

Effect of the female size on egg quality and fecundity of the wild Atlantic salmon in the sub-arctic River Teno

Sirkka Heinimaa* and Petri Heinimaa

*Finnish Game and Fisheries Research Institute, Inari Fisheries Research and Aquaculture, FIN-99870 Inari, Finland (*e-mail: sirkka.heinimaa@rktl.fi)*

Heinimaa, S. & Heinimaa, P. 2004: Effect of the female size on egg quality and fecundity of the wild Atlantic salmon in the sub-arctic River Teno. *Boreal Env. Res.* 9: 55–62.

Reproduction of the northern Atlantic salmon population was studied to find out the effect of female size on quantity and quality of eggs. Total and relative fecundity of females were used for quantity measures. Size, energy and water contents of eggs and changes in them as well as mortality of eggs during the incubation were used as quality measures. The size of wild female Atlantic salmon had a positive effect on their total number of eggs and on the energy content of eggs. However, the effect of the female size on the egg size was weak and there was no correlation between the female size and relative fecundity. Overall, the benefit of body size was not only quantitative but also qualitative in reproduction success of the River Teno salmon.

Introduction

The age and size of maturing individuals varies widely between and within river stocks of the Atlantic salmon (*Salmo salar* L.) (Alm 1959, Power 1981, Thorpe and Mitchell 1981, Hutchings and Jones 1998). Both genetic and growing conditions affect the age of maturity and the size of brood fish (Thorpe *et al.* 1983, Gjerde 1984, Jonsson *et al.* 1991, Friedland and Haas 1996). The size of the female salmon influences the breeding success in many ways. In a natural salmon population, firstly the egg number and size are both dependent on the female size (Thorpe *et al.* 1984, Brännäs *et al.* 1985, Kallio 1986), and secondly the juvenile size is positively correlated with the egg size (Flower 1972, Elliott 1989, Beacham and Murray 1985, Einum and Fleming 1999, 2000a, 2000b). Moreover, in nature, there is a joint effect of the egg size on the egg number and offspring survival, which creates stabilizing phenotypic selection for an

optimal egg size in a population (Einum and Fleming 2000, Heath *et al.* 2003). Females can either produce many but small eggs or fewer but large eggs. The benefit of a large egg is a large juvenile, which increase its possibility of survival during the first critical days after emergence (Flower 1972, Beacham and Murray 1985, Elliott 1989, Einum and Fleming 1999, 2000a, 2000b). Usually, the relative fecundity (number of eggs per body weight) is higher in small females than in large ones (Kallio 1986, Lobon-Cervia *et al.* 1997). However, under poor growing condition or high degree of intraspecific competition also small females produce large eggs (L'Abée-Lund and Hindar 1990, Hutchings 1991, Olofsson and Mosegaard 1999).

Can large females offer some other benefits to their offspring, like high nutrient reserves available to developing embryos and alevins? This is the topic to which little attention has been paid in previous studies. However, there are some observations of the positive effect of the

female size on egg dry weight and alevin's yolk reserves (Beacham and Murray 1985, Ojanguren *et al.* 1996). At least partly, the vitellogenesis of ascending salmon females occurs in the river at the time when they have already ceased eating (Randall *et al.* 1986, Wootton 1990, Fleming 1996). In this case, the large females have higher body-energy reserves to be used during the vitellogenesis of eggs than the smaller ones (Shearer *et al.* 1994).

The objectives of this study were to determine the effect of the female size on the egg quality and size and also on the total and relative fecundities in the one of the northernmost Atlantic salmon population. In this work, the egg quality was studied by analyzing their energy content. The energy content was chosen because it is positively dependent on the lipid and protein contents of the eggs (Srivastava and Brown 1991). Also other quality measurements like water content increase during egg swelling (*see* Lahnsteiner *et al.* 1999) and hatching time mortality were used.

Better understanding of the effect of the female size on reproduction allows for better evaluation of the consequences if the size of ascending females changes as a result of fishing, climate changes or stocking practices (Salminen 1997, Friedland 1998, Parrish *et al.* 1998).

