackish water, full-strength seawater), hence many environmental aspects differ and have potential to select for differences in SMR.

In this study, the southernmost Neva stock had higher rSMR values at the yolk-sac stage than the two other stocks, which is in agreement with the study of Lahti *et al*. (2002) who suggested natal stream productivity to be a possible masking agent for the selection of SMR against countergradient variation (i.e. cogradient variation) because southern streams have usually more abundant food resources due to more productive environment. However, this is not a plausible explanation for the present results since the stocks did not differ in rSMR of UMG fish in later trials. Rather, it is possible that a longer natural egg incubation period of northern stocks under ice cover has favoured lower metabolic rate in the embryonic stage to ensure yolk sufficiency. In the present study, day degrees required to 50% hatching in the Neva, Saimaa and Teno stocks were 441, 456 and 468, respectively, and there were no differences in fresh masses of the alevins.

Although we detected a significant population-specific difference in SMR at the yolk-sac stage, the difference is not necessarily related to life stage of the fish. The trials were conducted at different temperatures, and the temperature response of the northernmost Teno stock was steeper than that of the other stocks (Fig. 5). Hence, it is possible that variation in SMR among trials is connected with temperature. Billerbeck *et al*. (2000) observed that a northern population of the Atlantic silverside (*Menidia menidia*) had significantly higher routine metabolism at high temperature than a southern population, whereas at low and intermediate temperatures the populations did not differ. According to Spicer and Gaston (1999), differences in physiological traits between populations can be plastic physiological adaptations, irreversible non-genetic differences or genetic differences. All populations in this study were reared under similar conditions and they experienced same handling procedures. Hence, the differences in SMR between stocks could have a genetic basis (Pakkasmaa *et al*. 2006), and therefore be susceptible to selection (Arnott *et al*. 2006). Differences influenced by acclimatization disappear after keeping populations in similar conditions for a long time but genetic differences exist in the later generations (Spicer and Gaston 1999).

Hatchery rearing of the population may affect SMR, although in a study on brown trout populations, Lahti *et al*. (2002) did not find any difference in SMR between the populations originat-

ing from the wild or having hatchery origin. All salmon populations in this study represented the second hatchery generation, and thus variation in the hatchery-rearing period is excluded as an explanation for variation in rSMR between populations. Maternal effects must not be forgotten as the traits were measured in the early life history stages of fish, some of the influences may reflect maternal effects (Rossiter *et al*. 1993, McAdam *et al*. 2002, Kotiaho *et al*. 2003, Dupont-Nivet *et al*. 2005, Pakkasmaa *et al*. 2006, Roff 2008).

Since high-latitude populations experience lower temperatures and shorter growing seasons than low-latitude populations, different populations may have adopted differing growth trajectories. In southern Atlantic salmon populations, development of a bimodal size-frequency distribution during the first growing season and its concomitant smolting at the age of one or two years is common (Thorpe 1977, Heggenes and Metcalfe 1991, Nicieza *et al*. 1991). In addition, formation of the modal groups is commonly known in hatchery-reared populations of Atlantic salmon (Thorpe 1977). In this study, a bimodal size-frequency distribution during the first year of growth was observed in each stock, however, in Teno stock, the number of individuals in the UMG was slightly smaller, and respectively, the number of individuals in the LMG was larger than those in the other two stocks. According to Conover and Present (1990), many species with a large north–south distribution area show a larger growth potential in the northern as compared with that in the southern populations. When reared in identical conditions, high-latitude populations of ectotherms have been found to have higher growth rates than low-latitude ones and furthermore, populations from hostile environments (low temperatures, short season for growth, strong competition) are suggested to perform better at all temperatures (Conover and Schultz 1995). Our results agree with earlier findings that suggest genetic influences favour rapid growth at high latitudes, opposing the environmental effect of a shorter growing season according to countergradient variation (Schultz *et al*. 1996); UMG fish of the northernmost Teno stock had the highest SGR values. At a population level, however, the situation was more complicated because smaller proportion of Teno fish entered the UMG than in the other two populations. Growth and food consumption are strongly temperature-dependent and seasonal changes in temperature control energetic processes. The level of growth rate in the first period (March 2006–September 2006) was ca. two-fold higher than that in the second period (September 2006–May 2007) (Fig. 3), which can be explained by differences in temperatures and fish sizes between these two periods: water temperature during the latter period was much lower and SGR of the smaller fish was higher than that of the larger ones (e.g. Brett and Groves 1979).

