

**JUVENILE YEARS OF ATLANTIC
SALMON IN THE WILD
AND IN THE HATCHERY:
ECOPHYSIOLOGICAL
DIFFERENCES**

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Oulu, Finland
2003

Abstract

This study investigated the ecophysiology of one of the world's northernmost Atlantic salmon (*Salmo salar* L.) stocks in the River Teno. The juvenile years of salmon of same genetic background were studied in the wild and in the hatchery conditions. In addition, the maternal size effect on reproduction was studied in wild females.

Benefit of body size was not only quantitative but also qualitative in reproduction success of the wild female salmon in the River Teno. Total number of eggs and energy content of eggs were higher in big females than in smaller ones.

In the hatchery, under natural day length and water temperature conditions, the growth rate, liver glycogen content and condition factor of the parr was higher than in the wild. The liver glycogen content of the hatchery-reared parr increased throughout the growing season and decreased during winter, whereas that of the wild parr was the lowest in summer, and stayed relative stable from September to May. The observed differences in annual fluctuation in liver glycogen content may reflect the differences in carbohydrate content of feed and in behaviour between the hatchery and wild.

Overall, the hatchery-reared juveniles matured and smoltificated 1–2 years earlier than the wild fish. The mean age of wild precocious males was 3 years and that of wild smolts 4 years. However, there was considerable variation in the age of precocious males (1–6 yr) and smolts (2–8 yr) in the wild. The maturing and smolting juvenile age groups were restricted to two (1–2 yr and 2–3 yr, respectively) in the hatchery.

In June, the hypo-osmoregulatory ability of hatchery smolts was developed parallel to the wild smolts. Some differences in physiological parameters between different smolt groups could be observed in the wild and between hatchery-reared and wild smolts indicating that completing of smolting process varies to some extent under different conditions. However, the hatchery-reared smolts showed higher levels of fin damage and body energy stores than the wild smolts.

As the hatchery practices should aim at controlling the quantity and quality of the juvenile salmon in production, the environmental conditions governing the physiological development of the juvenile fish should be taken into account. Hatchery practices should be planned so that the seasonal timing of smolting would follow the wild fish as close as possible.

Keywords: ecophysiology, life-history, maternal reproduction, parr, *Salmo salar*, smolt

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Inari, November 2003

Sirkka Heinimaa

List of original papers

The thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Heinimaa S & Heinimaa P. Effect of female size on egg quality and fecundity of the wild Atlantic salmon in the subarctic River Teno. Submitted manuscript.
- II Heinimaa S. Seasonal changes of liver glycogen content and condition factor of wild Atlantic salmon parr in a sub-arctic river. Submitted manuscript.
- III Heinimaa S (2003) Liver glycogen content of Atlantic salmon (*Salmo salar* L.) parr decreased despite the unchanging carbohydrate content of feed in the hatchery in winter. *Aquacult. Res.* 34: 1–3.
- IV Heinimaa S, Erkinaro J & Soivio A (1998) Differences in the physiology status of Atlantic salmon smolts in three tributaries of the River Teno. *Aquaculture* 168: 85–94.
- V Heinimaa S. Proportion of smolts and precocious males in different age groups of Atlantic salmon in sub-arctic hatchery conditions. Submitted manuscript.
- VI Heinimaa S & Erkinaro J (2004) Characteristics of mature male parr in the northernmost Atlantic salmon populations. *J. Fish Biol* 64, in press.

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1 Introduction

Naturally-reproducing Atlantic salmon exist all along the North Atlantic coast from Maine to northern Labrador in North America, throughout Iceland, Ireland and Great Britain, and in mainland Europe from northern Spain to the Ural Mountains in Russia (Hutchings & Jones 1998 and references therein). Within the distribution area in a south-north direction, environmental conditions vary considerably. Juvenile salmon in northern Spain, for instance, are able to grow for at least 10 months of the year in a river (Nicieza *et al.* 1994), whereas in northernmost Scandinavia, in contrast, growth is possible for juvenile for only two-three months during a year (e.g. Jensen & Johnsen 1985, Erkinaro & Niemelä 1995).

Nevertheless, the general life-cycle of the Atlantic salmon is very similar throughout the geographical range of the species (Marschall *et al.* 1998). The reproduction and juvenile stages are in a river from where migratory juveniles (smolts) emigrate to growing areas: sea, brackish water or in landlocked forms to lakes (Hoar 1976, Marschall *et al.* 1998). The migratory stage is lacking only in some rear stream-resident forms (Berg 1985, Gibson *et al.* 1996). Male parr, and to a limited extent female parr of migratory form, can mature in a river before migration to growing areas (Bagliniere & Maisse 1985, Berg 1985).

The development of the individual begins from fertilization of the egg. The offspring receive from the parents the gene material that will direct their development through their life. During the early development stage, egg and yolk sack stages, the individual is entirely dependent on the nutrients and other compounds that it has received from its mother during the vitellogenesis of the egg (Brooks *et al.* 1997). The size and body tissue weight of the alevin positively correlate with the size and energy content of the egg (Thorpe *et al.* 1984, Beacham & Murray 1985, Srivastava & Brown 1991). It is most likely that early-feeding fry have inherited from their parents a high standard metabolic rate and they tend to be more aggressive and dominant than the siblings of low standard metabolic rate (Metcalf *et al.* 1995, Cutts *et al.* 1998, Yamamoto *et al.* 1998). The dominant fry occupy the best feeding territories and hence their growth rate is higher than that of the subdominant siblings (Cutts *et al.* 1998).