Material and methods

Study area

The River Teno is a large sub-arctic salmon river (drainage area 16 386 km²) in northern-

most Scandinavia (70°N, 28°E) and it runs into the Barents Sea. It forms the border between northern Finland and Norway and it is the most productive salmon river of both countries with annual river catches varying between 100 and 200 tonnes (Niemelä *et al.* 1996). More than 1000 km of different stretches of the river system are accessible to the Atlantic salmon. The salmon of the River Teno exhibit a very wide range of both age and size at maturity, but the majority (71%) of the ascending females have been more than one winter in the sea (Erkinaro *et al.* 1997, Niemelä *et al.* 2000). Growing conditions in this sub-arctic river system are poor and the growing season is short (Erkinaro and Niemelä 1995). The age of smolts varies from two to seven years, the most abundant age group being four-year-old (Englund *et al.* 1999).

Collection and analyses of material

In the years 1994–1998, salmon brood fish of the River Teno, 56 multi-sea-winter females and 64 males and 96 one-sea-winter males (Table 1), were bought from local fishermen. The brood fish were caught from the main stream within a 100 km section (69°56'N, 26°33'E–70°04'N, 27°41'E) in the middle part of the River Teno in the late August at the end of the upstream migration. The multi-sea-winter females and males were kept in their own 4.5 m² and one-sea-winter males in 1.5 m² plywood fish chests. The fish chests were placed on the bottom of the River Teno at about 1-m depth allowing river water to run through the mesh ends of the fish chests.

The fish were stripped between the end of September and early October at the time when the mean daily water temperature was about 5 °C. Before stripping, the brood fish were anaesthetised with neutralized tricaine methanesulfonate (MS-222, 1 g l⁻¹), after which their bladders were emptied and the fish were dried with a towel. The eggs from each female were stripped into a basin and then the egg mass was weighed without the ovarian fluid to the nearest g. Mean egg diameter of unfertilized eggs was calculated by dividing 20-cm length by the number of eggs that fitted into that distance. In 1997, the egg diameters of nine females were measured from eggs at the

Table 1. The number of stripped multi-sea-winter (MSW) females and males and one-sea-winter (1SW) males in 1994–1998.

Year	MSW female	MSW male	1SW male
1994	13	19	13
1995	5	6	3
1996	6	8	21
1997	9	18	23
1998	13	13	36
Total	56	64	96

beginning, middle and end of their stripping. The eggs of each female were divided into portions that were fertilized with milt of 2–6 different multi-sea-winter males and 2–12 different one-sea-winter males. The water-hardened eggs of each individual female were pooled so that these two male groups were kept separately. Hardened eggs were disinfected with buffered iodophore liquid (Betadine 10 ml l⁻¹, ten minutes). The eggs were moved to the quarantine hatchery of the Inari Fisheries Research and Aquaculture.

The total lengths (to the nearest mm) and weights (to the nearest g) of the fish were measured. The egg mass left in the body cavity of the fish was also weighed. The total egg mass of each female was calculated by summing up the weights of stripped and leftover eggs. The number of eggs per female was calculated by dividing its total egg mass by the mean wet weight of their eggs. The total body weight of the female was calculated by summing the stripped egg mass with the body mass after stripping. The gonadosomatic index (GSI) was calculated by dividing the total egg mass by the total body weight and the relative fecundity was calculated by dividing the total egg number by the total body weight. The age of the salmon was determined from scale samples taken between the adipose fin and lateral line.

The eggs were incubated in Ewos flat screen hatching trays, in which water ran through the egg layer. Water temperature during egg incubation was regulated to the same level as that measured on the bottom of the River Teno and recorded daily. The daily mean water temperature was about 0.5 °C from the beginning of November to the end of April. Water oxygen level was about 80%–100% in the incoming water. The hatchery trays were covered with a black plastic plate to protect the eggs from light. The dead eggs were removed and counted at the eyed stage. The living eggs were disinfected again as described earlier. The mean mortality of each female's eggs from the time of fertilization to the eyed stage was calculated by dividing the number of dead eggs by the number of incubation groups.

The water and energy contents of the unfertilized, fertilized, eyed stage eggs and newly hatched alevins were analysed. The wet weights

of ten eggs/alevins from each female were measured to the nearest mg. The water content of the samples was analysed gravimetrically after drying them to a constant weight (105 °C for 24 h). Another ten eggs/alevins were stored in liquid nitrogen for later measurement of the energy content. Energy contents (kJ g⁻¹ wet weight) were determined with a microbomb calorimeter.

