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Influence of parental life history on maturation and smoltification in brown trout (*Salmo trutta* L.)

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Abstract. The developmental pathways of the offspring of three groups of trout, *Salmo trutta* L., with known life histories were compared: one group from a freshwater resident population and two groups from an anadromous population (fish that have smoltified and fish that have not). The fish were hybridized within a group, and 27 families were obtained and reared mixed in two tanks. Tracking fish specimens was possible thanks to individual passive integrated transponder (PIT) tagging. All families followed different life pathways. Faster growth favored early smoltification and maturation at the age of 1+ in males that had not smoltified. In addition, both processes were clearly also influenced by inherited factors. Fish of freshwater resident origin smoltified more infrequently, and males matured earlier than did fish from the migratory population. The offspring of parents from the migratory population, which did smoltify during their individual histories, smoltified early (in the second year) more often than offspring of non-smoltified members of the population.

Keywords: salmonids, developmental path, inheritance, anadromy

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Introduction

Brown trout, *Salmo trutta* L. exhibit both anadromous and non-migratory biological lifestyles (e.g., Elliott 1994, Klemetsen et al. 2003, Cucherousset et al. 2005). They are often in close relationships, which means that when they occur together there is substantial gene flow among them (Charles et al. 2006), and this renders them genetically indistinguishable (Hindar et al. 1991, Pettersson et al. 2001 Charles et al. 2005, Heath et al. 2008). Genetic differences have been noted among generatively isolated populations (Hindar et al. 1991, Jonsson 1982, Pettersson et al. 2001). It was observed that some freshwater resident populations could produce migratory offspring (Rounsefell 1958, Skrochowska 1969a, Kallio-Nyberg et al. 2010), and transferring non-migratory fish to the sea evokes in them behaviors that are typical of anadromous forms (Skrochowska 1969a). It has also been observed that during trout introduction one form often gives rise to the second (Frost and Brown 1967, Ayllón et al. 2006). Fish from various anadromous populations can have very different life histories, and they differ in maturation age and smoltification (Fahy 1978, L'Abee-Lund et al. 1989). Many different life histories can occur even within a single population (Jonsson 1985), and this can influence the success of undertakings such as stocking material production.

Table 1
Characteristics of spawners used in the experiment. Sea trout-like (S) – sea trout that smoltified at the age of 1+ and matured at ages 2+ (males) or 3+ (females); brown trout-like (B) – sea trout which did not smoltify and matured at ages 1+ (males) or 3+ (females); and non-anadromous trout (R)

Fish type	Sex	Fish's number	Smolt 1yr	Smolt 2yr	Age of maturity	Caudal length (mm)	Weight (g)
S	F	1	yes	no	3+	502	1380
	F	2	yes	no	3+	500	1466
	F	3	yes	no	3+	477	1276
	M	1	yes	no	2+	488	1402
	M	2	yes	no	2+	544	1350
	M	3	yes	no	2+	520	1616
B	F	1	no	no	3+	473	1244
	F	2	no	no	3+	467	1254
	F	3	no	no	3+	465	1184
	M	1	no	no	1+	509	1504
	M	2	no	no	1+	554	1820
	M	3	no	no	1+	515	1740
R	F	1				510	1716
	F	2				510	1726
	F	3				470	1422
	M	1				490	1344
	M	2				520	1742
	M	3				480	1460

This is particularly apparent when there is no smoltification, which is the developmental path of non-migratory forms (Dębowski 2002). The question remains of whether differentiation is determined exclusively by disproportional access to environmental resources stemming from the heterogeneity of the fish and/or differences in their social status, or if other factors, such as inherited characters, can also have an influence. Studies performed on other anadromous salmonids, mainly salmon, *Salmo salar* L., indicate that the developmental path of parents, particularly the age at maturation, influence the choice of the developmental path in the young (Thorpe and Morgan 1978, 1980, Nævdal 1983, Thorpe et al. 1983, Bailey and Friars 1990, Herbinger and Newkirk 1990, Pineda et al. 2003, Duston et al. 2005, Paez et al. 2010, 2011). There is also some evidence for this in studies of sea trout (Skrochowska 1969b, Jonsson 1982, Näslund 1993, Palm and Ryman 1999, Cucherousset et al. 2005).