Day length, water temperature and availability of food are the most important factors, which regulate the growth of the salmon (Thorpe *et al.* 1989). With shortening day length the growth rate of parr decreases, but the specific growth rate of parr with high standard

metabolic rate and dominance decreases less than that of the subdominant siblings (Metcalf *et al.* 1989, Thorpe *et al.* 1989, Metcalf *et al.* 1990, Solbakken *et al.* 1994, Forsberg 1995, Skilbrei *et al.* 1997, Duncan & Bromage 1998). As a result of this the size distribution of the salmon cohort develops bimodally till autumn (Thorpe 1977, Saunders *et al.* 1989, Metcalf *et al.* 1990, Heggenes & Metcalf 1991, Nicieza *et al.* 1991, Skilbrei *et al.* 1997). The smolting is possible if the upper modal group parr have reached the threshold size of about 7 cm at the time when the day length is 12 h (in the wild at the autumn equinox) and the water temperature allows their further growth so that they will reach the adequate size of smolts (about 15 cm in the wild, Hoar 1976) the following spring (Metcalf *et al.* 1989, Skilbrei *et al.* 1997). In northern latitudes, the growth of the parr is very slow from the autumn equinox till following May (Eriksson *et al.* 1979, Berglund 1992, Erkinaro & Niemelä 1995) and also the autumnal threshold size for smolting is higher than in the southern latitudes (Berglund 1995, Metcalf 1998). In general, the better the opportunity for growth is, the sooner the parr in the cohort reach the threshold size and growth rate of smolting, and the larger is their proportion (Thorpe 1986, Metcalf 1998). In southern Atlantic salmon rivers, parr become smolts at ages of 1- and 2-years (Metcalf & Thorpe 1990, Heggenes & Metcalf 1991, Nicieza *et al.* 1991, Hutchings & Jones 1998), whereas smolt age and its variation within rivers increase towards northern latitudes to 2–7 years (Metcalf & Thorpe 1990, Englund *et al.* 1999).

The fastest growing parr reach first the body's fat content threshold for maturation (Rowe & Thorpe 1990a, Simpson 1992), and some of the males can mature already at the age of 0+ and at the length of 7 cm (Myers 1984, Berglund 1992). Adequate body lipid stores in autumn and spring are important preconditions for maturation (Rowe & Thorpe 1990a, Rowe *et al.* 1991, Simpson 1992). Those juveniles that have adequate size in autumn for smolting next spring have two choices, smolting in the next spring or maturation in the following autumn (Thorpe *et al.* 1998), and the direction of development depends on the decrease of their body's lipid content during winter and spring (Morgan *et al.* 2002). During winter, the visceral fat content of smolting juveniles decreases more than that of non-smolting juveniles (Morgan *et al.* 2002). During spring, the body lipid content of smolting individuals continues to decrease (Morgan *et al.* 2002), whereas in non-smolting and maturing individuals the carcass fat content increases first, followed by the visceral fat content (Rowe *et al.* 1991, Morgan *et al.* 2002). However, the incidence of maturation among the fastest growing parr undoubtedly varies among populations and may primarily depend upon the age at which individuals get large enough to become smolts (Marschall *et al.* 1998). Depending on the growing conditions, especially in spring, the proportion of precocious males can vary considerably between years (Bagliniere & Maisse 1985, Glebe & Saunders 1986) but also between rivers (Hutchings & Jones 1998).

The threshold values of size and body lipid stores as well as the physiological changes that occur during maturation and smolting processes are under genetical control. The environmental conditions control when these threshold values are reached and in what time of the year the physiological changes occur. From the point of view of the salmon stock, the number of males that mature in a river is a significant factor, because they increase the effective size of population by contributing to reproduction (Saunders & Scholm 1985, Hutchings & Myers 1988, L'Abée-Lund 1989, Jordan & Youngson 1992). Parr maturation, however, may also increase the mortality of the male parr and hence reduce the later number of ascending anadromous males (Myers 1984, Whalen & Parrish 1999). The size of smolt may also have a further effect on the composition of ascending

salmon. The increased smolt size may increase the possibility of the fish to mature after one year in the sea (Ritter *et al.* 1986, Salminen 1997), and therefore the environment in which juvenile salmon grow is a significant factor on a population level.

In Finland, there are only four wild Atlantic salmon stocks: two in the rivers running into the Bothnian Bay, Baltic Sea, and two in the rivers emptying into the Arctic Ocean. Hydroelectric constructions and decreased water quality have destroyed most of the Baltic salmon rivers in Finland. To compensate for the lack of juvenile production in these rivers, about 2.2 million smolts and about 1 million parr and newly hatched fry are stocked yearly (Anonymous 2002). Over 90% of Atlantic salmon smolts annually entering the Baltic Sea are of hatchery origin (Salminen 2000). The juvenile salmon are reared mainly in private hatcheries from eggs of captive brood fish.

In a hatchery, the growth of juvenile salmon is faster and they become smolts and mature at younger ages than in nature (Thorpe 1991). From the point of view of the fish farming industry, where the results are measured by the amount of production, the fast growth of the fish is beneficial. However, when salmon are produced for stocking purposes, many other things beside the growth rate should be taken into account. The egg quality, behaviour, metabolic activity and maturation of the hatchery-reared fish can be different from those of the wild fish (Kleckner & Sidell 1985, Segner & Braunbeck 1990, Srivastava & Brown 1991, Bates & McKeown 2003). It has been shown that the stocking results, i.e. survival, of hatchery-reared juveniles is often lower than that of wild juveniles (Poole *et al.* 2003), although the stocking success can be increased by increasing the size of the smolts (Lundqvist *et al.* 1994, Salminen *et al.* 1995) especially the stocking success of previously mature males (Berglund *et al.* 1992). The other way to increase the stocking results is to increase the quality, e.g. hypo-osmoregulatory ability, of the smolts (Morán *et al.* 1991, Farmer 1994).

To be able to improve the quality of hatchery products, it should be known how environmental conditions affect the well being of fish and the timing of different life-cycle events in a hatchery. Although the biology of Atlantic salmon has been studied widely, most of the studies have been carried out in southern Atlantic salmon rivers and hatcheries. The present study has a focus on sub-arctic conditions where the cold and long winter may place challenges to physiology and ecology of juvenile salmon that could not be detected in more temperate conditions. Moreover, parallel data have been collected from nature and from hatchery to be able to study juveniles of the same origin in these environments under corresponding day length and water temperature conditions. In this study, the major difference between the natural and hatchery environments affecting the growth of juveniles was the availability and content of food. As the environmental conditions also affect the reproduction and egg and alevin development in the wild, these subjects were also accounted for here.