Statistical methods

Linear regression analyses were used to calculate the relationships between the female size and fecundity, between the egg size and energy content, and also between the egg water and energy contents, between the hatching time mortality and the egg size and between the alevin and egg sizes ($\alpha = 0.05$). One-way ANOVA was used to test the egg size differences within striping and wet weight differences during hatching. For statistical analysis the normality of the residuals was tested with the Lilliefors test and the homogeneity of variances with the Levene test. When necessary, the data were normalised by logarithmic and relative numbers by arcsine transformations. The energy content changes of the eggs during the incubation were tested with the Friedman nonparametric test. Computations were carried out with SYSTAT 8.0 statistical software.

Results

The fecundity, measured as number of eggs per female, was positively related to body size (Fig. 1 and Table 2). The mean total length of the females was 99.2 ± 9.0 cm (mean \pm SD), the mean total weight 9.0 ± 3.0 kg and the mean number of eggs per female $16\,436 \pm 5\,827$ (Fig. 1). There were nine different river/sea age combinations from 3/2 (3-river years and 2-sea years) to 5/4, 39% of the females belonging to the age group 4/3.

There was no significant relationship between the female size and GSI or relative fecundity (Table 2). Mean GSI was $20.0\% \pm 3.9\%$ and the mean relative fecundity was 1845 ± 392 eggs

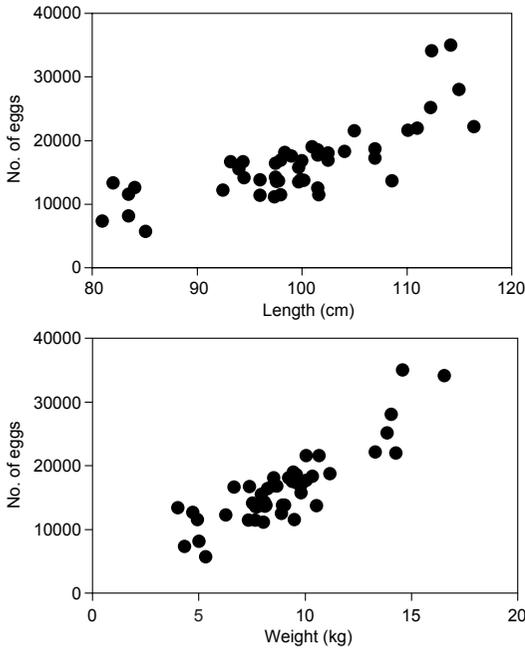


Fig. 1. Fecundity (no. of eggs) of different sized (length and weight) wild female Atlantic salmon of the River Teno.

per kg. The relationship between the female length and unfertilized egg wet weight was just barely significant, but there was no significant relationship between the female weight and egg wet weight nor between the female size and egg

diameter (Table 2). The mean diameter of unfertilized eggs was 5.3 ± 0.2 mm and the mean egg wet weight was 111 ± 13 mg. The egg diameter did not differ statistically between eggs taken at the beginning, middle or end of stripping (ANOVA $F_{2,21} = 0.072$, $P = 0.931$).

The female size had a significant positive effect on the energy content of the eggs (Fig. 2 and Table 2). The mean energy and water contents of the unfertilized eggs were 10.5 ± 0.5 kJ g^{-1} and $61.2\% \pm 1.0\%$, respectively. The energy content of the unfertilized eggs was negatively related to their water content (Table 2). After fertilization, the increase in the water content of the eggs was also negatively related to the water content of the unfertilized eggs (Table 2). During water hardening the water content of the eggs increased on average by $6.9\% \pm 1.0\%$ and the wet weight increased by about $17.9\% \pm 4.0\%$. The mean water content and wet weight of the hardened eggs were $68.1\% \pm 1.3\%$ and 135 ± 17 mg, respectively.

The eggs developed to the eyed stage on average in 112 ± 9 days (117 ± 16 degree ($^{\circ}C$) days), between the end of January and the beginning of February, except in 1995 when the period began at the end of December. The mean incubation mortality from fertilization to the eyed egg stage was $14.5\% \pm 8.7\%$. There was a positive

Table 2. Equations of linear regressions, squared multiple R and P values ($\alpha = 0.05$) of the ANOVA test and the number of samples (N) of the River Teno female material.