The aim of the current study was to test the effect of parental phenotype on the age of maturation and smoltification in trout from a migratory population in comparison with trout from a freshwater resident population in controlled conditions in a hatchery.

Material and methods

Comparisons were made of the progeny of selected parent fish that were reared under the same conditions: two groups of trout from an anadromous population (sea trout), with different individual life histories, and a group of trout from a non-anadromous population, but with a life history similar to that of one the sea trout groups. Sea trout

Table 2
The 27 families of progeny created in the experiment: fish type, sex, and fish's number are adapted from Table 1

SF1 x SM1	BF1 x BM1	RF1 x RM1
SF1 x SM2	BF1 x BM2	RF1 x RM2
SF1 x SM3	BF1 x BM3	RF1 x RM3
SF2 x SM1	BF2 x BM1	RF2 x RM1
SF2 x SM2	BF2 x BM2	RF2 x RM2
SF2 x SM3	BF2 x BM3	RF2 x RM3
SF3 x SM1	BF3 x BM1	RF3 x RM1
SF3 x SM2	BF3 x BM2	RF3 x RM2
SF3 x SM3	BF3 x BM3	RF3 x RM3

parents, kept in ponds, were derived from sea-run fish caught in the lower Vistula River (18.9518° E, 54.3583° N) during their spawning migration. They were tagged with PITs (Passive Integrated Transponder) at the age of 0+ and their development, including smoltification and maturation, was followed until the age of 6+ (*i.e.* for use in the present experiment) (Dębowski 2002). For the sake of comparison, non-anadromous parents were also observed, and these fish are also held in the ponds and were the progeny of fish from a local population in the Radunia River (18.3394° E, 54.3334° N), which is a tributary of the lower Vistula that has been inaccessible to migratory trout for over a century. Their age and life history are unknown. Three males and three females were chosen from each of three groups of fish: sea trout-like (S) – sea trout that smoltified at the age of 1+ and matured at ages 2+ (males) or 3+ (females); brown trout-like (B) – sea trout which did not smoltify and matured at ages 1+ (males) or 3+ (females); and non-anadromous trout (R). The characteristics of the spawners are presented in Table 1. The experiment was conducted at the Department of Salmonid Research in Rutki, Inland Fisheries Institute in Olsztyn, Poland.

Artificial spawning was performed on November 14, 2001. Within each of the three groups, a 3×3 factorial mating design created nine families, for a total of 27 families (Table 2). They were incubated separately. After the eyed-egg stage was reached, 300 eggs were retained from each family. In the subsequent May, 200 fry from each family were stocked into separate tanks with volumes of 1 m^3 that were supplied with the river water and kept under natural light conditions. In January 2003, all of the surviving fish (2,023 individuals) were tagged with PITs. Each of the families that had been held separately up to this point were randomly divided in half and transferred to two large tanks with volumes of 9 m^3, which constituted the two replicates of the experiment.

The fish were examined in the spring (March-May) three times because of the differentiation and duration of the smoltification periods. The examinations included measurements of caudal length, height, weight, and silvering (Kazakov and Kozlov 1985). The degree of smoltification was determined with these data using methodology based on silvering and caudal length (Dębowski et al. 1999). The fish were classified as smolts if they exhibited smolt characteristics during at least one of the examinations. The fish were examined again in the fall (November/December), and in addition to measurements, the sexual maturity of the fish was evaluated. This same procedure was applied in subsequent years. The fish were monitored until the fall when they reached an age of 3+. The sex of the fish was determined when they achieved sexual maturity, so the sex of the fish that died before maturity is

Table 3
Smoltification in the first year. Percentage of smolts and mean (±SD) caudal length of fish in parental groups, and parameters of generalized linear model of influence of length (L), parental group R (resident population) in relation to B (anadromous population – non-smoltified fish)(R-B) and S (anadromous population – smoltified fish) in relation to B (S-B) in two replicates (tanks) and both sexes separately. Lengths (L) sharing the same letter in categories are not significantly different (P≥0.05)