The main questions addressed in this study were:

1. How female size affects the egg quality and fecundity of wild salmon females in a northern salmon population?
2. How the body's energy stores of juvenile salmon develop in the wild and in the hatchery?
3. At what age and size male parr mature and juveniles become smolts in the wild and in the hatchery?
4. What is the physiological status of smolting juveniles in the wild and in the hatchery?

2 Material and methods

2.1 The rivers

The River Teno is the border river between northern Finland and Norway (70°N) and it runs into the Barents Sea (Fig. 1). The drainage basin of the river is large, 16 386 km², in which more than 1 000 km of different stretches are accessible to salmon. The River Teno is the most productive salmon river in Finland and Norway with annual river catch from 100 to 200 tonnes of salmon (Niemelä *et al.* 1996). Salmon production in the river is purely based on natural reproduction and many tributaries support distinct spawning stocks (Elo *et al.* 1994). The salmon of the River Teno exhibit a very wide range of ages and sizes at maturity (1–5 sea-winters, total age 3–10 years, length 40–130 cm; Niemelä *et al.* 2000). Some 80% of the ascending male salmon are 1-sea-winter fish, but among females the proportion is only 30% (Niemelä *et al.* 2000). The mean density of fry varies from 10 to 60 and of parr from 10 to 50 fish per 100 m² in the River Teno system (Niemelä *et al.* 1999). Growing conditions in this sub-arctic river system are poor and the growing season is short (Fig. 2). The water in the rivers is of a good quality for juvenile salmon (pH 7.0–7.7, alkalinity 140–150 meq l⁻¹, conductivity 2.8–6.1 mS m⁻¹ and total P 9.8–27.1 mg l⁻¹, Lapland Regional Environment Centre unpublished data). There are differences in growing conditions between the different parts of the river system, growth of parr being better in nursery brooks and lacustrine habitats than in the main spawning rivers (Erkinaro & Niemelä 1995, Erkinaro *et al.* 1995). Many parr spend their last freshwater years in the tributaries (Erkinaro *et al.* 1997), in where the typical age is 2–4 years, whereas in spawning rivers it is 0–2 years (Erkinaro 1995). Smolt age has varied between 2 and 7 years in the River Teno (Englund *et al.* 1999, Niemelä *et al.* 2000) but recently also some 8-year-old smolts have been observed (unpublished data).

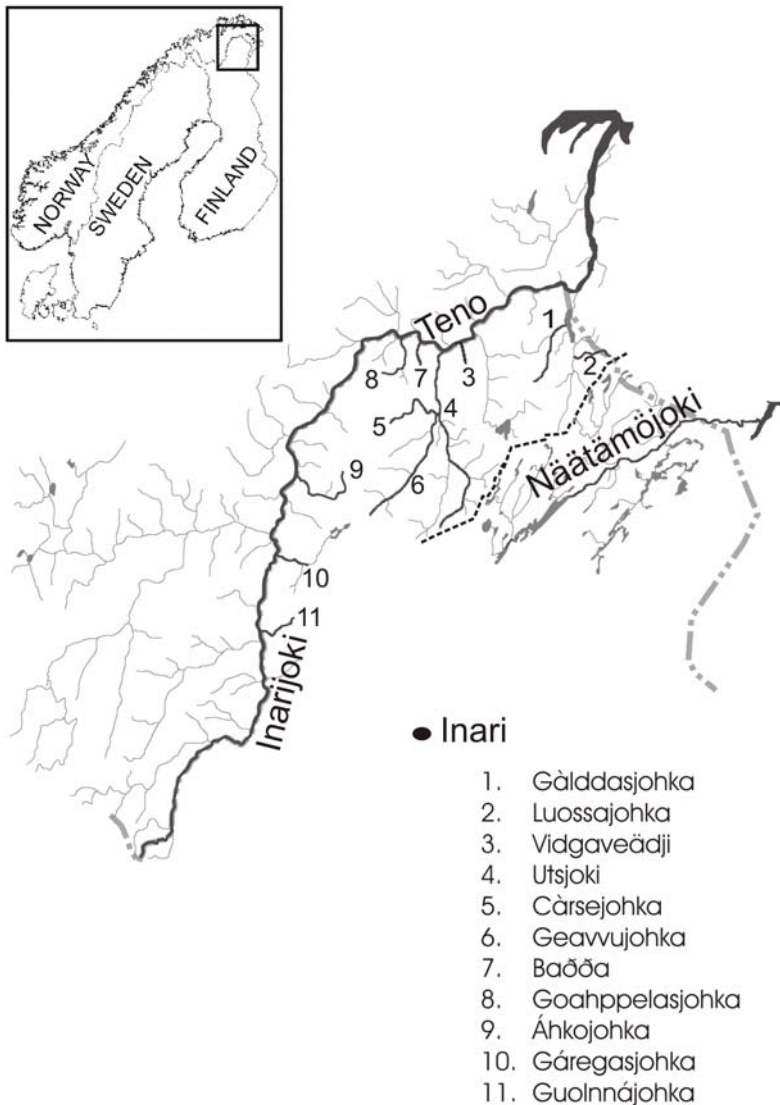


Fig. 1. Rivers Teno and Näätämöjoki watercourses and the tributaries included in the study. Location of the Inari hatchery is also indicated in the figure.

Some reference was also made here to the ages and sizes of precocious males in the neighbouring river system to the southeast, that of the River Näätämö basin (69°N, Fig. 1). The drainage basin of the river is 2 962 km², in which about 220 km of river system are accessible to salmon. Salmon production in the river is purely based on natural reproduction and annual river catch varies from 3 to 15 tonnes (Länsman *et al.* 1998). The mean density of fry varies from 5 to 20 and that of parr between 10 and 60 fish per 100 m² (Niemelä *et al.* 2001). The age of smolts varies from 2 to 6 years (Niemelä *et al.* 2001) and the age of ascending salmon from 1 to 4 sea-winters (Länsman *et al.* 1998).

