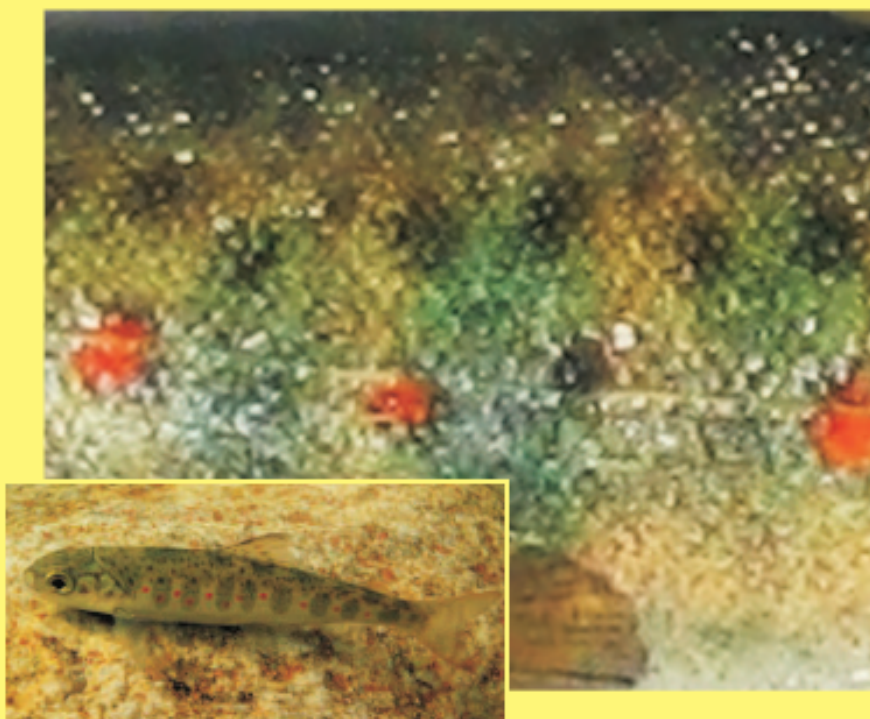


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Relationships between metabolic rate,  
growth rate, smolting and  
parasite infection  
in salmonid fishes

by  
Eila Seppänen



Joensuu  
2008

Eila Seppänen

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ACADEMIC DISSERTATION

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*Keywords:* aggressive behaviour, cataract, *Diplostomum* spp., growth rate, *Salmo salar*, *Salvelinus alpinus*, sexual maturation, smoltification, standard metabolic rate

The central themes in this thesis are standard metabolic rate (SMR) and its relationship to other traits. SMR is required for maintaining the critical physiological functions: it is the minimal metabolic rate of unfed fish performing no swimming activity. I investigated the variation in SMR, growth rate, behaviour and life-history characteristics as well as the intensities of *Diplostomum*-induced cataract among three geographically distinct Atlantic salmon (*Salmo salar*) populations: the Saimaa, River Neva and River Teno stocks. These populations represent the same species, but they differ in their geographical origin and the habitat of adult fish (fresh water, brackish water and full-strength seawater, respectively). The basic hypothesis was that, as a consequence of geographical isolation, the different stocks of the same species have genetically diverged from one another and have adapted to different environmental conditions, which is expressed in their physiology and behaviour. The factors studied were the associations between SMR and growth rate, aggressiveness and life-history strategy, as well as the repeatability of relative SMR. Furthermore, the relationship between SMR and parasite infection was studied in the three Atlantic salmon populations and also in Arctic charr (*Salvelinus alpinus*).

The results of my thesis demonstrated variation in physiological traits at different life-stages among the Atlantic salmon stocks. SMR differed among the stocks: the southernmost Neva stock had the highest values immediately after hatching, and the northernmost Teno stock had the highest values in winter. The trials were conducted at different temperatures, and the temperature response of the northernmost Teno stock was steeper than that of the other stocks. Hence, it is possible that variation in SMR among trials is connected with temperature rather than with the life stage of the fish. Growth rate differed among the stocks, and there was a positive correlation between growth and SMR: the Neva stock having high growth rates also showed high SMR values. Furthermore, the highest values in aggressiveness were found in the Neva stock but the association between SMR and aggressiveness was not statistically significant.

The energetic pattern of the smolting process in each population was revealed, and a relationship was found between SMR status and life history strategy: post-smolts and smolts had higher SMR than non-smolts. The post-smolts in the Teno stock had the highest values in SMR. Furthermore, temporal consistency of SMR was found: from autumn to late spring, fish were mainly observed to maintain their relative SMR level, indicating a significant repeatability of individual SMR status over the period.

The prevalence of cataract-bearing fish and cataract intensities differed among the three salmon populations. Most cataract-bearing individuals and the highest cataract intensities were found in the Saimaa stock, supporting the theory of a parasite being most infective to the local population. SMR and cataract intensity correlated positively, revealing a possibility that parasite infection affects the SMR of the fish.

In Arctic charr, however, a decrease in SMR as well as enlargement in spleen and liver sizes were observed in the *Diplostomum*-infected fish compared to the control fish. This indicates that a chronic parasite infection might not cause direct energetic costs, but it may weaken the efficiency of energy metabolism and thus lead to lowered SMR. I acknowledge that the host-parasite relationship between Arctic charr and *Diplostomum* may be a special case and, in further research, at least the influence of warmer water on this relationship should be studied.

Finally, my thesis gives new information about differences in SMR and growth rate among the salmon stocks and the relationship between these parameters and their association with smolting. Furthermore, my thesis produced new knowledge on the connection between SMR and chronic parasite infection, and this information may be advantageous in fish farming, where parasite-induced cataract is a serious problem.

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## LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following articles, which are referred to in the text by their Roman numerals I-V:

- I Seppänen, E., Piironen, J. & Huuskonen, H. (2009). Standard metabolic rate, growth rate and smolting of the juveniles in three Atlantic salmon stocks. *Boreal Environment Research* **14** (in press).
- II Seppänen, E., Huuskonen, H. & Piironen, J. Consistency of relative standard metabolic rate in juvenile Atlantic salmon and life history strategy. Manuscript.
- III Seppänen, E., Tiira, K., Huuskonen, H. & Piironen, J. Metabolic rate, growth and aggressiveness between three Atlantic salmon populations. *Journal of Fish Biology* (in press).
- IV Seppänen, E., Kuukka, H., Huuskonen, H. & Piironen, J. (2008). Relationship between standard metabolic rate and parasite-induced cataract of juveniles in three Atlantic salmon stocks. *Journal of Fish Biology* **72**, 1659-1674. doi: 10.1111/j.1095-8649.2008.01832.x
- V Seppänen, E., Kuukka, H., Voutilainen, A., Huuskonen, H. & Peuhkuri, N. Metabolic depression and spleen and liver enlargement in juvenile Arctic charr exposed to chronic parasite infection. *Journal of Fish Biology* (in press).