					Model parameters (confidence interval)				
Category	Parental group	n	Smolts (%)	Length (mm)	B_0	L	R-B	S-B	Chi^2/df
Tank 1	R	304	21	$113±17^A$	-19.771	0.158	-0.627	0.839	
	S	257	31	$109±18^A$	(-22.697; -16.845)	(0.134; 0.182)	(-0.944; -0.311)	(0.521; 1.157)	0.673
	B	281	23	$111±17^A$	P<0.001	P< 0.001	P< 0.001	P< 0.001	
Tank 2	R	298	28	$114±17^A$	-14.541	0.120	-0.665	0.574	
	S	262	38	$110±17^B$	(-16.572; -12.509)	(0.103; 0.137)	(-0.939; -0.392)	(0.304; 0.843)	0.833
	B	266	33	$110±17^B$	P<0.001	P <0.001	P< 0.001	P< 0.001	
Females	R	182	33	$114±16^A$	-18.674	0.155	-0.409	0.613	
	S	91	47	$115±16^A$	(-22.623; -14.730)	(0.122; 0.188)	(-0.808; -0.010)	(0.151; 1.075)	0.771
	B	84	38	$116±16^A$	P< 0.001	P <0.001	P< 0.001	P< 0.001	
Males	R	206	17	$114±15^A$	-17.302	0.139	-1.304	0.989	
	S	145	35	$110±16^B$	(-20.662; -13.942)	(0.111; 0.167)	(-1.729; -0.879)	(0.570; 1.408)	0.662
	B	110	36	$115±17^A$	P< 0.001	P< 0.001	P< 0.001	P< 0.001	

Table 4
Maturation of 1+ males that did not smoltify the previous spring. Percentage of mature fish and mean (±SD) caudal length of fish in parental groups, and parameters of generalized linear model of influence of length (L), parental group R (resident population) in relation to B (anadromous population – not smoltified fish)(R-B) and S (anadromous population – smoltified fish) in relation to B (S-B) in two replicates (tanks). Lengths (L) sharing the same letter in categories are not significantly different (P≥0.05)

					Model parameters (confidence interval)				
Category	Parental group	n	Matured (%)	Length (mm)	B_0	L	R-B	S-B	Chi2/df
Tank 1	R	83	63	$229±17^A$	-7.979	0.033	1.087	0.047	
	S	35	29	$212±21^B$	(-12.794; -3.163)	(0.011; 0.054)	(0.569; 1.605)	(-0.602; 0.695)	1.165
	B	31	16	$224±21^A$	P<0.002	P<0.003	P<0.001	P>0.887	
Tank 2	R	89	70	$243±21^A$	-7.625	0.031	0.959	0.064	
	S	59	41	$230±23^B$	(-11.355; -3.896)	(0.016; 0.047)	(0.508; 1.411)	(-0.431; 0.558)	1.177
	B	35	26	$237±27^A$	P <0.001	P<0.001	P<0.001	P>0.800	

unknown, and the numbers of fish in tanks are higher than the sums of males and females. Smolts were excluded from the following analysis to mimic the natural situation in which smolts migrate to the sea.

Average lengths were compared with ANOVA. Generalized linear models were used to analyze parental influence and fish growth, and the dependent variables were binomial ("smolt/not smolt" or "mature/not mature"), and independent variables were nominal (parental groups) and continuous (length). Each nominal variable had three categories, so it was represented in the model by two factors in relation to group B (in all models). The link function of the models was logit. Statistica (StatSoft Inc. 2005) was used to perform the analysis.

Results

Smoltification in the first year

In both tanks, the fish from group R were bigger than those from the other groups; however, the difference was only significant in tank 2 (Table 3). A total of 29% of all fish smoltified in the first year (38% of females and 27% of males), and the proportions were the highest for the S groups. The models show that the probability of smoltification increased with the length of the fish and with origin from group S, and decreases when the fish originated from group R. All these relationships were highly significant in both tanks and in both sexes, but they seemed to be stronger in males than in females.

Maturation at age 1+

Only males matured at this age, with a total of 49% of them doing so. In both tanks, fish from group S were smaller than those from the other groups (Table 4). In addition, in both tanks the probability of maturation increased with the length of the fish and with those belonging to group R.