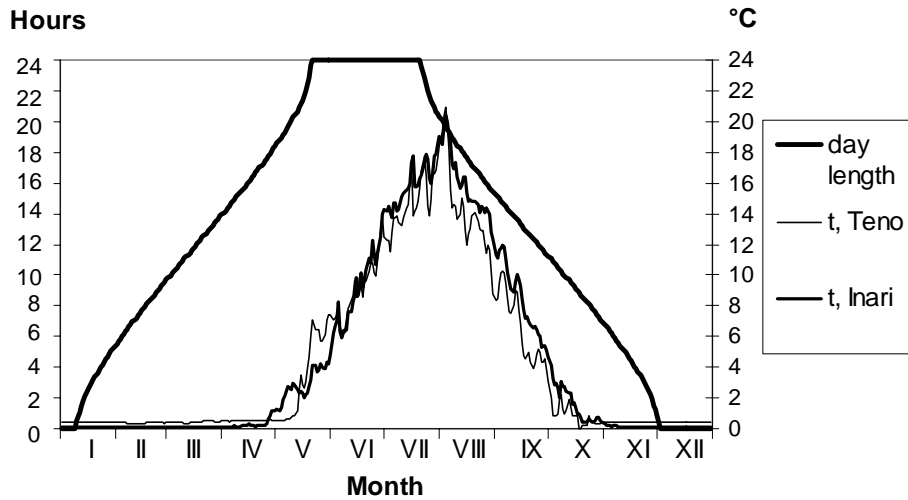


Fig. 2. Day length (from sun rise to sun set) in hours in Inari (69°N) and mean daily water temperatures (t) in the River Teno and in the Inari hatchery during a year.

2.2 The Inari hatchery

Although the salmon stock of the River Teno has remained vital, human activities and environmental changes pose a threat to it. In 1993, the Finnish Game and Fisheries Research Institute decided to store the genetical material of the Atlantic salmon stocks of the Rivers Teno and Näätämö in a frozen gene bank and establish a brood stock in the Inari hatchery of the Finnish Game and Fisheries Research Institute. This gave an opportunity to study the egg production and egg quality of wild females, the development of the eggs and juveniles in hatchery conditions, and also the incidence of precocious maturation of parr in the wild.

The Inari hatchery of the Finnish Game and Fisheries Research Institute is in the Inari village at the same latitude (69°N, 27°E) as the headwaters of the River Teno (Fig. 1). The rearing water comes from the River Juutuanjoki. The differences in water temperature and its annual fluctuations are minor between the Rivers Juutuanjoki and Teno (Fig. 2). The eggs are incubated and fish are reared in natural water temperature and photoperiod conditions in the hatchery (I, III, V). Water quality is good in the hatchery: suspended solid concentration is $1-4 \text{ mg l}^{-1}$ and colour is 14–40 Pt $\text{mg l}^{-1}</math> (unpublished data).$

2.3 Sampling of brood fish and eggs

The ascending brood fish were caught from the middle part of the River Teno in late August in years 1994–1998 (I), whereas precocious males were electrofished in different parts of the River Teno system and from the River Näätamö in September in 1993–1999 (VI). The brood fish were kept in fish chests in the river until stripping at the end of September–early October. The size and age of the brood fish were determined, and in addition the total amount of eggs produced by females and their relative fecundity. The quality of the egg of individual females was analyzed from unfertilized eggs by determining the size (diameter and wet weight) and energy content of eggs and from wet weight increase after fertilization (I). Fertilized and disinfected eggs were moved to the quarantine hatchery of the Inari hatchery.

The eggs were incubated in Ewos flat screen hatching trays covered with black plastic covers. The mean mortality of the eggs of individual females from fertilization to the eyed egg stage was calculated. The development of the embryos was studied by analysing the water and energy contents of eyed eggs and newly hatched alevins and by calculating days and degree-days from fertilization to these development stages (I).

2.4 Sampling of wild and hatchery-reared parr

The feeding of alevins was started at the end of June in the hatchery. Fry were reared in fibreglass tanks of 1 m² and 4 m² with typical rearing densities of the hatchery up to 3 years (III, V). The fry were fed with dry pellets of 0.6–1.7 mm in size (BioMar Ecostart 17) using automatic feeders (III, V). The routine hatchery work consisted of checking water inflow, of collecting dead fish daily, and of cleaning the tanks every second week in winter and twice a week in summer.

In order to obtain different aged juveniles (0–4 years) from nature, the wild parr were electrofished from the River Teno and the tributaries Utsjoki and Baðða. The electrofishing operations were carried out in different seasons (July, September, December and May) in 1994–1995 (II). The liver glycogen content and condition factor of wild and hatchery-reared parr were analyzed to obtain information on seasonal changes in body energy stores (II, III).

2.5 Sampling of wild and hatchery-reared smolts

The migrating wild smolts were sampled with counting fences from the lowest part of the tributaries Guolnná, Gáregas and Baðða at the end of June in 1994 (IV). In the hatchery, the size distribution of the 1-, 2- and 3-year-old juveniles was studied in June 1999 (V). The proportions of lower and upper modal fish and precocious males were calculated for each group. The smolt samples were taken from the upper modal group of the 2-year-old salmon and from the lower modal group of the 3-year-old salmon (V).

In order to obtain resting values of the measured physiological parameters, 20 smolts were introduced into individual restrainers for 48 h (IV, V). For testing the ion regulation ability of the smolts, 10–20 fish were challenged to 30‰-balanced sea water for two days (IV, V). The physiological smolting phase was studied by analyzing silver coloration, visibility of parr marks, blood haematocrit (Hct) and hemoglobin (Hb) values as well as plasma glucose, lactate, protein and electrolyte (Cl^- , Na^+ , K^+ and Mg^{2+}) concentrations of the smolts (IV, V). The appearance of fin damage was checked from sampled smolts (IV, V). The body energy stores of smolts were studied from tissue samples by analyzing liver glycogen, muscle lipid, protein and water contents (IV, V).

3 Results and discussion

3.1 Maternal effect on egg and alevin stages

There was considerable variation in the smolt age – sea age combinations and in the size of the multi-sea-winter (MSW) females in the River Teno (I). The size of the female salmon influenced the breeding success in many ways. The absolute fecundity of the female increased with the size of the fish as has been observed also in earlier studies in Atlantic salmon (Thorpe *et al.* 1984, Brännäs *et al.* 1985, Kallio 1986, Eskelinen & Ruohonen 1989, Erkinaro *et al.* 1997). Moreover, the energy content of eggs increased with female size although the correlation between size of females and eggs was weak and the relative fecundity (number of eggs per body kg) remained stable in different sized female salmon (I). In earlier studies, a positive relationship between female size and egg dry weight and between female size and yolk reserves and body tissue of alevins have been observed (Beacham & Murray 1985, Ojanguren *et al.* 1996). These results are in accordance with the results of the River Teno salmon that female size had a positive effect on egg quality.