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## 1 INTRODUCTION

### 1.1 METABOLIC RATE

Metabolism, usually comprising the major part of energy budgets in animals, has a central role to play in physiological traits, such as growth and energy storage, which 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 and it is influenced by environmental factors (e.g., Claireaux & Lagardere, 1999; McNab, 2002), body size and composition (e.g., Daan *et al.*, 1990; Chappell *et al.*, 1999), nutritional status and activity. Of the environmental factors, temperature is considered to be a controlling, and dissolved oxygen concentration a limiting factor for metabolic rate (Fry, 1971). Furthermore, metabolic rate is a genetically variable, non-specific parameter and thereby has potential to respond to natural selection (Pough & Andrews, 1984; Garland & Bennett, 1990; Moody *et al.*, 1997; Steyermark & Spotila, 2000; Khazaeli *et al.*, 2004; Nespolo *et al.*, 2007). Consequently, metabolic rate may be higher or lower, depending also on genetic factors.

Energy costs in fish consist of minimal costs, those related to activity and those associated with the digestion, absorption and processing of food (Adams & Breck, 1990; Jobling, 1994). Since direct measurement of the energy losses of fish is difficult, it is usual to use oxygen consumption as an indirect measure of energy metabolism. SMR, which is the minimal or resting metabolic rate of unfed fish performing no swimming activity, is required for maintaining the critical physiological functions (Brett & Groves, 1979; Priede, 1985; Jobling,

1994). The two most important functions of SMR are “service” and “cellular maintenance” functions (Jobling, 1994). The first includes the expenditures of respiratory and circulatory systems that aim at supplying the body tissues with oxygen and nutrients, whereas the latter relates to the costs of ion transport and those associated with the synthesis and turnover of the biochemical constituents of cells (Jobling, 1994). Normally, fish live above this resting level, having normal activity such as daily feeding without stress, and this is termed the routine metabolic rate. The upper limit of aerobic metabolic rate with maximum sustained swimming is known as the active metabolic rate (AMR) (Jobling, 1994). According to Priede (1985), both the standard and active metabolic rates of healthy fish are mandatory, and healthy fish cannot regulate their magnitude. However, SMR can be lowered or raised by starvation and stress, respectively (O’Connor *et al.*, 2000; Sloman *et al.*, 2000).

In many studies, it has been suggested that variation in the SMRs of organisms both within and between species reflects adaptations to specific environmental conditions (e.g., Lahti *et al.*, 2002; Broggi *et al.*, 2004; Álvarez *et al.*, 2006). Generally, in populations from higher latitudes or altitudes, SMR tends to be higher, reflecting adaptation to a more seasonal climate (Cossins & Bowler, 1987; Garland & Adolph, 1991; Spicer & Gaston, 1999), though opposite results (Lahti *et al.*, 2002) and results indicating no between-population differences in SMR have also been found (Finstad *et al.*, 2004).

In salmonids, a positive relationship has been observed between SMR and growth rate at individual level (e.g., Metcalfe *et al.*, 1995; Huuskonen & Karjalainen, 1998; Yamamoto *et al.*, 1998; Álvarez & Nícieza, 2005) and



also between SMR and aggressiveness, both at the individual (Metcalf *et al.*, 1995; Cutts *et al.*, 1998, 1999) and at the population level (Lahti *et al.*, 2002).

## 1.2 SMOLTIFICATION AND MATURATION

Smolting and maturation are the two major developmental events during post-emergence life in salmonids, both processes being circannual and synchronized by photoperiod (Thorpe *et al.*, 1998; Metcalfe, 1998). Sexual maturation is necessary for the continuity of a species, but smolting migration is optional: salmonids can also mature without smolting (Thorpe, 1994). Smoltification is thus considered to be a subsidiary developmental event in relation to sexual maturation (Thorpe, 1994; Thorpe & Metcalfe, 1998). Salmonids show considerable variation in life-history patterns, growth rate, and age and size at sexual maturation as well as at smolting, both between and within species (Hutchings & Morris, 1985; Thorpe, 1989; Elliott, 1994; Tallman *et al.*, 1996). 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, juvenile salmonids, parr, have to reach certain genetically-determined threshold values in body size and energy stores for both events (Thorpe *et al.*, 1998; Metcalfe, 1998).

Sexual maturation among male parr is an alternative life-history pattern to smolting (Thorpe, 1986). Male Atlantic salmon may mature at the one-year-old parr stage while still living in fresh water (Fleming, 1996). Favourable growth rates and high energy balances increase the incidence of early maturation (Rowe & Thorpe, 1990; Rowe *et al.*, 1991; Shearer &

Swanson, 2000). Early maturing male parr compete as "sneakers" with large anadromous males at the spawning sites. In the following year, early maturing males that have survived over the winter may either remature or undergo smoltification and migrate to the sea.

In the southern Atlantic salmon populations, growth bimodality is common during the first growing season, and fast-growing individuals, the upper modal group (UMG) become smolts at least one year earlier than the slower growing ones in the lower modal group (LMG) (Thorpe, 1977; Metcalfe *et al.*, 1990; Heggnes & Metcalfe, 1991; Nicieza *et al.*, 1991). During smolting, the transformation of freshwater-adapted parr to the seaward-migrating smolt, various morphological, physiological, biochemical and behavioural changes occur in fresh water before they enter the sea (Hoar, 1976, 1988; Folmar & Dickhoff, 1980; McCormick & Saunders, 1987; Boeuf, 1993).