Equation	R^2	P	N
$\text{Log}[\text{number of eggs}] = 3.070\text{log}[\text{length}(\text{cm})] - 4.460$	0.632	< 0.001	46
$\text{Log}[\text{number of eggs}] = 0.891\text{log}[\text{weight}(\text{kg})] + 1.583$	0.662	< 0.001	46
$\text{Arcsine}[\text{GSI}] = 0.055\text{log}[\text{length}(\text{cm})] + 0.208$	0.011	0.458	53
$\text{Arcsine}[\text{GSI}] = 0.010\text{log}[\text{weight}(\text{kg})] + 0.370$	0.005	0.632	53
$\text{Log}[\text{number of eggs per kg}] = -0.358\text{log}[\text{length}(\text{cm})] + 9.143$	0.025	0.298	46
$\text{Log}[\text{number of eggs per kg}] = -0.109\text{log}[\text{weight}(\text{kg})] + 8.491$	0.029	0.260	46
$\text{Log}[\text{egg weight}(\text{mg})] = 0.390\text{log}[\text{length}(\text{cm})] - 3.996$	0.089	0.043	46
$\text{Log}[\text{egg weight}(\text{mg})] = 0.103\text{log}[\text{weight}(\text{kg})] - 3.136$	0.077	0.061	46
$\text{Egg diameter (mm)} = 0.714\text{log}[\text{length}(\text{cm})] + 2.043$	0.072	0.075	45
$\text{Egg diameter (mm)} = 0.165\text{log}[\text{weight}(\text{kg})] + 3.828$	0.049	0.146	45
$\text{Log}[\text{egg energy cont. (kJ g}^{-1}\text{)}] = 0.178\text{log}[\text{length}(\text{cm})] + 1.530$	0.140	0.035	32
$\text{Log}[\text{egg energy cont. (kJ g}^{-1}\text{)}] = 0.053\text{log}[\text{weight}(\text{kg})] + 1.866$	0.165	0.021	32
$\text{Log}[\text{egg energy cont.}] = -1.224\text{arcsine}[\text{egg water cont.}] + 3.448$	0.165	0.021	32
$\text{Arcsine}[\text{water increase}] = -0.722\text{arcsine}[\text{egg water cont.}] + 0.913$	0.146	0.014	41
$\text{Arcsine}[\text{proport. of dead eggs}] = 0.993\text{log}[\text{egg diameter}] - 1.285$	0.125	0.020	43
$\text{Alevin wet weight (mg)} = 1.145[\text{egg wet weight (mg)}] + 0.009$	0.463	< 0.001	43
$\text{Alevin wet weight (mg)} = 0.074[\text{egg diameter (mm)}] - 0.257$	0.539	< 0.001	43

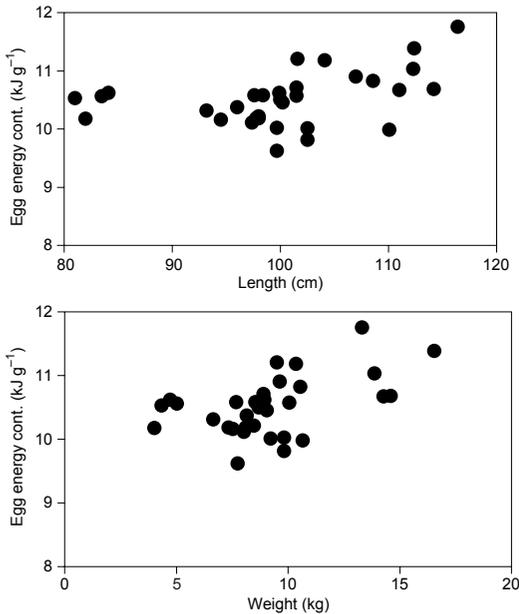


Fig. 2. Egg wet energy content (kJ g^{-1}) of different sized (length and weight) wild female Atlantic salmon of the River Teno.

relationship between the egg diameter and the embryo mortality during the incubation time to the eyed egg stage with increasing variation in embryo mortality with the egg size (Fig. 3 and Table 2). The mean wet weight of eyed eggs was 134 ± 16 mg and the mean energy content was 8.7 ± 0.7 kJ g^{-1} .

Alevins started to hatch on average after 220 ± 6 days (181 ± 15 degree ($^{\circ}\text{C}$) days) after fertilization, at the time when the water temperature began to rise in May. The mean wet weight of the hatched alevins was 136 ± 22 mg and their mean energy content was 6.9 ± 1.4 kJ g^{-1} . The wet weight did not change during the incubation from fertilized eggs to newly hatched alevins (ANOVA $F_{2,133} = 0.092$, $P = 0.912$) but the energy content decreased (Friedman $F = 14.889$, d.f. = 2, $P = 0.001$). The size of newly hatched alevins was positively related to the size of the unfertilized eggs (Fig. 4 and Table 2).