Developing eggs receive the nutrients and other compounds from their mother during the vitellogenesis in the ovary (Brooks *et al.* 1997). This typically takes place during and after the upstream migration when brood fish have already ceased eating (Randall *et al.* 1986, Wootton 1990, Fleming 1996). In the river, big females have large energy stores to be used during vitellogenesis than small females as the energy stores of the fish positively correlate with the size of the fish (Shearer *et al.* 1994).

Instead of producing more eggs per unit body weight the big females invested more in the egg energy content and not so much in egg size (I). The relative fecundity of female can even decrease with increasing female size (Lobon-Cervia *et al.* 1997, Määttä 2000) as the egg size increases with the size of the female (Kazakov 1981, Thorpe *et al.* 1984, Brännäs *et al.* 1985, Kallio 1986). However, in nature there is a joint effect of egg size on egg number and offspring survival, which creates stabilizing phenotypic selection for an optimal egg size in a population (Einum & Fleming 2000a, Heath *et al.* 2003).

The optimal size of eggs depends on selection pressures, which have various influences in different developing stages of the fish. Beyond the certain optimal egg size, an increase of egg diameter may not be beneficial anymore because the small surface-to-

volume ratio increases the sensitivity of a big egg to low water oxygen content (Beacham & Murray 1985) increasing mortality of eggs with egg size during incubation (I). However, large egg size is generally a favourable trait as the size of alevins is positively related to the size of eggs (I), and the big alevin size is beneficial in a competition situation (Cutts *et al.* 1998, Einum & Fleming 2000a,b). The mean unfertilized egg size of the River Teno salmon females was relatively large, 5.3 mm and 111 mg (I). According to Thorpe *et al.* (1984), slow growth during the juvenile years increases the egg size. This could partly explain the large egg size in the MSW Teno salmon, as the juvenile growth in the River Teno is very slow and smolt age is high (Erkinaro & Niemelä 1995, Englund *et al.* 1999). During the sea migration, an increase in sea-age increases the size of females and further their fecundity and egg size (Kazakov 1981, Thorpe *et al.* 1984). About 70% of the ascending females in the River Teno are MSW fish (Niemelä *et al.* 2000), and the mean size of the MSW female spawners in the present material was 99 cm and 9 kg (I).

In a hatchery brood stock, smolting age (V) and also the maturation age are lower (Thorpe 1991), and the size of mature females is smaller than in nature (see for example Eskelinen & Ruohonen 1989, Määttä 2000). Moreover, the egg size of the hatchery-reared salmon is smaller than that of wild salmon of the same size (Srivastava & Brown 1991, Määttä 2000). The small alevins from the small eggs, however, may still have high survival since competition pressure is lower in hatchery than in nature (Einum & Fleming 1999, Heath *et al.* 2003). The increased survival of offspring of the female chinook salmon (*Oncorhynchus tshawytscha*) with small egg size in a hatchery decreased the egg size of ascending females in salmon stock subject to stocking (Heath *et al.* 2003). This may be a concern also in the Atlantic salmon stocks that are supplemented by stocking.

Egg quality – high lipid, protein and energy content of eggs (Srivastava & Brown 1991) – is influenced by many factors such as the diet of the brood fish and the endocrine status of the female during the growth of oocyte in the ovary (Brooks *et al.* 1997). Usually, the egg quality is better in the wild than in hatchery-reared salmon females (Srivastava & Brown 1991). The energy and water contents of unfertilized eggs and wet weight increase during water hardening are all related to each other (I). As the water content of high-energy eggs was low the water content increase of the eggs was high during water hardening (I). A sufficient increase ($\geq 13\%$) of wet weight during water hardening is considered one indicator of egg quality (I, Lahnsteiner *et al.* 1999) as well as the low mortality during incubation (Brooks *et al.* 1997). All characteristics of good egg quality (high average energy content of 10.5 kJ/g and low average 14.5% mortality) were found in the eggs of the wild Atlantic salmon females in the River Teno (I).

3.2 Growth and body energy stores of wild and hatchery-reared parr

3.2.1 Growth

The northern populations of salmon experience a more pronounced seasonal variation in growth opportunity than the southern ones. The first growing season is very short as the external feeding of fry begins at the end of June in the hatchery (V) or even as late as in July in the River Teno (unpublished data). The daily food consumption and growth rates

of juveniles as well as the amount of available drifting food begin to decrease already at the end of July (Erkinaro & Niemelä 1995, Erkinaro & Erkinaro 1998, Amundsen *et al.* 1999). Thus, the growth increment of the juveniles during the first summer is small both in the wild (Erkinaro & Niemelä 1995) and in the hatchery (III,V).

Under these growing conditions, it is not surprising that none of the parr could reach the autumnal threshold size for smolting and bimodal size distribution did not develop during the first growing season in the hatchery (V, see also Eriksson *et al.* 1979). Possible bimodal size distribution of salmon population has not been studied in the River Teno. There are no observations of 1-year-old smolts in the River Teno system (Englund *et al.* 1999) and thus it is most likely that a bimodal size distribution does not develop during the first growing season.

The growth of the parr is interrupted during the coldest winter months (Fig. 2) in northern salmon rivers (see also Berglund 1992). In May, the daylight time is already 24h, but the low water temperature (Fig. 2) keeps the growth hormone levels low until water temperature begins to rise (Schmitz *et al.* 1994, Björnsson *et al.* 1998). The feeding activity and growth of the wild parr and the amount of the available drifting prey organisms are the highest in early summer in the River Teno system (Erkinaro & Niemelä 1995, Erkinaro & Erkinaro 1998). Also in the hatchery, the growth of the parr was fastest during early summer (III).