Heritable traits, biotic and abiotic factors influence the age of maturation (Powers, 1986). It is suggested that the primary physiological decision whether or not an individual salmon will mature is made in autumn (Thorpe, 1994), while the determination of smolting is made in late summer during the same year (Thorpe, 1989). Maturation may be interrupted if performance thresholds, such as sufficiently large energy reserves, are not met (Thorpe, 1986; Rowe *et al.*, 1991; Thorpe, 1994; Thorpe *et al.*, 1998), but smolting, once started, cannot be obstructed by reducing feeding (Thorpe & Metcalfe, 1998).

## 1.3 AGGRESSION AND GROWTH

Although the level of aggressiveness in salmonids is partly genetically determined (Ferguson & Noakes,

1982), environment has also a large influence on aggressiveness; e.g. variation in food resources (Rosenau & McPhail, 1987; Dunbrack *et al.*, 1996), predation pressure (Huntingford, 1982; Magurran & Seghers, 1991) and an abiotic environment (Grant & Noakes, 1988) are known to affect the level of aggression. Most of the studies in aggressiveness have been conducted in laboratory, and thus they do not necessarily reflect fully the situation in the field. Variation in environmental complexity may induce fluctuating selective pressures (Höjesjö *et al.*, 2004), indicating that habitat complexity reduces the growth of aggressive and dominant fish relative to subordinates. Within populations, behavioural differences among individuals are affected by size differences (Newman, 1956), the degree of kinship (Olsén, 1999) and earlier loss or victory experiences (Huntingford & Turner, 1987). Aggressiveness can be seen as a fitness-related behavioural trait in salmonids, as more aggressive Atlantic salmon, *Salmo salar* L., with higher metabolic rates are more likely to grow faster, migrate earlier and also mature earlier than less aggressive conspecifics (Metcalf *et al.*, 1989; Metcalf, 1991; Metcalf, 1998; Nicieza & Metcalf, 1999). According to Nicieza & Metcalf (1999) fast-growing juvenile Atlantic salmon (upper modal group, UMG) fish are more aggressive than slow-growing (lower modal group, LMG) fish, suggesting that there is a strong connection between aggression and growth bimodality. However, although aggressive and dominant juvenile salmonids often grow better than less dominant individuals (Fausch, 1984; Huntingford *et al.*, 1998), no significant correlations between dominance status and specific growth rate have been reported (Martin-Smith

& Armstrong, 2002; Vøllestad & Quinn, 2003). Individuals with higher social status frequently obtain preferential access to a food source and grow faster than lower ranked individuals (Chapman, 1962; Fausch, 1984; Grant, 1990; O' Connor *et al.*, 2000), and thus large size can be a consequence of high social status (Huntingford *et al.*, 1990; Thorpe *et al.*, 1992). In salmonids, a positive association has been observed between aggressiveness and growth rate, both at the individual (Metcalf, 1990; Nicieza & Metcalf, 1999) and at the population level (Lahti *et al.*, 2001), which is due to better competitiveness of the more aggressive and dominant individuals. The cause and effect relationship may also be the opposite: when an individual fish for different reasons (inheritable factors, higher metabolic rate, the amount of genetic variability) has a higher growth rate, it becomes a better competitor and possibly a dominant individual. Furthermore, dominant and aggressive Atlantic salmon (*Salmo salar* L.) individuals have a higher SMR than subordinate fish: as salmonids have indeterminate growth, high SMR also favours fast growth (Metcalf *et al.*, 1995; Yamamoto *et al.*, 1998). It has been suggested that growth rates are faster at higher latitudes. According to Schultz *et al.* (1996), the higher growth rate in northern fish populations is an adaptation to the short growing season. However, studies on Atlantic salmon (Elliott & Hurley, 1997; Jonsson *et al.*, 2001) and Arctic charr (*Salvelinus alpinus* L.) (Larsson *et al.*, 2005) suggest that the variation in growth rates among populations appeared unrelated to thermal conditions in the river from which the populations originated.

#### 1.4 PARASITISM

Parasites are known to be ecologically important stressors causing physiological and behavioural changes that may reduce host fitness (Møller *et al.*, 1996; Klein *et al.*, 2004; Östlund-Nilsson *et al.*, 2005). Fitness costs may be due, in part, to the energetic costs of maintenance and activation of the immune system (Sheldon & Verhulst, 1996; Zuk & Stoehr, 2002). Exposure to parasites (Morand & Harvey, 2000; Shinagawa *et al.*, 2001; Khokhlova *et al.*, 2002) or other short-term challenges to the immune system (Freitak *et al.*, 2003; Martin *et al.*, 2003) elevate the metabolic rate, demonstrating that activation of the immune system is costly in terms of energy. Parasitism is known to affect host metabolism in fish (Walkey & Meakins, 1970; Lemly & Esch, 1984; Östlund-Nilsson *et al.*, 2005), and changes in SMR can reflect an alteration in the host's energy metabolism due to parasitic infection.

The spleen has a central role in immune defence and haematopoiesis, (Rose, 1981; John, 1994), and increased size is a possible reflection of investment in the immune function (Rose, 1981; John, 1994). It has also been suggested that spleen size reflects adaptation to the level of parasite load in the host population, or species (Gregory, 1991; John, 1995; Morand & Poulin, 2000).

Liver enlargement occurs for various reasons such as infection, direct toxicity, hepatic tumours, storage diseases, or metabolic disorders. Changes in liver metabolism can affect the quantities of metabolites available to the peripheral tissues and consequently influence the metabolism of the whole organism (Huntington & Reynolds, 1987; Marceau *et al.*, 1999; Cortez-Pinto *et al.*, 1999). In fish, liver mass indicates energy reserves and reflects overall

body condition (Wootton, 1984; Lambert & Dutil, 1997).

*Diplostomum* spp., including *D. spathaceum* and *D. pseudospathaceum*, are ubiquitous parasites that develop into metacercariae in the eye lens of fish and cause cataracts due to their metabolic products and mechanical destruction of the lens tissue. Cataracts reduce vision and may even cause total blindness (Ersdal *et al.*, 2001). Fish farming produces fish for many purposes, such as human consumption and stocking for conservation of endangered species, and for fisheries. Currently, there are many problems in the cultivation of fish, one of them being the large number of cataract-bearing fish. Indeed, major economical losses due to cataracts have recently been reported (Menzies *et al.*, 2002).