Discussion

The egg quality, as evaluated by its energy content, was found to be positively dependent on the female size. However, the egg size itself

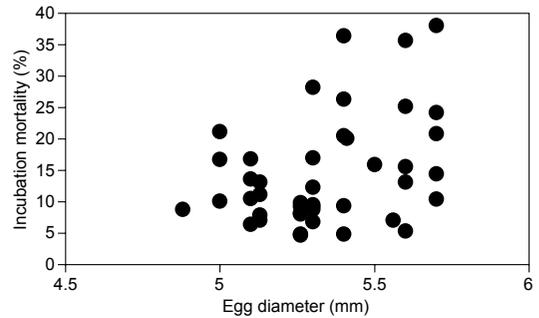


Fig. 3. Mortality during incubation of the different sized eggs from fertilization to the eyed stage of the wild female Atlantic salmon of the River Teno.

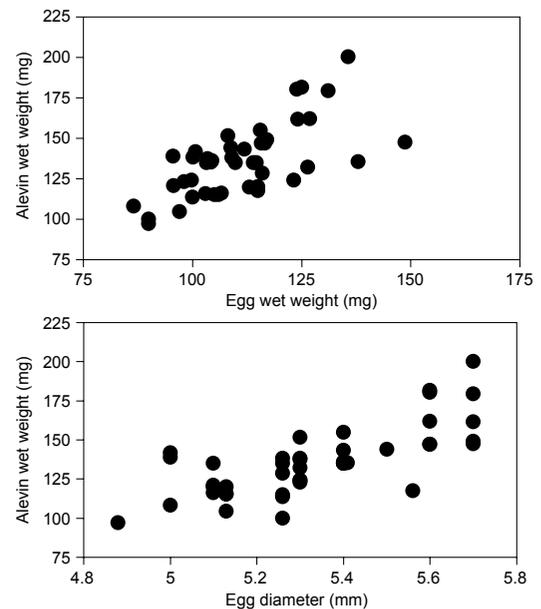


Fig. 4. Relationships between the unfertilized egg and alevin wet weights and between the unfertilized egg diameters and alevin wet weights of the wild female Atlantic salmon of the River Teno.

was not so evidently size-dependent in the River Teno salmon females. The relative fecundity of females was not size dependent, but as expected the total fecundity was. The embryo mortality during the incubation from fertilization to eyed egg stage was positively size dependent, and the mortality of large eggs varied more than the smaller ones. The wet weight of the eggs did not change during the incubation and the egg size had a positive effect on the alevin size.

The positive effect of female size on fecundity has been shown previously in wild and

hatchery-reared Atlantic salmon (Thorpe *et al.* 1984, Brännäs *et al.* 1985, Kallio 1986, Eskelinen and Ruohonen 1989, Erkinaro *et al.* 1997), in other salmonid species in many studies (Bagenal 1969, Beacham and Murray 1985, Ojanguren *et al.* 1996, Lobon-Cervia *et al.* 1997, Morita *et al.* 1999, Olofsson and Mosegaard 1999) as well as in this study.

Although the positive correlation between female size and egg size has been reported in many previous studies in wild Atlantic salmon (Kazakov 1981, Thorpe *et al.* 1984, Brännäs *et al.* 1985, Kallio 1986), brown trout (*Salmo trutta* L.) (Ojanguren *et al.* 1996, Lobon-Cervia *et al.* 1997, Lahnsteiner *et al.* 1999, Olofsson and Mosegaard 1999), *Oncorhynchus* species (Beacham and Murray 1985) and *Salvelinus* species (Morita *et al.* 1999) many other things also influence the egg size. They are age and physiological condition of a female, as well as the time of spawning and arrangement of ova in the ovaries, amongst others (Kazakov 1981). However, in this study there were no size differences between eggs taken at the beginning, middle or the end of the stripping. Reasons for poor correlation between the female and egg sizes observed in this study could be a result of the relatively large size of the multi-sea-winter females and complicated age structure of the River Teno salmon (*see also Niemelä et al.* 2000). Both the river-age and sea-age of salmon have a positive effect on the egg size (Kazakov 1981, Thorpe *et al.* 1984). Unfortunately, due to the small sample size of the River Teno salmon females they could not be divided into different age groups.