The bimodal size distribution of the hatchery-reared parr developed during the second growing period (V). In the wild, there is large individual variation in growth rates of juvenile salmon between feeding territories of different quality (Keeley & Grant 1995) and between different parts of the river system with varying productive capacity of the habitats (Erkinaro & Niemelä 1995, Erkinaro *et al.* 1995, Heggberget *et al.* 1986). Although there are some observations from 2-year-old smolts in the River Teno, the detection of bimodal size distribution may be difficult in conditions where the variation of smolt age is high, the proportion of smolt ages varies yearly (Englund *et al.* 1999) and where age-related shifts in habitat preference exist (Erkinaro 1995).

3.2.2 Liver glycogen content

In the hatchery, liver glycogen content increased during the period from May to the end of September (III). The liver glycogen content of the wild parr was considerably lower (0.5–5.7%) than that of hatchery-reared parr (9.3%) in July (II, III). One reason for this may be the high digestible carbohydrate content of commercial feed (15%, III) compared to that of natural insect food (Reinecke & Owen 1980). The liver glycogen contents of hatchery-reared fish are positively related to dietary carbohydrate levels in water temperature above 12°C (Kim & Kaushik 1992, Hemre *et al.* 1995). The content of nitrogen-free extract, i.e. sugars and starches, of insect food can vary considerably between 0.8–33.8% (Reinecke & Owen 1980), but it is not known how well fish can digest these compounds. Generally, fish cannot utilize starches very efficiently (Bergot & Brèque 1983, Spannhof & Plantikow 1983).

It could be possible that the need to use glucose is lower in the hatchery than in the natural environment in summer. Growth hormone increases the swimming activity as well as the dominant feeding behaviour of juvenile salmonids (Björnsson 1997). Burst

swimming activity connected with drift-feeding (Kalleberg 1958, Wankowski & Thorpe 1979) and territorial defence (Kalleberg 1958) as well as the stress reactions are energised by glucose (Vijayan & Moon 1992, Mehrani & Storey 1993, Hemre & Krogdahl 1996). Growth hormone also promotes glycogen breakdown (Björnsson 1997). At the same time with increasing growth hormone levels, the relative capacity for aerobic glycolysis also increases with water temperature (Thibault *et al.* 1997). The lowest glycogen levels of the wild parr were detected in the River Teno system in July at the same time when the growth hormone concentration, as well as the metabolic need and ability to use glucose, are the highest. Also the sampling stress could have decreased the liver glycogen content of the wild parr (Vijayan & Moon 1992, Hemre & Krogdahl 1996). However, in the hatchery there is no territorial behaviour (although there is hierarchical behaviour (MacLean *et al.* 2000)), no need to escape predators, plenty of food available and low water flow in tanks. Anyhow, the carbohydrate content of food was so high that it satisfied the metabolic needs of the hatchery-reared parr and additional glucose was stored in the liver as glycogen (III, see also Segner & Braunbeck 1990, Hemre *et al.* 1995, Hemre & Krogdahl 1996).

In decreasing water temperature, the liver glycogen content may increase even in fish with a low carbohydrate diet (Hemre *et al.* 1995) as the growth hormone level, the metabolic need and capability to use glycogen decrease (Weatherley & Gill 1987, Hemre *et al.* 1995, Björnsson 1997, Thibault *et al.* 1997). The highest liver glycogen contents of wild parr were observed as late as in December (II) in the outlet of the lake, where the water temperature and the food supply is higher than in riffle sections (Gibson & Galbraith 1975, Erkinaro & Erkinaro 1998). The liver glycogen levels of the wild parr remained at a lower level (2.1–9.5%) than that of the hatchery-reared parr (11.7–14.4%) also in September and December (II, III). Bæverfjord (1992) has argued that the liver glycogen content of 14% may impair the function of liver cells. In this case, the liver glycogen content of the hatchery-reared parr was near the upper limit value in autumn.

The liver glycogen content of the hatchery-reared parr decreased significantly during winter (III), whereas that of the wild parr remained relatively stable between September and May (II). The efficiency of feed conversion, especially that of carbohydrates, decreases in cold water (<2°C; Hemre *et al.* 1995, Björnsson 1997) inhibiting replenishing of liver glycogen stores (III). Unlike in summer (see above), the need to use glucose might be higher in hatchery than in the wild in winter. In cold water, the activity of the wild parr is low, and the parr hide beneath stones in the river habitat most of the time (Cunjak 1988a, Metcalfe & Thorpe 1992, Bremset 2000). In the hatchery, there are no hiding places for parr in a tank. Movement and routine work in the hatchery disturb the parr, causing burst swimming and stress reaction, and this, in turn, consumes the liver glycogen stores. The decrease in liver glycogen content *per se* is not harmful to hatchery-reared parr (III) but it may indicate different behaviour in the hatchery than in the wild during winter. The hatchery parr have no need to conserve liver glycogen, as may be the case in wild parr with low glycogen content (Plisetskaya 1980, Woo & Cheung 1980, Sheridan & Mommsen 1991, Pereira *et al.* 1995). The liver glycogen content of the hatchery-reared parr (7.0–8.3%) was still higher than that of the wild parr (2.4–7.3%) in May (II, III), except for the 1-year-old parr (7% and 7.3% in hatchery and wild, respectively).

It is interesting that the annual changes in the liver glycogen content were more steady in the main river than those of the older parr in tributaries (II). There are differences in food and feeding between different rivers and different aged parr (Erkinaro & Erkinaro

1998), in carbohydrate concentrations between different insect species (Reinecke & Owen 1980) and also in the efficiency of carbohydrate metabolism in different sized fish (Phillips *et al.* 1948, Kitamikado *et al.* 1964, Austreng *et al.* 1977). Therefore, differences in the liver glycogen content of fish between different age groups and habitats are possible in nature (II).

3.2.3 Condition factor

In the hatchery, the condition factor (CF) of parr increased during the period from May to the end of September (III). The lipid and protein contents of wild parr have also been shown to increase during the growing period from April to September in more southern Atlantic salmon rivers (Gardiner & Geddes 1980, Berg & Bremset 1998). In the River Teno, the increase of CF was most pronounced from May to the beginning of July (II) simultaneously with the highest feeding activity and growth rate of the parr (Erkinaro & Niemelä 1995, Erkinaro & Erkinaro 1998). The CF of the wild parr does not usually increase in late summer anymore, but some exceptions have been observed (II, Erkinaro & Niemelä 1995). It is known, that the appetite and growth can vary between individuals especially in late summer and the body energy stores are higher in smolting and maturing juveniles than in other juveniles in autumn (Metcalf *et al.* 1989, Rowe *et al.* 1991, Morgan *et al.* 2002).