## 2 OUTLINE OF THE THESIS

In this study, I have investigated SMR and its relationship to other traits in salmonid fishes, measuring variation in SMR (**I**, **II**, **III**, **IV**), growth rate (**I**, **III**, **IV**), behaviour (**III**), life-history characteristics (**I**, **II**) and intensities of parasite-induced cataract (**IV**, **V**). As research objects, I used three geographically distinct, farmed Atlantic salmon (*Salmo salar*) stocks (landlocked Saimaa; migrating Neva, down to the Baltic Sea, and migrating Teno, down to the Arctic Sea) and farmed Arctic charr (*Salvelinus alpinus*).

The main aims of this thesis were

1) to investigate whether the three populations of Atlantic salmon originating from different geographical locations and measured at different water temperatures, fish sizes and at different life stages differed with regard to SMR (**I**, **II**, **III**, **IV**), aggressive behaviour (**III**) and

specific growth rate (**I**, **III**, **IV**), and to discover associations between these variables within populations (**I**, **III**)

2) to examine whether individual variation in relative SMR in juvenile Atlantic salmon is consistent over time (**II**) and furthermore, to check whether different stocks differ in the consistency of relative SMR (**II**)

3) to clarify whether the variation in relative SMR is related to parr-smolt transformation and/or maturation and hence, to the life history strategy (age at smolting and/or maturing) (**I**, **II**)

4) to study the relationship between chronic parasite infection and SMR in three Atlantic salmon stocks (**IV**) and Arctic charr (*Salvelinus alpinus*) (**V**)

### 3 MATERIALS AND METHODS

The main material and methods used in the experiments for my thesis are briefly summarized below. More detailed descriptions can be found in the original papers.

#### 3.1 FISH

The main experimental animal in this thesis, Atlantic salmon (*Salmo salar* L.) (**I**, **II**, **III**, **IV**) belongs to the Salmonidae family, which is found in the northern Atlantic Ocean and rivers that flow into the Atlantic Ocean. Several life-history strategies can be adopted by Atlantic salmon (Thorpe, 1994; Fleming, 1996). Most Atlantic salmon follow an anadromous migration pattern, i.e. their highest feeding and growth takes place in salt water, and as adults they return to spawn in their native freshwater streams. Atlantic salmon spawn in freshwater in autumn (September-November), and the eggs develop during winter and hatch in the following spring. The duration of the

freshwater stay varies from 1 to 5 years, according to river location. During spring-early summer, immature parr undergo parr-smolt transformation and migrate downstream to the sea. Having left their natal streams, they experience a period of rapid growth during the 1 to 4 years they live in the ocean. However, Atlantic salmon do not necessarily require salt water, and numerous examples of fully freshwater, "landlocked", populations of the species exist throughout the Northern Hemisphere.

Three salmon stocks that differed in their geographical origin (Fig. 1 in paper **IV**) and native habitats were used: a landlocked, non-anadromous and freshwater-adapted Saimaa stock and two anadromous, sea-run populations, the River Neva and River Teno stocks, adapted to brackish water and full-strength seawater, respectively. The fish were reared at Saimaa Fisheries Research and Aquaculture in Enonkoski (Finnish Game and Fisheries Research Institute, FGFRI). The fish were maintained from the fertilization of eggs onwards in freshwater under similar experimental conditions to ensure constant environmental rearing conditions in the different stocks. Since the growth season in Finland is relatively short we accelerated the early development of the 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 used routinely at Saimaa Fisheries Research and Aquaculture. From then on, a simulated natural photoperiod and ambient water temperature were used to avoid any disturbance of endogenous rhythms in the fish. The fish were fed *ad libitum* with commercial pellet feed. The

pellet size was adjusted according to the size of the fish. The experimental fish were selected to represent the measured size distribution of each stock. To study the influence of the environment on the traits of salmon, some of the experimental fish were reared in seminatural raceways for five months (IV). As a species, Atlantic salmon is not considered threatened. However, two of the populations used in this study, the Saimaa and Neva stocks, are endangered. The stocks are maintained by annual stocking of hatchery-reared smolts (Pursiainen *et al.*, 1998). The study fish were farmed fish and not captured from the wild. Farming produces these fish in excess and therefore the wild stocks in nature were definitely not harmed.

Another experimental fish species in this thesis was the Arctic charr (*Salvelinus alpinus* L.) (V), which was one of the first species to colonise the northern lakes when the ice cover retreated after the last glaciation period. Arctic charr are among the salmonids that are least resistant to high temperatures, but probably the most resistant to low temperatures (Wandsvik & Jobling, 1982; Baroudy & Elliott, 1994; Lyytikäinen *et al.*, 1997). The arctic charr in the Saimaa lake system is a glacial relict in eastern Finland. It is endangered and relies almost completely on stocking for its existence (Makkonen *et al.*, 1997). FGFRI in Enonkoski has taken the Saimaa Arctic charr for aquaculture since 1983.

### 3.2 GENERAL STUDY DESIGN AND TAGGING METHODS (I - V)

All my experiments were conducted over the years 2005-2007. Respirometry measurements were carried out at different life stages of the fish and different times of year, and the size and temperature ranges

were wide (0.2 – 134.7 g and 2.7 – 13.9 °C, respectively). Behavioural trials were conducted in early summer, approximately one month after yolk-sac absorption. The fish were anaesthetized with a buffered MS-222 (tricaine methane sulphonate) solution before size measurements, tagging and eye examinations.

The fish were marked by two methods according to their size. The larger fish (total length > 8 cm) were tagged with passive integrated transponders (EURO-ID-tags; Trovan®). The ID-tag (length 12 mm and diameter of 2 mm) was inserted into the body cavity of the fish. The smaller ones (total length < 8 cm) were tagged with fluorescent elastomeric colorants (VIE; Northwest Marine Technology, Inc., Washington). A small amount of colour agent was injected under the skin of the fish in two places: at the dorsal and caudal fins.

### 3.3 RESPIROMETRY (I, II, III, IV, V)

Oxygen consumption was measured by an automated three-chamber intermittent-flow respirometer equipped with a 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<sup>-1</sup>. The experimental design enabled chambers of different sizes, depending on body mass, to be used. This allowed the ratio of fish volume to water volume to be kept approximately constant. Before experiments, the fish were fasted for 24 hours in the aquaria. During that time the fish were also acclimatized to the experimental temperature.