When the egg size increases, the relative fecundity has been reported to decrease, either with female size (Kallio 1986, Lobon-Cervia *et al.* 1997) or with female age (Belding 1940, Baum and Meister 1971). In our material from the River Teno, the relative fecundity of the salmon was uninfluenced by the female size, probably due to a weak correlation between female size and egg size. Also the GSI of the River Teno salmon was independent of the female size as has been reported for the Baltic salmon (Kallio 1986).

The effect of female size on the egg and alevin quality has been measured in different ways in earlier studies. Ojanguren *et al.* (1996)

reported a positive relationship between egg dry weight and female size and Beacham and Murray (1985) found a positive relationship between the female size and the egg yolk reserves of alevins. The egg quality of the River Teno salmon was judged by their energy content as was suggested by Srivastava and Brown (1991). The large females of the River Teno salmon produced eggs that had higher energy content than the small ones. This result is in accordance with the results of the studies cited above.

In brown trout, high egg viability ($\geq 80\%$) during incubation has been associated with an increase in egg wet weight by $\geq 13\%$ during swelling (Lahnsteiner *et al.* 1999). The energy and water contents of the unfertilized eggs of the River Teno salmon were inversely related to each other and the water content increase during swelling was inversely related to the water content of the unfertilized eggs. So, the energy content of an egg and increase in its wet weight are correlated with each other and are both indicators of good egg quality which could also be seen in this study as low mortality of the embryos during incubation to the eyed stage.

Positive correlation between the embryo mortality and the egg size has been observed in earlier studies (Flower 1972, Beacham and Murray 1985) as well as in this study. It has been argued that large eggs can be more sensitive to water oxygen deficiencies than smaller ones because of their smaller surface-to-volume ratio (Beacham and Murray 1985). In the study of Einum *et al.* (2002), however, this hypothesis was refuted and it was found that embryos mortality decreased with increasing egg size (*see also Brännäs et al.* 1985). In this study, the results of embryo mortality during incubation in 1994–1998 were pooled and the increased variation in embryo mortality related to egg size may have been more dependent on year than the egg size.

During incubation, the yolk is used for embryo development and metabolism (Hansen and Møller 1985, Srivastava and Brown 1991). The energy content of the eggs decreased during the incubation (*see also Srivastava and Brown 1991*) but the wet weight of the eggs remained the same in the River Teno salmon. The positive relationship between the egg size and the alevin size was observed in this study as well

as in many previous studies on Atlantic salmon (Kazakov 1981, Thorpe *et al.* 1984), brown trout (Ojanguren *et al.* 1996, Olofsson and Mosegaard 1999) and Pacific salmon (Beacham and Murray 1985, 1990). Moreover, it has been observed that the size of newly hatched alevins is positively related to the energy content of the eggs (Srivastava and Brown 1991).

Benefit of the body size was not only quantitative but also qualitative in reproduction success of the River Teno salmon. Total number of eggs was higher in large females than in smaller ones but when the number of eggs was related to the body weight there was no difference amongst females of different sizes. Instead of producing more eggs per unit of body weight, large females invest more in the egg quality (energy content of eggs) than small females. Overall, the quality of eggs of the River Teno salmon females was good, which is typical of the wild Atlantic salmon (*see also* Srivastava and Brown 1991).

Acknowledgements: We thank the Finnish Game and Fisheries Institute for giving the possibility to collect this research material. We also thank J. Guttorm and M. Ikonen for collecting the brood fishes and for taking good care of them during maintenance, the personnel of Inari hatchery for taking care of the eggs during incubation, J. Haantie for the age analyses of the fish, L. Kytömaa for energy content analyses, M. Julkunen for statistical advice, A. Soivio and J. Erkinaro for reviewing the manuscript, and the Foundation for Research of Natural Resources in Finland for financial support to the corresponding author.