In agreement with many earlier studies (e.g. Cutts *et al*. 1998, Yamamoto *et al*. 1998), rSMR and SGR correlated positively in the third trial i.e. after the period of high growth rate. As mentioned above, the fast-growing individuals (UMG) and the slow-growing ones (LMG) can be unequivocally assigned to two distinct life-history pathways, differing in the timing of seaward migration and probabilities of early maturation and mortality (Thorpe 1987, Lundqvist *et al*. 1988). Both in nature (Metcalfe and Thorpe 1990) and in hatchery-reared (Metcalfe 1998, Thorpe *et al*. 1998) salmon, the age at smolting is dependent on growth. Fast-growing fish with high SMR and aggression levels can smolt as one-year-old, whereas slower growing fish with low SMR and aggression levels smolt at the age of two years or later (Thorpe 1977, 1986, Bailey *et al*. 1980, Kristinsson *et al*. 1985, Myers *et al*. 1986, Metcalfe and Thorpe 1992, Bohlin *et al*. 1994, Metcalfe *et al*. 1995, Bull *et al*. 1996, Nicieza and Metcalfe 1999) but there is variation among populations in the incidence of smoltification and maturity of the fastest growing parr (Thorpe 1977, 1986).

Majority of the UMG fish in each stock apparently smolted at the age of one year as external indicators of smolting were observed in a large part of the test fish in the third trial in autumn 2006. The prevalence of post-smolts was highest and furthermore, the values in condition factor were lowest in Teno stock. The post-smolts had significantly higher rSMR than the non-smoltified fish. It is known, that UMG fish have higher rSMR than LMG fish (Maxime *et al*. 1989), and high SMR as early as five weeks after first feeding was proportional to the probability of a fish entering UMG (McCarthy 2000). In the

present study, it was demonstrated that there can be significant differences in SMR within UMG fish as well. In the second trial in March 2006 at 2.7 °C, no external indicators of smolting were observed, on the other hand, all except one fish could be classified as smolts on the basis of their external appearance in the fourth trial in May 2007 at 10.0 °C. These results are in accordance with the study of Shrimpton *et al*. (2000) who reported that Atlantic salmon can smolt twice under laboratory conditions although in the natural life cycle smolting is a once-in-a-lifetime event (Björnsson and Bradley 2007). It is interesting that not all UMG fish smolted as one-year-old although they did not differ in size, condition factor or SGR from the smolted fish. The majority in the group of post-smolts and the minority among the non-smoltified fish were females. This is in agreement with earlier studies (Leyzerovich and Melnikova 1979, Heinimaa *et al*. 1998) suggesting that generally females constitute a majority of migrating smolts, due to early maturation of male parr. The fastest growing parr either migrate to sea as smolts or mature as parr (Thorpe 1977, 1986, Myers *et al*. 1986, Bohlin *et al*. 1994). Atlantic salmon parr do not usually mature sexually in the same year in which they smolt and migrate, and vice versa (Thorpe 1987, Hansen *et al*. 1989). Elevated SMR during smolting is caused by energetic costs associated with physiological and biochemical transformations, adapting the fish for marine environment. These transformations are known to be reversible: fish lose their smolt characteristics if they remain in fresh water beyond the period of normal spring migration (e.g. Kiiskinen *et al*. 2002, 2003). In this study, the difference in rSMR values between smolted and non-smolted fish was found in autumn at the time of desmolting when marine adaptations exchanged back for freshwater ones (e.g. Pirhonen *et al*. 1998).

To conclude, this study gives new information about differences in SMR and SGR among the three Atlantic salmon stocks as well as the relationship between these parameters and their association with smolting. The salmon stocks differed in their geographical origin and native habitat presumably selecting for differences in physiological parameters. Our results demonstrated the presence of both cogradient and countergradient variation in physiological traits of Atlantic salmon at different life-stages. The southernmost Neva stock had higher rSMR values at yolk-sac stage than the Teno stock, and the northernmost Teno stock had higher SGR values at smolt stage than the two other stocks. In addition, the stocks differed in physiological parameters characteristic of smolting: the post-smolts in the northernmost Teno stock had higher rSMR and SGR, and lower condition factor values than the fish in the two other stocks.

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