Each experiment lasted for 24 h, of which 16 h in the light and 8 h in the

dark. During this period the oxygen consumption of each chamber was recorded for 15 min every hour and the average rate during this time was extrapolated to an hourly value. The signals from the polarographic oxygen sensor were fed on-line into the computer and integrated every 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 and it was subtracted from the total decline of oxygen. The respirometer system was cleaned and disinfected every week. 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 in 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 ( $\mu\text{mol O}_2 \text{ h}^{-1}$ ) and body mass (g) data. Using this procedure, fish with higher SMR than expected for their mass had positive values, whereas those with lower SMR than expected had a negative rSMR (Metcalfe *et al.*, 1995).

### 3.4 BEHAVIOURAL TRIALS (III)

A series of aquarium trials was conducted to investigate the level of aggressiveness in each population. Several trials were always run concurrently for each population to avoid temporal separation. From the three salmon populations, 144 individuals were used in the aggression trials. Twelve trials with four fish were run for each population. Behaviour was recorded for 20 min once a day (between 8.00 and 12.00 am) for a period of two days. As food stimulates aggressiveness (Newman,

1956), the fish were fed three times with food pellets similar to those used in the rearing tanks during each observation period using an automatic feeder (Eheim®). The frequency of all aggressive behaviours and the frequency of the different behaviours exhibited by all the four fish in one aquarium during 20 min observation period were used as measures of aggressiveness. The averaged data over two observation periods from each aquarium formed one replicate in the later analyses.

### 3.5 EYE EXAMINATIONS (IV, V)

Cataract measurements of the three salmon populations were carried out twice, in January 2005 and after raceway cultivation in October 2005. The eyes of the salmon and Arctic charr were investigated for parasites at the same time as tagging was carried out. A KOWA sl-15 slit-lamp microscope was used for cataract measurements and detection of parasites in fish lenses.

## 4 RESULTS AND DISCUSSION

### 4.1 SMR IN THREE SALMON STOCKS

The results of the thesis demonstrated the presence of both cogradient (**I**, **III**) and countergradient (**IV**) variation in the physiological traits of Atlantic salmon at different life-stages. SMR differed between the stocks in the year class 2005, the southernmost Neva stock having the highest values immediately after hatching (**I**, **III**) and in the year class 2004, the northernmost Teno stock having the highest values in winter (**IV**). Hence, these results partly disagreed and partly agreed with several earlier studies (Cossins & Bowler, 1987; Garland & Adolph, 1991; Spicer & Gaston, 1999), suggesting that SMR

tends to be higher in populations from higher latitudes/altitudes, reflecting adaptation to a more seasonal climate. Latitudinal and altitudinal variation in climate is an important environmental factor, producing variation in physiological and life history traits in ectotherms (Conover & Schultz, 1995; Arendt, 1997). Many studies have suggested that variation in the SMRs of organisms, both within and between species, reflects adaptation to specific environmental conditions (e.g., Lahti *et al.*, 2002; Broggi *et al.*, 2004; Álvarez *et al.*, 2006). As the Atlantic salmon populations originated from geographically distinct habitats, many other environmental aspects (e.g., habitat of adult stage: fresh water, brackish water, full-strength seawater) in addition to latitude may differ and presumably select for differences in SMR between the stocks (**I**, **II**, **III**, **IV**). Metcalfe *et al.* (1995) suggested food level and its variability as being the factors influencing the evolution of SMR, while Lahti *et al.* (2002) proposed natal stream productivity as a possible masking agent in the selection of SMR against countergradient variation (i.e. cogradient variation). More abundant food resources are usually found in southern streams, so the amount and stability of food resources may be a relevant factor, food being presumably more abundant in the River Neva than in the River Teno. Hence, it may be possible that a better nutritional environment has favoured higher SMR for the Neva fish in comparison to the Teno stock. However, this is not a plausible explanation, since the stocks did not differ in SMR in later trials (**I**). Rather, it is possible that the longer natural egg incubation period of the northern Teno stock under ice cover has favoured a lower metabolic rate in the embryonic stage to ensure yolk adequacy. Day degrees required for 50% hatching in the Saimaa, Neva

and Teno stocks were 456, 441 and 468, respectively, and there were no differences in the fresh masses of the alevins (**I**). Finally, it is possible that the significant population-specific difference in SMR detected at yolk-sac stage is not related to the life stage of the fish at all. The trials were conducted at different temperatures, and the temperature dependence of SMR in the northernmost Teno stock was steeper than it was in the other stocks. Hence, it is possible that variation in SMR among trials is a direct temperature effect (**I**). According to Spicer & Gaston (1999), differences in physiological traits between populations may be plastic physiological adaptations, irreversible non-genetic differences or genetic differences. Differences induced by acclimatization should disappear after keeping populations in similar conditions for a long time, while genetic differences persist (Spicer & Gaston, 1999). All the populations were reared under similar conditions, starting from fertilization, and they experienced the same handling procedures (**I**, **II**, **III**, **IV**). Hence, the differences noticed in SMR between stocks are expected to have a genetic basis (**I**, **II**, **III**, **IV**, Pakkasmaa *et al.*, 2006), and therefore to be susceptible to selection (e.g., Pough & Andrews, 1984; Garland & Bennett, 1990; Moody *et al.*, 1997; Harchman *et al.*, 1999; Steyermark & Spotila, 2000; Arnott *et al.*, 2006).

#### 4.2 TEMPORAL CONSISTENCY OF RELATIVE SMR

In paper **II**, the consistency of individual variation in SMR was examined during a period when growth was sustainable and when maturing or smolting could take place for the first time. The results for consistency in SMR partly agreed and partly disagreed with earlier studies

that have suggested that SMR in juvenile Atlantic salmon is consistent over time under conditions of high food availability (O'Connor *et al.*, 2000; McCarthy, 2000). In the first period from March to September 2006, no correlation was found between the relative SMR status of individuals, whereas in the second period from September 2006 to May 2007, relative SMRs correlated mainly positively with only one exception: the individual that showed no external smolting indicators in May 2007. Within the stocks, repeatability between measurements in September 2006 and May 2007 appeared to be similar although not statistically significant in all the stocks.

In paper **I**, it was observed that the temperature response of SMR differed between the populations. It is possible that the responses may also vary at individual level, which would result in no consistency of SMR when fish are measured at different temperatures. In fact, in paper **II**, relative SMR at a low temperature (2.7 °C) during the first measurement did not correlate with those at higher temperatures (13.9 °C and 10.0 °C) in later measurements. At higher temperatures, relative SMRs were significantly repeatable among fish with a similar life-history strategy (**II**).