The CF of the wild parr decreased during winter (II), whereas the decrease in the hatchery-reared parr was not significant (III). The CF of the hatchery-reared parr was not significantly higher in the first autumn and the following May than that of the wild parr, unlike the following year (II, III). Parr continue feeding during winter but at lower level than in summer (Metcalf *et al.* 1986, Metcalf & Thorpe 1992, Koskela *et al.* 1997, Berg & Bremset 1998, Bremset 2000). The efficiency of feeding decreases with decreasing water temperature as the energetic cost of swimming activity increases (Webb 1978, Metcalf *et al.* 1986). As the digested energy may not satisfy the whole energy demand of the parr (Berg & Bremset 1998), the deficiency in energy is compensated by catabolising the body's lipid stores in winter (Gardiner & Geddes 1980, Cunjak & Power 1986, 1987, Cunjak 1988b, Berg & Bremset 1998).

3.3 Mature male parr in the wild and in the hatchery

For maturation parr need to reach certain minimum size, which is about 7 cm (VI, see also Myers 1984, Berglund 1992, Arndt 2000) and certain fat content (Rowe & Thorpe 1990b, Rowe *et al.* 1991, Simpson 1992). Only a few male parr in the hatchery (4%) and only one male parr in the wild reached this threshold values during second growing period and matured at the age of 1+ (V, VI). The proportion of precocious males increase with age and size in the wild and in the hatchery (V, VI). The fat content of the fish increases with size (Simpson 1992) and correspondingly, the proportion of the precocious males increased up to 3+ in the Rivers Teno and Näättäjäjoki (VI). The

increase in maturation rate among 2+ hatchery-reared males (V) is also accordance with the increase of CF described previously. However, there is, considerable variation in ages (1–6 years) and sizes (7.4–20.4 cm) of precocious male in the sub-arctic rivers studied here (VI).

Maturation of male parr is favoured by short winters (Prévost *et al.* 1992) and good growing conditions in spring allowing replenishing of carcass and visceral fat contents (Rowe & Thorpe 1990b, Rowe *et al.* 1991, Simpson 1992, Berglund 1995). In the northern Atlantic salmon rivers, the fat content of parr decrease during winter (Gardiner & Geddes 1980, Cunjak 1988b, Berg & Bremset 1998) and water temperature limits the growth in spring (Fig. 2) so that the lowest CF of parr were detected in May (II). Thus, it appears natural that the proportion of the precocious males was low (0–25%) in the River Teno system (VI) and even in the hatchery (4–35%, V) compared to more southerly Atlantic salmon rivers (Bagliniere & Maise 1985, Whalen & Parrish 1999). The yearly differences in growing seasons cause variation not only in the abundance of precocious males (Bagliniere & Maise 1985), but also in the age structure and size of precocious males between years (VI). The differences in the age structure and size of precocious males between rivers (VI) indicate differences in growing conditions between different parts of the river systems (Heggberget *et al.* 1986, Erkinaro & Niemelä 1995).

In the River Teno system, most of the parr smoltify at the age of 4 years (IV, Englund *et al.* 1999), which naturally decreases the proportion of older precocious males in the rivers (VI). The mean size of the precocious wild males increased very little after the age of 3+ (VI), and their size was smaller than that of the wild smolts of same ages. Only the oldest precocious males barely reached the average length of smolts in the River Teno (IV, VI). Thus, male parr are able to, and usually do mature before they reach smolt size. Moreover, possibility for growth is very limited from autumn to next spring (Erkinaro & Niemelä 1995) implying that parr have to reach adequate size for smolting already in autumn (see also Metcalfe 1998). However, maturation decreases growth when energy is used for gonad development in late summer and autumn (Rowe & Thorpe 1990a, Whalen & Parrish 1999, Arndt 2000). In addition, testicular resorption is slow in cold water (Berglund *et al.* 1991). These in turn decrease the possibility of mature males for smolting in the next spring (Berglund *et al.* 1992, Fängstam *et al.* 1993).

3.4 Smolting in the wild and in the hatchery

In the hatchery, parr of the upper modal group smolted at the age of 2 years and those of the lower modal group at the age of 3 years (V). The smolt ages vary considerably, from 2 to 8 years in the River Teno system (see 2.1.). Under similar water temperature and photoperiod conditions, the hatchery-reared parr smolted 1–2 years earlier than the wild parr (IV, V). Smolt age groups were restricted to two (1–2 years) in the hatchery instead of seven (2–8) in the wild (IV, V, see 2.1.). The 2-year-old upper modal group smolts were similar in size (about 15 cm) to the wild smolts (IV, V). After the third growing season in the hatchery, upper modal smolts exceeded well the natural smolt sizes and the mean length of the lower modal smolts was 20 cm (IV, V). Smolts of this size exist also in nature, but they are not common in the River Teno system (unpublished data, see also Hutchings & Jones 1998).

In the hatchery, 60% of the 2-year-old juveniles belonged to the upper modal group, the smolt group (V). If the 2-year-old fish were stocked in the river as a smolts, the individuals of the lower modal group should effectively be regarded as parr. Anyhow, it is important that both modal groups are used in stocking because there may be genetic differences between the individuals of the modal groups (Crozier 1998). If the 3-year-old smolts of this study (V) would have been hypothetically used in releases, it should be taken into account that large smolts of these sizes do not necessarily migrate as far as small smolts (Salminen *et al.* 1994, Kallio-Nyberg *et al.* 1999), and they have a higher probability to reach maturity after only one year in the sea (Salminen 1997). These factors should be concerned when releasing smolts of different origin, ages and sizes.

