Life history traits of sea trout in two Icelandic rivers

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ABSTRACT
Smolt age, smolt size, number of sea sojourns, longevity, sexual maturation, growth in fresh and sea water were explored in two Icelandic stocks of sea trout. Better juvenile growth was observed in the river Grenlækur stock than the river Leirvogsá stock, especially during the last year in fresh water. It is suggested that this difference may be caused by the behaviour of the juveniles in Grenlækur which at this time migrate to more favourable feeding grounds in the lower reaches of the river where competition is less pronounced. After their third seaward migration 69.6% of the Grenlækur population was sexually mature against 40.0% of the Leirvogsá population, possibly as a consequence of bigger smolt in the River Grenlækur. The longevity of the Grenlækur sea trout was 7.7 years for males and 8.5 years for females compared to 7.8 years for males and 7.3 years for females in the Leirvogsá. The study demonstrates well how local conditions affect productivity of salmonid juveniles, reflected in the spring-fed influence in the Grenlækur and diverse habitat whereas the Leirvogsá is mainly a run-off river with more uniform habitat.

Keywords: age at maturity, growth, migration, repeated spawning, smolt

YFIRLIT
Lífssögulegir þættir hjá sjóbirtingi í tveimur íslenskum ám
Aldur gönguseiða, stærð þeirra, fjöldi ferða til sjávar, langlífi, kynþroski, vöxtur í ferskvatni og sjó voru rannsakaðir hjá tveimur íslenskum sjóbirtingsstofnum. Vöxtur seiða í ferskvatni reyndist mun meiri í Grenlæk heldur en í Leirvogsá, sérstaklega síðasta árið í ferskvatni. Þessi munur kann að skýrast af atferli seiða í Grenlæk en þau ganga árið fyrir sjávargöngu niður á neðri svæði lækjarins þar sem fæðuskilyrði eru hagstæðari heldur en ofar í ánni auk minni samkeppni, sem seiði í Leirvogsá gera ekki. Eftir þriðju sjávargöngu var 69,6% af Grenlækjarstofninum orðinn kynþroska en 40,0% af Leirvogsárstofninum, en þennan mun má líklega rekja til stærri gönguseiða í Grenlæk. Langlífi sjóbirtingsins í Grenlæk var 7,7 ár hjá hængum en 8,5 ár hjá hrygnum en samsvarandi í Leirvogsá 7,8 ár hjá hængum og 7,3 ár hjá hrygnum. Niðurstöður þessarar rannsóknar undirstrika hvernig aðstæður og umhverfi á hverjum stað geta haft áhrif á seiðaframleiðslu í ánum sem endurspeglast í því að Grenlækur er lindá með fjölbreyttari búsvæðum en Leirvogsá er dragá og einsleitari búsvæði fyrir urriðaseiði.

INTRODUCTION

Differences in life history among salmonids are clearly reflected in their ecology. This can for instance be seen in phenotypic plasticity such as the development of fully freshwater resident forms to anadromous populations dwelling 1-5 years in the sea before returning to their spawning grounds in fresh water (Klemetsen et al. 2003).

A great variability exists in the life history and survival of brown trout (*Salmo trutta* L.), which is heavily affected by environmental conditions (Elliott 1994, Klemetsen et al. 2003, Harris & Milner 2006, Jonsson & Jonsson 2009a). The species spawns in late autumn in the rivers and tributaries to lakes which serve as nursery areas for the juveniles. In rivers trout parr prefer stony bottoms but are also found on fine grained substratum like sand, silt and mud. The larger trout have increasing preferences for deep, slow stream areas (Heggenes et al. 1999). Habitat selection is generally seen as the result of a trade-off between potential energy intake and risk, and variation in these two factors causes individual variation in survival, growth and reproductive success (Heggenes et al. 1999, Heggenes & Saltveit 2007).

In anadromous brown trout populations the parr smoltify in the spring and migrate to coastal waters where they feed during the summer. In late summer to autumn both immature and mature fish return to their home river and spend the winter in fresh water. These annual migrations are repeated each year throughout their lifespan (Jonsson & Jonsson 2009a).

Even though smolt emigration of sea trout is more dependent on body size than age (Bohlin et al. 1996), additional factors also influence smolt age and size. Økland et al. (1993) showed that smolt age was negatively correlated with parr growth and positively correlated with smolt size. L'Abée-Lund et al. (1989) studied 34 stocks of sea trout along the coastline of Norway and found that smolt age and size increased with higher latitude, whereas smolt age decreased with increased river and sea temperatures. The same relationship was observed by Jensen & Johnsen (1986) for smolts of Atlantic salmon (*Salmo salar* L.), i.e. smolts were generally older and larger at higher latitudes, probably because of climatic conditions (Metcalfe & Thorpe 1990). Considerable difference in smolt age was seen within a short latitudinal range in two stocks of Atlantic salmon in Iceland, living in different environmental and climatic conditions (Antonsson & Gudjonsson 2002). Hence, life history traits of brown trout are obviously flexible and respond to different environmental conditions, even on a relatively small spatial scale.