Other possible reasons for variation in the measurements of relative SMR between March 2006 and September 2006 and in September 2006 and May 2007 are probably changes in individual nutritional status and growth rate (**II**, Brett & Groves, 1979). The length of the period between the repeated measurements affects the degree of consistency in aerobic performance. In the short term (from some hours to a week) repeatability is very high, but as the length of the period increases (from several months to years), repeatability decreases or even disappears (van

Berkum *et al.*, 1989; Chappell *et al.*, 1995). Repeatability of aerobic metabolism has been studied earlier in terms of maximum oxygen consumption rates (Hayes & Chappell, 1990; Friedman *et al.*, 1992; Chappell *et al.*, 1995), field metabolic rate (Berteaux *et al.*, 1996; Peterson *et al.*, 1998) and SMR (DeVera & Hayes, 1995; McCarthy, 2000; O'Connor *et al.*, 2000; Cutts *et al.*, 2001).

There has been discussion whether a single individual measure of a trait can be used to make predictions over a longer time scale. If the trait exhibits long-term consistency, a single measure is suggested as being representative of the whole lifetime (Austin & Schaffer, 1992). The results of the present study (**II**) could be interpreted according to McCarthy (2000), who suggested that changes in performance may take place during the life cycle as a result of ontogenic shifts, and hence, individual consistency of a trait is not established for the whole ontogeny. Furthermore, during early ontogeny, the validity of a single measure to predict long-term performance has been both supported (van Berkum *et al.*, 1989; McCarthy, 2000) and rejected (Chappell *et al.*, 1995). Moreover, it has been suggested that the predictive power is trait-dependent (Austin & Schaffer, 1992).

#### 4.3 SMOLTIFICATION, MATURATION AND SMR

The results in papers **I** and **II** demonstrate a connection between SMR and smolting in juvenile Atlantic salmon. The post-smolts had a significantly higher relative SMR than the non-smoltified fish: in September 2006, the fish that showed external indicators of smolting had higher relative SMR values than the non-smoltified fish, indicating that high SMR individuals had smoltified in the



previous spring and were now desmolting. Elevated SMR during smolting is caused by the energetic costs associated with physiological and biochemical transformations pre-adapting the fish for a 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). Contrary to the case of landlocked salmon, however, this is not a natural process in their anadromous conspecifics. The difference in relative SMR values between smolted and non-smolted fish was found in autumn at the time of desmolting, when marine adaptations changed back to freshwater ones (**I**, **II**, e.g., Pirhonen *et al.*, 1998). The majority of the UMG (upper modal group) fish in each stock apparently smolted at the age of one year. The prevalence of post-smolts was slightly higher in the northernmost Teno stock (66.7%) than in Saimaa and Neva stocks (63.6% and 60.0%, respectively). In March 2006 at 2.7 °C, no external indicators of smolting had yet been observed, but in September 2006 at 13.9 °C they were found and, on the other hand, all except one fish could be classified as smolts on the basis of their external appearance in May 2007 at 10.0 °C (**I**, **II**). 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 & Bradley, 2007).

It is interesting that not all UMG fish smolted at one year although they did not differ in size, condition factor or growth rate from the smolted fish (**I**, **II**). The direction of the developmental route in Atlantic salmon is dependent on the

individual's prior feeding opportunities and its current metabolic performance (Thorpe, 1989), i.e. certain genetically-determined threshold values in body size and energy stores are decisive (Metcalf, 1998; Thorpe *et al.*, 1998). The fast-growing individuals (UMG) and the slow-growing ones (LMG) can be assigned unequivocally to two distinct life-history pathways, differing in the timing of seaward migration and the probabilities of early maturation and mortality (Thorpe, 1987; Lundqvist *et al.*, 1988); faster growing individuals are more likely to surpass the thresholds that trigger early maturation or smolting (Metcalf, 1998). Both in nature (Metcalf & Thorpe, 1990) and in hatchery-reared (Metcalf, 1998; Thorpe *et al.*, 1998) salmon, the age at smolting is dependent on growth.

It has also been observed that during the parr-smolt transformation of Atlantic salmon, fish with high growth rates also have high SMR values (Maxime *et al.*, 1989; McCarthy, 2000). Further, fast-growing fish with high SMR and aggression levels can smolt at one year or mature as parr, 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; Metcalf & Thorpe, 1992; Bohlin *et al.*, 1994; Metcalf *et al.*, 1995; Bull *et al.*, 1996; Nicieza & Metcalf, 1999), but there is variation among populations in the incidence of smoltification and maturity of the fastest growing parr (Thorpe, 1977, 1986).

In any case, Atlantic salmon smolts do not mature sexually in the same year in which they migrate, and *vice versa* (Thorpe, 1987; Hansen *et al.*, 1989). If juvenile salmon do not smolt, they may become sexually

mature, and then migrate the following year. If they smolt and migrate, their sexual maturation will take place after the years in the sea. The condition factor and relative SMR values of the post-smolts correlated negatively, indicating that high SMR fish grew more in length than in mass (streamlined body shape), resulting in a reduced condition factor (**I, II**). By contrast, a positive correlation was found between relative SMR and condition factor in the group of males (**I, II**). As some of the males were precocious (in the Saimaa and Teno stocks), this may indicate that these mature males grew more in mass than in length (the opposite of the development in post-smolts), resulting in an increased condition factor (**I, II**). The majority in the group of post-smolts and the minority among the non-smoltified fish were females (**I, II**). This is in agreement with earlier studies (Leyzerovich & Melnikova, 1979; Heinimaa *et al.*, 1998) suggesting that females generally constitute a majority of the migrating smolts, due to the early maturation of the male parr. In May 2007 females and males did not differ in relative SMR (**I, II**).

#### 4.4 SMR, GROWTH AND AGGRESSIVENESS

Fast-growing fish have higher SMR than the slow-growing ones (Maxime *et al.*, 1989; McCarthy, 2000), and furthermore, high SMR as early as five weeks after first feeding was proportional to the probability of a fish entering UMG in Atlantic salmon (McCarthy, 2000). In papers **I** and **II**, it was demonstrated that there may be significant differences in SMR within UMG fish as well.