References

- Alm G. 1959. Connection between maturity, size and age in fishes. *Rep. Inst. Freshw. Res. Drottningholm* 40: 5–145.
- Bagenal T.B. 1969. The relationship between food supply and fecundity in brown trout *Salmo trutta* L. *J. Fish Biol.* 1: 167–182.
- Baum E.T. & Meister A.L. 1971. Fecundity of Atlantic salmon (*Salmo salar*) from two Maine rivers. *J. Fish. Res. Bd. Canada* 28: 764–767.
- Beacham T.D. & Murray C.B. 1985. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. *Can. J. Fish. Aquat. Sci.* 42: 1755–1765.
- Beacham T.D. & Murray C.B. 1990. Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. *Trans. Am. Fish. Soc.* 119: 927–945.
- Belding D.L. 1940. The number of eggs and pyloric appendages as criteria of river varieties of the Atlantic salmon. *Trans. Am. Fish. Soc.* 67: 285–289.
- Brännäs E., Brännäs K. & Eriksson L.-O. 1985. Egg characteristics and hatchery survival in a Baltic salmon, *Salmo salar* L., population. *Rept. Inst. Freshw. Res. Drottningholm* 62: 5–11.
- Einum S. & Fleming I.A. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. *Proc. R. Soc. Lond. B* 266: 2095–2100.
- Einum S. & Fleming I.A. 2000a. Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature* 405: 565–566.
- Einum S. & Fleming I.A. 2000b. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution* 54(2): 628–639.
- Eimum S., Hendry A.P. & Fleming I.A. 2002. Egg-size evolution in aquatic environments: does oxygen availability constrain size? *Proc. R. Soc. Lond. B* 269: 2325–2330.
- Elliott J.M. 1989. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. The critical time for survival. *J. Anim. Ecol.* 58: 987–1002.
- Englund V., Niemelä E., Lämsmä M. & Heino M. 1999. Variations in Atlantic salmon, *Salmo salar* L., smolt age in tributaries of the River Teno, Finland. *Fish Manage. Ecol.* 6: 83–86.
- Erkinaro J. & Niemelä E. 1995. Growth differences between the Atlantic salmon parr, *Salmo salar*, of nursery brooks and natal rivers in the River Teno watercourse in northern Finland. *Environ. Biol. Fish.* 42: 277–287.
- Erkinaro J., Dempson J.B., Julkunen M. & Niemelä E. 1997. Importance of ontogenetic habitat shifts to juvenile output and life history of Atlantic salmon in a large subarctic river: an approach based on analysis of scale characteristics. *J. Fish Biol.* 51: 1174–1185.
- Eskelinen U. & Ruohonen K. 1989. Reproduction parameters of hatchery-reared Atlantic salmon broodstocks and a model to optimize the rearing cycle. In: De Pauw N., Jaspers E., Ackefors H. & Wilkins N. (eds.), *Aquaculture – a biotechnology in progress*, European Aquaculture Society, Brendene, Belgium, pp. 507–516.
- Fleming I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Rev. Fish Biol. Fish.* 6: 379–416.
- Fowler L.G. 1972. Growth and mortality of fingerling chinook salmon as affected by egg size. *Prog. Fish-Cult.* 34: 66–69.
- Friedland K.D. 1998. Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. *Can. J. Fish. Aquat. Sci.* 55(Suppl. 1): 119–130.
- Friedland K.D. & Haas R.E. 1996. Marine post-smolt growth and age at maturity of Atlantic salmon. *J. Fish Biol.* 48: 1–15.
- Gjerde B. 1984. Response to individual selection for age at sexual maturity in Atlantic salmon. *Aquaculture* 38: 229–240.
- Hansen T.J. & Møller D. 1985. Yolk absorption, yolk sac constrictions, mortality, and growth during first feeding of Atlantic salmon (*Salmo salar*) incubated on Astro turf. *Can. J. Fish. Aquat. Sci.* 42: 1073–1078.