Smoltification in the second year

Males that had matured at age 1+ did not smoltify in the subsequent spring and were excluded from this analysis. A total of 52% of fish, which thus far had not smoltified or matured, smoltified in the second year (53% of females and 50% of males). Fish from group S were generally smaller (Table 5). The probability of smoltification decreased with the length of the fish and among those in group R. The probability of smoltification increased in the fish in group S in both tanks and among both sexes (the last relationship was not significant in tank 1 or in males).

First maturation at age 2+

Among the immature fish, all of the males matured as did 95% of the females in the third year of life (Table 6).

Discussion

A relationship between smoltification age and fish size has been noted repeatedly in salmon (e.g., Thorpe 1977, Thorpe and Morgan, 1980, Thorpe et al. 1982, Nicieza et al. 1991) and in trout (Bohlin et al. 1994, Tanguy et al. 1994, Dębowski 2002). This was confirmed in relation to both sexes: the probability of smoltification at the age of 1+ increased with fish length. Based on the analysis performed for this study, the origin of the fish was identified as a significant factor. Smoltification occurred both in fish from either residential or anadromous populations. There was a relatively smaller number of smolts in the former group, whereas in the latter there were more smolts among the offspring of smoltified fish, i.e., fish that followed an anadromous life cycle. In addition, this applied to both females and males, although the effect of origin was stronger in males. Thus, we can conclude that the probability of early smoltification is heritable both for population and parental life history.

Table 5
Smoltification in the second year of fish that had not matured or smoltified previously. Percentage of smolts and mean (±SD) caudal length of fish in parental groups, and parameters of generalized linear model of influence of length (L), parental group R (resident population) in relation to B (anadromous population – non-smoltified fish)(R-B) and S (anadromous population – smoltified fish) in relation to B (S-B) in two replicates (tanks) and both sexes separately. Lengths (L) sharing the same letter in categories are not significantly different ($P \geq 0.05$)

					Model parameters (confidence interval)				
Category	Parental group	n	Smolts (%)	Length (mm)	B_0	L	R-B	S-B	Chi^2/df
Tank 1	R	94	33	239 ± 20^A	7.500	-0.029	-1.228	0.091	
	S	46	72	224 ± 20^B	(3.326; 11.675)	(-0.047; -0.012)	(-1.682; -0.775)	(-0.462; 0.643)	1.124
	B	46	83	236 ± 22^A	P<0.001	P<0.001	P<0.001	P>0.747	
Tank 2	R	86	16	249 ± 22^A	7.122	-0.028	-1.830	0.690	
	S	62	73	238 ± 25^B	(3.460; 10.784)	(-0.043; -0.014)	(-2.326; -1.335)	(0.205; 1.175)	0.917
	B	59	73	252 ± 27^A	P<0.001	P<0.001	P<0.001	P<0.006	
Females	R	122	29	243 ± 24^A	7.483	-0.028	-1.774	0.596	
	S	48	81	235 ± 26^B	(3.815; 11.152)	(-0.042; -0.013)	(-2.245; -1.303)	(0.013; 1.178)	0.994
	B	52	85	247 ± 26^A	P<0.001	P<0.001	P<0.001	P<0.046	
Males	R	57	16	245 ± 20^A	9.071	-0.038	-1.592	0.373	
	S	60	65	230 ± 22^B	(4.727; 13.414)	(-0.056; -0.020)	(-2.166; -1.019)	(-0.143; 0.889)	1.006
	B	53	70	244 ± 26^A	P<0.001	P<0.001	P<0.001	P>0.156	

Table 6
Maturation of 2+ fish that had not matured or smoltified previously. Percentage of mature fish and mean (±SD) caudal length of fish in parental groups, in two replicates (tanks) and the sexes separately