Relative SMR and growth rate correlated positively after the period of high growth rate (**I, II**). Previous

laboratory studies have also found high SMR to favour fast growth (Metcalf *et al.*, 1995; Cutts *et al.*, 1998; Huuskonen & Karjalainen, 1998; Yamamoto *et al.*, 1998), but see; Steyermark, 2002; Álvarez & Nicieza, 2005; Sears, 2005). According to Álvarez & Nicieza (2005), in the wild, the variability of the environment mainly determines the relationship between SMR and growth, and thus studies conducted in the laboratory do not necessarily reflect the situation in the wild.

Geographical location causes intraspecific variation in metabolic processes (Hochachka & Somero, 1971), digestive performance (Nicieza *et al.*, 1994a) and growth (Nicieza *et al.*, 1994b; Conover & Schultz, 1995). Since high-latitude populations experience lower temperatures and shorter growing seasons than low-latitude populations, different populations may have adopted differing growth trajectories: the higher growth rate of northern fish is interpreted as an adaptation to a short growing season (Conover & Present, 1990; Schultz *et al.*, 1996). In Atlantic salmon populations, the 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 general (Thorpe, 1977; Heggenes & Metcalfe, 1991; Nicieza *et al.*, 1991) both in hatchery-reared (Thorpe, 1977, 1986) and wild (Nicieza *et al.*, 1991) populations. A bimodal size-frequency distribution during the first year of growth was observed in each stock in the present study, too (**I, II**). However, in the Teno stock, the proportion of individuals in the UMG was slightly lower and respectively, the proportion of individuals in the LMG was higher than those in the other two stocks (**I, II**). This may reflect a longer natural parr period in this northernmost population.

Although no association was found between SMR and aggressiveness among Atlantic salmon populations, the results were indicative: the highest values in SMR and aggressiveness were found in the Neva population (III). The explanation for the lack of correlation between SMR and aggressiveness might be the small between-population variation in total aggressiveness due to the low frequency of aggressive acts. In an earlier study, a significant correlation was found between SMR and the frequency of different aggressive behaviours in brown trout (Lahti *et al.*, 2002), indicating that populations with low SMR have energetically less costly and less risky aggressive behaviour, while populations with high SMR, on the other hand, display energetically costly aggressive behaviour. Different aggressive behaviours, whether mild or overt aggression, had no correlation with SMR (III). The concordance found between metabolic rate and behaviour is general in many organisms. SMR has been suggested as affecting an individual's social status in birds (Røskoft *et al.*, 1986; Högstad *et al.*, 1987; Bryant & Newton, 1994) as well as in fish (Metcalf *et al.*, 1995; Cutts *et al.*, 1998, 1999, 2001; Yamamoto *et al.*, 1998), high metabolic rate raising the dominance status. Dominant individuals frequently obtain preferential access to a food source and grow more rapidly than subordinates (Chapman, 1962, Fausch, 1984, Grant, 1990). As mentioned earlier, fast growing fish are likely to have higher SMR compared to their slow-growing conspecifics (Metcalf *et al.*, 1995; Yamamoto *et al.*, 1998). They are also forced to seek food more actively to cover the high energetic costs of maintenance and growth. Hence, there is a trade-off between growth rate and predation risk.

It is suggested that the developmental pathway adopted by fish is linked to aggression; the fast-growing, more aggressive juveniles would migrate in the spring, while the slow-growing fish with less aggressive behaviour would delay migration for another year (Nicieza & Metcalfe, 1999). Growth rate and aggressiveness were positively associated among the three Atlantic salmon populations, although the statistical significance was lost after correction for multiple tests (III). It is important to note that the number of populations in our study was only three, and using more populations would have increased the strength of the results. Nevertheless, the population-level positive association between growth rate and aggressiveness (III), taken together with earlier evidence from brown trout (ten populations; Lahti *et al.*, 2001), indicate the existence of a common genetic background for these two traits in salmonids. At the individual level, the most aggressive individuals often grow rapidly, in which case higher growth rate may either be a cause or a consequence of higher aggression level.

#### 4.5 PARASITE INFECTION AND SMR

The results in paper IV showed a population-specific difference in SMR in the first trial in winter and in cataract intensity and *Diplostomum* count in the third trial in the following autumn. In the second and third trials in spring and autumn, respectively, SMR values did not differ between the stocks.

It has been suggested that there is a genetic basis for susceptibility to *Diplostomum* (Betterton, 1974). Earlier studies suggest that local parasite populations infect fish originating from the same geographical location more effectively

(Ballabeni & Ward, 1993; Ebert *et al.*, 1998; Carius *et al.*, 2001). According to the results of this study, too (**V**), the parasite population at the Enonkoski hatchery may have 'specialized' in the Saimaa stock because this stock is geographically the nearest one and, in addition, the most farmed at this particular hatchery. On the other hand, the Teno stock, having the least prevalence and the least intensive cataracts, is the most distant one. It should be noted that in the first trial, the fish had only minor *Diplostomum* infections, probably because cercariae are mostly released in the late summer months (Karvonen *et al.*, 2006) and because large snail populations and therefore a greater infection risk exist at the ground-based outside pools and not in the tanks inside the hatchery, where these fish were held during their first year.

The results of the first trial agreed with the earlier studies (Garland & Adolph, 1991; Spicer & Gaston, 1999): SMR correlated positively with the latitude of population origin, the most northern Teno stock having the highest SMR values (**IV**). However, in the later trials, no correlation was found between SMR and the latitudes of the stocks. Hence, it seems possible that some other factor influencing SMR against the latitudinal gradient may mask the climatic effect. One possible explanation would be parasite infections that are common in rearing conditions (Muzzall *et al.*, 1990; Buchmann & Bresciani, 1997). In the Saimaa and Neva stocks, SMR and cataract intensity, as well as SMR and *Diplostomum* count, correlated positively after raceway cultivation, where the fish were exposed to natural *Diplostomum* spp. infection. The fish in the Teno stock diverged from the pattern, as no correlation was found between SMR and cataract intensity. SMR did not differ between the three populations, so the connection

between cataract formation and SMR cannot be explained only by the origin of the fish. Thus, the results suggest that in the Neva and Saimaa populations, parasite infection affected metabolic rate. The results in paper **IV** agree with earlier studies, where parasite infection has been observed to increase SMR (Booth *et al.*, 1993; Delahay *et al.*, 1995; Morand & Harvey, 2000; Shinagawa *et al.*, 2001; Khokhlova *et al.*, 2002; Nilsson, 2003). In the Teno stock, the parasite infection was lowest, and only 58% of the fish had cataracts (**IV**). Therefore the infection was possibly not severe enough to cause an increase in metabolic rate in the Teno stock.