Growth in both fresh water and sea varies considerably among individuals and populations of anadromous brown trout (Klemetsen et al. 2003). Different growth rates in fresh water have been positively correlated with river temperature and length of the growing season in the rivers (L'Abée-Lund et al. 1989) and negatively with juvenile density (Elliott 1994, Jenkins et al. 1999) due to food competition and habitat availability. Both frequency of sea sojourn and growth at sea are different among stocks of sea trout. Data from 25 stocks of sea trout in Norwegian rivers show that mean length increment for each stock during the first summer at sea ranged from 94 – 204 (mm) and longevity from 4.7 to 11.1 years (Jonsson et al. 1991).

Timing of emigration to the sea and immigration to the river varies among stocks and age groups of sea trout. Over the range of the species geographical distribution, the time of downstream migrations of the first time migrants (smolts) takes place from March to June but second or multi-time migrants leave the river earlier in the spring. The general trend is that smolt of sea trout migrate earlier and younger at lower latitudes but later and older at higher latitudes (Klemetsen et al. 2003, Jonsson & Jonsson 2009b).

Knowledge of the life history of sea trout in Icelandic rivers is rather scarce, though information on catch data and stock sizes is fairly good (Guðbergsson 2010). Sea trout occur in all regions of Iceland but are most abundant in

South Iceland where they are the dominant salmonid fish in many rivers. In other parts of the country, either Atlantic salmon or Artic charr (*Salvelinus alpinus* L.) are the dominant species. Studies on sea trout have mostly been limited to juvenile studies in fresh water and counting of immigrants in some rivers. Gudjónsson (1993) studied sea trout smolts in a small river in south-western Iceland. The smolt migrated to sea in May and June and the migrants ranged in size from 8.4-20.7 cm with a mean size of 16.0 cm. Jóhannsson & Einarsson (1993) reported that the mean size of sea trout smolt was 25.3 cm and at age 3-4 years in the River Skaftá, south-eastern Iceland. The food of sea trout was analysed in a brackish lagoon in South Iceland. The main food items were sand eels (*Ammodytidae*), mysids and amphipods (Jóhannsson 1995). By tagging sea trout in the River Grenlækur with data storage tags, Sturlaugsson & Johannsson (1996 and 1998) reported that while dwelling in the sea the trout were feeding inshore and in the surface layers of the sea, usually in the uppermost 5 meters. Johannsson et al. (2001) studied migration behaviour of sea trout with an electronic fish counter in the same river. Migrations into the river were from the middle of June to the middle of October.

The objective of this study was to investigate and compare the life history traits between two populations of anadromous brown trout in Iceland. The study focused on smolt age, smolt size, number of sea sojourn, longevity, sexual maturation, growth in fresh and sea water. It is hypothesized that differences in environmental factors and behaviour can explain variability in life history traits between these two populations of sea trout.

MATERIALS AND METHODS

Study area

Sampling of data was conducted in two rivers, the Grenlækur and the Leirvogsá in south-eastern and south-western Iceland, respectively (Figure 1). The River Grenlækur is a spring-fed river and originates in the lava field Eldhraun but enters the sea at a sandy coastline