- Heath D.D., Hearsh J.W., Bryden C.A., Johnson R.M. & Fox C.W. 2003. Rapid evolution of egg size in captive salmon. *Science* 299: 1738–1740.
- Hutchings J.A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout, *Salvelinus fontinalis*. *Evolution* 45: 1162–1168.
- Hutchings J.A. & Jones M.E.B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.* 55(Suppl. 1): 22–47.
- Jonsson N., Hansen L.P. & Jonsson B. 1991. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. *J. Anim. Ecol.* 60: 937–947.
- Kallio I. 1986. Istutettujen ja luonnonkudusta peräisin olevien emolohien (*Salmo salar* L.) fekunditeetti ja mätimunan koko. *Riista- ja kalatalouden tutkimuslaitos, kalantutkimusosasto. Monistettu julkaisu* 44: 53–74.
- Kazakov R.V. 1981. The effect of the size of Atlantic salmon, *Salmo salar* L., eggs on embryos and alevins. *J. Fish Biol.* 19: 353–360.
- L'Abée-Lund J.H. & Hindar K. 1990. Interpopulation variation in reproductive traits of anadromous female brown trout *Salmo trutta* L. *J. Fish Biol.* 37: 755–763.
- Lahnsteiner F., Weismann T. & Patzner R.A. 1999. Physiological and biochemical parameters for egg quality determination in lake trout, *Salmo trutta lacustris*. *Fish Physiol. Biochem.* 20: 375–388.
- Lobon-Cervia J., Utrilla C.G., Rincón P.A. & Amezcua F. 1997. Environmentally induced spatio-temporal variations in the fecundity of brown trout *Salmo trutta* L.: tradeoffs between egg size and number. *Freshwater Biology* 38: 277–288.
- Morita K., Yamamoto S., Takashima Y., Matsuishi T., Kanno Y. & Nishimura K. 1999. Effect of maternal growth history on egg number and size in wild white-spotted char (*Salvelinus leucomaenis*). *Can. J. Fish. Aquat. Sci.* 56: 1585–1589.
- Niemelä E., Moen K., Kärki P. & Länsman M. 1996. Tenojoen vesistöalueen kalastus- ja saalistilastot vuodesta 1972 vuoteen 1995 Suomessa ja Norjassa. *Kala- ja riistataraportteja* nro 60.
- Niemelä E., Mäkinen T.S., Moen K., Hassinen E., Erkinaro J., Länsman M. & Julkunen M. 2000. Age, sex ratio and timing of the catch of kelts and ascending Atlantic salmon in the subarctic River Teno. *J. Fish Biol.* 56: 974–985. doi: 10.1006/jfbi.1999.1223.
- Ojanguren A.F., Reyes-Gavilán F.G. & Braña F. 1996. Effects of egg size on offspring development and fitness in brown trout, *Salmo trutta* L. *Aquaculture* 147: 9–20.
- Olofsson H. & Mosegaard H. 1999. Larger eggs in resident brown trout living in sympatry with anadromous brown trout. *Ecol. Freshwater Fish* 8: 59–64.
- Parrish D.L., Behnke R.J., Gephard S.R., McCormick S.D. & Reeves G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Can. J. Fish. Aquat. Sci.* 55(Suppl. 1): 281–287.
- Power G. 1981. Stock characteristics and catches of Atlantic salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in relation to environmental variables. *Can. J. Fish. Aquat. Sci.* 38: 1601–1611.
- Randall R.G., Thorpe J.E., Gibson R.J. & Reddin D.G. 1986. Biological factors affecting age at maturity in Atlantic salmon (*Salmo salar*). *Can. Spec. Publ. Fish. Aquat. Sci.* 89: 90–96.
- Salminen M. 1997. Relationships between smolt size, post-smolt growth and sea age at maturity in Atlantic salmon reared in the Baltic Sea. *J. App. Ichthyol.* 13: 121–130.
- Shearer K.D., Åsgård T., Andorsdóttir G. & Aas G.H. 1994. Whole body elemental and proximate composition of Atlantic salmon (*Salmo salar*) during the life cycle. *J. Fish Biol.* 44: 785–797.
- Srivastava R.K. & Brown J.A. 1991. The biochemical characteristics and hatching performance of cultured and wild Atlantic salmon (*Salmo salar*) eggs. *Can. J. Zool.* 69: 2436–2441.
- Thorpe J.E. & Mitchell K.A. 1981. Stocks of Atlantic salmon *Salmo salar* L. in Britain and Ireland: discreteness and current management. *Can. J. Fish. Aquat. Sci.* 38: 1576–1590.
- Thorpe J.E., Morgan R.I.G., Talbot C. & Miles M.S. 1983. Inheritance of developmental rates in Atlantic salmon, *Salmo salar* L. *Aquaculture* 33: 119–128.
- Thorpe J.E., Miles M.S. & Keay D.S. 1984. Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. *Aquaculture* 43: 289–305.
- Wootton R.J. 1990. *Ecology of teleost fishes*. London: Chapman & Hall.

Received 14 May 2002, accepted 3 November 2003