Although the fish of the Teno stock had higher initial SMR than the other two stocks, they did not grow faster (**IV**), the result being in contrast with many previous studies (e.g., Cutts *et al.*, 1998; Yamamoto *et al.*, 1998). The reason for this could be their lower infection rate, causing protracted growth due to the energetic costs of parasite resistance. In earlier studies, parasitism has been found to inhibit fish growth, e.g., Szalai & Dick (1991), Szalai *et al.* (1992), and Johnson & Dick (2001) suggested that parasites reduced fish growth in yellow perch *Perca flavescens* (Mitchill). By contrast, infected fish have been observed to grow faster in lake (Burrough, 1978), as well as in laboratory conditions (Arnott *et al.*, 2000; Ebert *et al.*, 2004). Lysne *et al.* (2006) reported a higher increase in body mass and length in *Lernaeocera branchialis*-infected cod *Gadus morhua* compared with uninfected conspecifics. It is possible that this phenomenon is associated with the energetic costs of parasite resistance which results in reduced growth in more resistant individuals (Lysne *et al.*, 2006).

In paper **V**, however, *Diplostomum* infected Arctic charr had significantly

lower SMR than the control fish. This finding is at odds with earlier studies, suggesting either a higher rate of oxygen consumption in parasitized fish in comparison to non-parasitized ones (e.g., Walkey & Meakins, 1970; Lemly & Esch, 1984; Östlund-Nilsson *et al.*, 2005), or no effect of parasite infection on basal metabolic rate (Meakins & Walkey, 1975). Genetic background did not explain the difference in SMR between infected and control fish, indicating that the response of fish energy metabolism to chronic *Diplostomum* infection was more or less similar in all ten Arctic charr families.

In addition to depressed metabolic rate, chronic *Diplostomum* infection was associated with increased host spleen and liver size (V). A positive correlation between splenic enlargement and parasitism in fish, including fish-cestode and fish-nematode systems, has been reported in several studies (Arnott *et al.*, 2000; Morand & Poulin, 2000; Lefebvre *et al.*, 2004). However, Ottova *et al.*, (2005) found no relationship between spleen size and parasitism in bream *Abramis brama* L. infected by *Diplostomum* spp. and two ectoparasites, *Gyrodactylus* spp. and *Argulus* spp. In the study by Ottova *et al.* (2005), splenic enlargement was associated with poor somatic condition. There was no difference in condition between the experimental groups (V). Consequently, the splenic enlargement observed in infected fish in the present study cannot be explained by condition-related changes in the spleen (V). Given that spleen is a lymphoid organ having a role in defence against infections (Press & Evensen, 1999), enlargement of the spleen can most probably be explained by increased leukocyte synthesis (V). The spleen also has a haematological function (Press & Evensen, 1999), but there is no

apparent reason to expect extra synthesis of erythrocytes during *Diplostomum* infection.

The liver mass of infected charr was higher than that of uninfected charr (V). Although liver mass is an indication of energy reserves in fish (Wootton, 1984; Lambert & Dutil, 1997), the higher liver masses observed in the infected charr may be related to disorders in the liver function, which may have secondary effects on other tissues due to the regulatory role of the liver in homeostasis of the body. Infection-induced changes in liver metabolism may change the proportions and/or the absolute quantities of liver metabolites that become available to the peripheral tissues and consequently can influence the function of the whole organism. In humans, fatty liver is associated with the metabolic syndrome (Marceau *et al.*, 1999; Cortez-Pinto *et al.*, 1999) that is characterized by a considerable reduction in the insulin sensitivity of tissues (Marchesini *et al.*, 2001), resulting in ineffective glucose and lipid metabolism. If chronic *Diplostomum* infection in Arctic charr harms the liver energetic function and/or decreases tissue sensitivity to insulin, depressed SMR in infected fish is actually a result of disturbed energy utilization.

The respirometry was carried out at low temperatures in winter (V), and it is known that only few signs of immunological responses are found in fish eye tissues (Koppang *et al.*, 2004), both the humoral and cellular response decelerating at cold temperatures (Rijkers *et al.*, 1980; Hardie *et al.*, 1994). The Arctic charr is, however, one of the most cold-stenotherm fish species (Sandlund *et al.*, 1992; Lyytikäinen *et al.*, 1997), and influence of water temperature on the immune function of the Arctic charr is minor (Pylkkö *et al.*, 2002). The possibility that splenic

enlargement and impaired liver condition may result from other factors, for example, bacteria, viruses or other parasites in unfiltered water, was considered. However, no bacterial or viral diseases or other parasites than *Diplostomum* were evident in the study fish, and therefore they were not examined more closely.

#### 4.6 EFFECTS OF HATCHERY REARING

The influence of hatchery rearing on the traits of the studied populations has to be considered, as hatchery conditions are much more homogeneous than the environment in the wild. A typical hatchery provides safe and constant conditions with adequate and easy access to food and without threat of predators. The effects of variation in growing conditions and hatchery background were minimized; all fish stocks were reared in similar conditions from fertilizations onwards, and they represented the second hatchery generation (**I**, **II**, **III**, **IV**). 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 originating all from the wild or of hatchery origin. Genetic and maternal effects were suggested as factors affecting embryonic metabolism in Arctic charr (Pakkasmaa *et al.*, 2006), with larger eggs or embryos having proportionately lower respiratory and metabolic rates (see e.g., Schmidt-Nielsen, 1984).

Hatchery rearing is known to affect the aggressive behaviour of fish and to weaken anti-predator responses. Growing and developing in a conventional hatchery prepares fish poorly for the transition to a natural environment, and when hatchery-reared juveniles are stocked in the wild, the majority of them die as a

result of starvation (Ersbak & Haase, 1983; Ellis *et al.*, 2002) or predation (Olla *et al.*, 1994, 1998). This may be due to their adaptation to a hatchery environment as a result of which, their behaviour after stocking may differ from that which would be optimal in the wild.

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