After the parr have reached the adequate size and accumulated sufficient body energy stores in autumn, the smoltification may begin in the next spring (Morgan *et al.* 2002). The physiological changes are energized by catabolizing the body's energy stores, which also increases the plasma glucose, protein and lactate levels and oxygen carrying capacity of the blood (Farmer *et al.* 1978, Virtanen 1987). These physiological changes transform the parr to smolt, which acquire a silvery coloration and an ability for ion regulation in saltwater (Farmer *et al.* 1978, Virtanen 1987).

The body energy reserves of the 2-year-old upper modal smolts were higher than those of the 3-year-old lower modal smolts in the hatchery (V). Larger smolts may start to lose their energy reserves earlier and/or at a higher rate and they may desmoltificate also earlier than the smaller ones (Virtanen 1987, Kiiskinen *et al.* 2002). The low social rank of the 3-year-old smolts in the group could also have an effect on lipid levels and especially on liver glycogen levels as the stress that sub-dominant individuals suffer consume their liver glycogen stores (Peters *et al.* 1988). Beside the differences in body energy stores, the physiological differences were minor between the above groups (V).

The body energy reserves of the hatchery smolts, especially in the 2-year-old fish, were higher than those of the wild smolts (IV, V, see also Poole *et al.* 2003). There were also differences in the size and body energy stores of the wild smolts between the nursery brooks and the spawning tributary, the values being higher in the former (IV). Again, these differences indicated differences in growing conditions within the river system (Erkinaro & Niemelä 1995). In the hatchery and in the wild, the smolt transformation succeed equally well in different sized smolts (IV, V, Farmer *et al.* 1978, Shrimpton *et al.* 2000).

Increasing day length and water temperature induce secretion of hormones that control the physiological changes during smoltification (McCormick *et al.* 2003). A water temperature of +10°C is often regarded as the triggering level for the beginning of smolt run (Ermolaev 1988, Jonsson 1991, Erkinaro *et al.* 1998). The physiological changes occur mainly before the migration starts (Farmer *et al.* 1978, Virtanen 1987, McCormick *et al.* 2003) and maximum seawater adaptability last about two weeks (Berglund *et al.* 1992). However, there can be considerable differences in the timing of smoltification between individuals in nature, where the smolt run can last over a month (Erkinaro *et al.* 1998). The smolts sampled at the beginning of the main smolt run in the River Guolinná had higher stress levels, lower plasma ion levels in freshwater and lower water and ion regulation ability in saltwater than the smolts sampled at the peak of migration in the other two tributaries (IV). According to Berglund *et al.* (1992), smolt migration may start before the optimal seawater adaptability is reached, and in the River Umeälven, the recapture rate was the highest for smolt released about two weeks before the time of optimal seawater adaptability. The smolts of the River Guolinná have a trip of 240 km to

the sea and hence probably enough time to finish the smoltification during the migration (IV, see also Ermolaev 1988, McCormick *et al.* 2003). In fact, the physiological stage of the hatchery-reared smolts reminded that of the wild smolts in the River Guolnná (IV, V). Considering that the samples from the hatchery-reared smolts were taken one week earlier than in nature, it is possible that the smoltification was not yet complete (IV, V).

The hatchery-reared smolts had considerably more fin damage than the wild smolts (IV, V), which has been shown also by Pelis & McCormick (2003). The fin damages may decrease the ability of station holding and prey capture in flowing water and increase the infection risk for diseases (Schneider & Nicholson 1980, Arnold *et al.* 1991).

In many earlier studies, differences in stress levels and ion regulation ability have been observed between the hatchery-reared and wild smolts. The differences may be attributed to various differences in growing conditions between hatchery and natural environments (McCormick *et al.* 2003, Poole *et al.* 2003 and references therein).

4 Management implications and further research needs

The carbohydrate content of the commercial dry feed may be unnecessarily high because the liver glycogen content of the hatchery-reared parr reached the unfavourably high level of 14% (Bæverfjord 1992), and it was significantly higher than that of the wild parr. In addition, the parr could not utilize effectively the carbohydrates of the dry feed in winter (III, Hemre *et al.* 1995). Thus, lower carbohydrate content of dry feed could be beneficial for hatchery-rearing of juvenile salmon.

The higher consumption of liver glycogen may indicate more restless behaviour of the parr in the hatchery than in the wild in winter. As the reason for this may be human activities in the hatchery, unnecessary disturbance in the hatchery should be avoided as much as possible during the cold water period.

The bimodal size distribution of salmon cohort should be taken into account when salmon smolts are produced for stocking. By determining the size distribution of the cohort, it is possible to separate the potentially smolting individuals from others. Both modal groups should be used in stocking to avoid genetic selection, but the lower modal group should be used and regarded as parr. If fish are reared in the hatchery for such a long time that also the lower modal group reach the smolt size, the hatchery smolts will be much larger than wild smolts. This may result in undesired migration behaviour and age at maturity in the sea. The longer rearing time in the hatchery increases also the proportion of precocious males in the cohort. It would also be beneficial to determine the proportion of precocious males in different age groups in the salmon hatcheries from time to time. Accurate information on the composition of the release groups would help to estimate the stocking results more precisely.

In hatchery rearing, the use of natural photoperiod and water temperature conditions similar to the river where the smolts will be released is recommended. This will enable a simultaneous smoltification in the hatchery and in nature. Knowing the timing of smoltification in the hatchery facilitates also the planning of the stocking schedule. The smolts can be stocked in a river before smoltification is complete, but stocking too late and the possibility of desmoltification should be avoided.

The results of this study raise interesting challenges for further studies. As the female size affected the egg quality in the wild, does the same phenomenon occur in hatchery brood stocks? More research is also needed on the relationships between the egg size/quality and the incubation mortality under different conditions in water temperature and quality.

Thorpe *et al.* (1984) have shown that juvenile salmon development, i.e. parr growth and smolt age, may influence the egg size of similar-sized females. Given the highly variation in life-history traits of the River Teno salmon, could the juvenile development have a similar effect in this complex system too?

As the carbohydrate content of the standard commercial dry feed appears unnecessarily high for hatchery-reared juvenile salmon, an optimal content of feed for subarctic, cold-water conditions should be studied. In wild parr of northern rivers, the role of fat and carbohydrate stores in seasonal energy use and their possible role as a bottleneck in winter survival requires more detailed studies.

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