Category	Parental group	n	Matured (%)	Length (mm)
Tank 1	R	63	98	239 ± 20^{A}
	S	13	100	224 ± 20^{B}
	B	8	100	236 ± 22^{A}
Tank 2	R	72	99	249 ± 22^{A}
	S	17	88	238 ± 25^{B}
	B	16	94	252 ± 27^{A}
Females	R	87	98	243 ± 24^{A}
	S	9	78	235 ± 26^{B}
	B	8	88	247 ± 26^{A}
Males	R	48	100	245 ± 20^{A}
	S	21	100	230 ± 22^{B}
	B	16	100	244 ± 26^{A}

Lengths (L) sharing the same letter in categories are not significantly different ($P \geq 0.05$)

In studies of salmon smoltification age, differences have often been found among populations (Refstie et al. 1977, Bailey and Friars 1990), and in some stationary populations smoltification did not occur at all (Birt et al. 1991). A similar pattern was observed in trout; stationary populations did not produce any smolts (Tanguy et al. 1994), or they produced smaller numbers compared to anadromous populations (Jonsson 1982). However, in some cases no such differences have been reported (Kallio-Nyberg et al. 2010). Views on the heritability of the tendency smoltify in the first year of life are divided. According to Refstie et al. (1977) and Thorpe and Morgan (1978), both salmon parents determine heritability; the first authors reported a stronger effect of mothers, the latter of fathers, while Paez et al. (2011) report only the effect of fathers. No information on this subject has been found in the literature available that is either related to the sexes or to trout.

Maturation at the parr stage, without anadromous migration, is an alternative male strategy in many migratory salmonid fish species (e.g., Thorpe 1989, 1990). This phenomenon has often been studied because of its significance to commercial fish farming, in particular for salmon (e.g., Nævdal 1983, Hansen et al. 1989). This is clearly associated with the growth of fish, for example, faster growing male salmon (e.g., Saunders et al. 1982, Rowe and Thorpe 1990, Berglund 1995) and trout (Dellefors and Faremo 1988, L'Abee-Lund et al. 1990, Dębowski 2002) mature earlier. High percentages of trout males can mature at the age of 1+, on average 57% according to Dellefors and Faremo (1988), from 6 to 60% according to L'Abee-Lund et al. (1990), 43 and 56% according to Dębowski (2002), and from 16 to 83% according to the experiment described in this paper. Piche et al. (2008) report that the size threshold of salmon parr maturation varies in different populations and is heritable. Differences in the maturation age among different populations transferred to one environment have also been observed in trout (Palm and Ryman 1999). According to Birt et al. (1991), salmon male parr maturation is a genetic trait of stationary fish populations. In this experiment, the effect of male length on maturation was not particularly strong, but it was statistically significant. Many more males matured at the age of 1+ among fish from the stationary population, while there was no such difference among fish from the anadromous population with different parental life histories.

There are no data available in the literature that indicate clearly the effect of trout male maturation age on that of their progeny, whereas this kind of correlation is repeatedly found with regard to Atlantic salmon (Thorpe et al. 1983, Kallio-Nyberg and Koljonen 1997, Duston et al. 2005, Kallio-Nyberg et al. 2007) and in Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum) (Heath et al. 1994).

Male maturation precluded smoltification. A similar phenomenon was observed by other researchers in trout (Skrochowska 1969b, Dellefors and Faremo 1988, Dębowski 2002). This relationship is not so clear in salmon. According to Hansen et al. (1989) and Whalen and Parrish (1998), maturation reduces the chances of subsequent smoltification, but, for example, Mitans (1973) reports that almost all mature parr salmon migrate to the sea in the following spring. Among fish that did not smoltify the previous spring or did not mature in fall, greater length decreased the chance of smoltification at the age of 2+. This relationship, which was weak but highly significant, was found in both males and females in both replicates. The probability of smoltification in both sexes significantly decreased in fish from the stationary population; the influence of parental life history within the migratory population was weak.

The current experiments confirmed that trout growth influences both maturation and smoltification, with faster growth favoring early smoltification and maturation at the age of 1+ in males that did not smoltify. In addition, both processes were also clearly influenced by inherited factors. Freshwater fish of resident origin smoltified more infrequently, and males matured earlier than fish from the migratory population. Offspring of parents from the migratory population, which did smoltify during their individual history, smoltified in the second year more often than did offspring of non-smoltified members of the population.

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