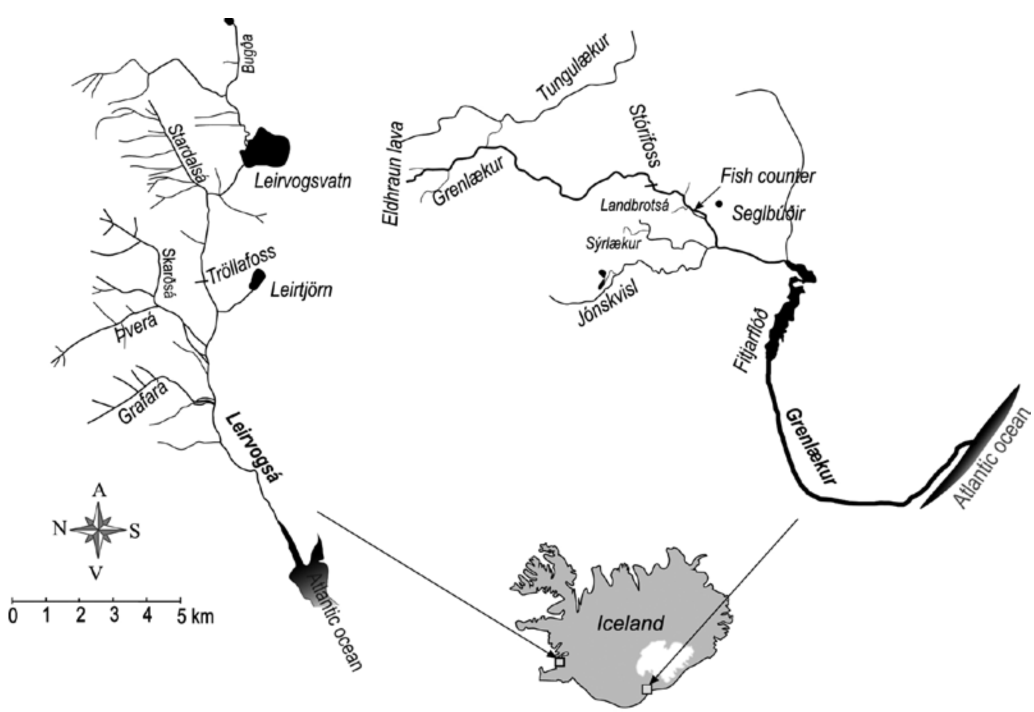

Figure 1. Location of the Icelandic study rivers.

(estuary: 63°38,966´N; 17°49,788´W). It is approximately 30 km long and is passable for migratory fish almost up to its origin. In the upper reaches of the Grenlækur the bottom habitat is characterized by rubble and boulders of lava, but is mostly sandy bottom in the lower reaches, where the water spreads out. In this part the river flows through the shallow lake, Fitjaflód. The catchment area of the river is of 22.2 km^2 and the average annual flow is 2.18 m^3 s^{-1} (Hróðmarsson 2010).

The River Leirvogsá (estuary: 64°10,881´N; 21°43,004´W) is characterized as a direct run-off river with a catchment area of 85 km^2 and an average annual flow of approximately 3.0 m^3 s^{-1}. It originates in Lake Leirvogsvatn and from small direct runoff tributaries in a mountainous area. The river is 18 km long and is passable for migrating fish up to the waterfall, Trollafoss, which is 8 km from the sea. Above the waterfall resident brown trout are present. Immediately below the waterfall the river bed is mainly bedrock but the bottom substrate in the main nursery area of the river consists mostly of gravel, rubble and boulders.

The River Grenlækur harbours two salmonid species, Arctic char and brown trout where the latter is the dominant species. The River Leirvogsá contains Atlantic salmon and brown trout where the Atlantic salmon is more abundant. In both rivers the brown trout is anadromous, i.e. sea trout. In addition to the salmonid species, three-spined sticklebacks (*Gasterosteus aculeatus* L.) and European eel (*Anguilla anguilla* L.) occur in both rivers. A new invader in Icelandic waters (Jónsson et al. 2001), flounder (*Platichthys flesus* L.), is found in the lower reaches of both these rivers.

Data sampling

In the last decade, monitoring programs have been conducted in both rivers. Electric fishing surveys are used to monitor density and growth of juvenile year-classes within the rivers. A single-pass electric fishing method was used as an index of juvenile densities (Arnason et al. 2005).

In both rivers adult fish are harvested in recreational (rod) fisheries. The rod catches are registered in logbooks (species, fish length, weight, sex and date of capture) (Guðbergsson 2010). In the River Leirvogsá an experienced fishing warden measures the fish and takes scale samples and through the years 2000-2009 they sampled 25-81 scale samples per year. In the River Grenlækur anglers collect the samples and through the years 1996-2004 they sampled 17-55 scale samples per year. Plastic imprints of the adult scales were used for determination of freshwater and sea age. Digital images of the scales were analysed and used to back-calculate the length between annuli (winter marks), both in the freshwater and seawater phase according to methods described in Heidarsson et al. (2006). If the marks were irregular or gaps were observed in the scales it was noted as a spawning mark (Figure 2). For calculations of the fish length after each year (end of the annulus) and length at smolting the Dahl-Lea equation was used (Francis 1990).

$L_i = L_c\,(S_i / S_c)$; *where:*
L_i *is the back-calculated length at annulus i*
L_c *is the fish length when captured*
S_i *is the length of the scale from the core to annulus i*
S_c *is the total scale radius (from the core to the edge)*

According to Jonsson et al. (1991) the longevity was defined as the age at the 90th percentile of the age distribution and we calculated the longevity for males and females separately for the sea trout stocks in Grenlækur and Leirvogsá. The body size was defined as the length at first maturity and calculated for both sexes separately.

Data analysis

The specific growth coefficient (G_L) was calculated using the equation

$G_L = (\ln length_2 - \ln length_1)\,\Delta t^{-1}$ (Wootton 1990)

where Δt is the interval of time and in this case it is a period of one year and therefore t = 1.

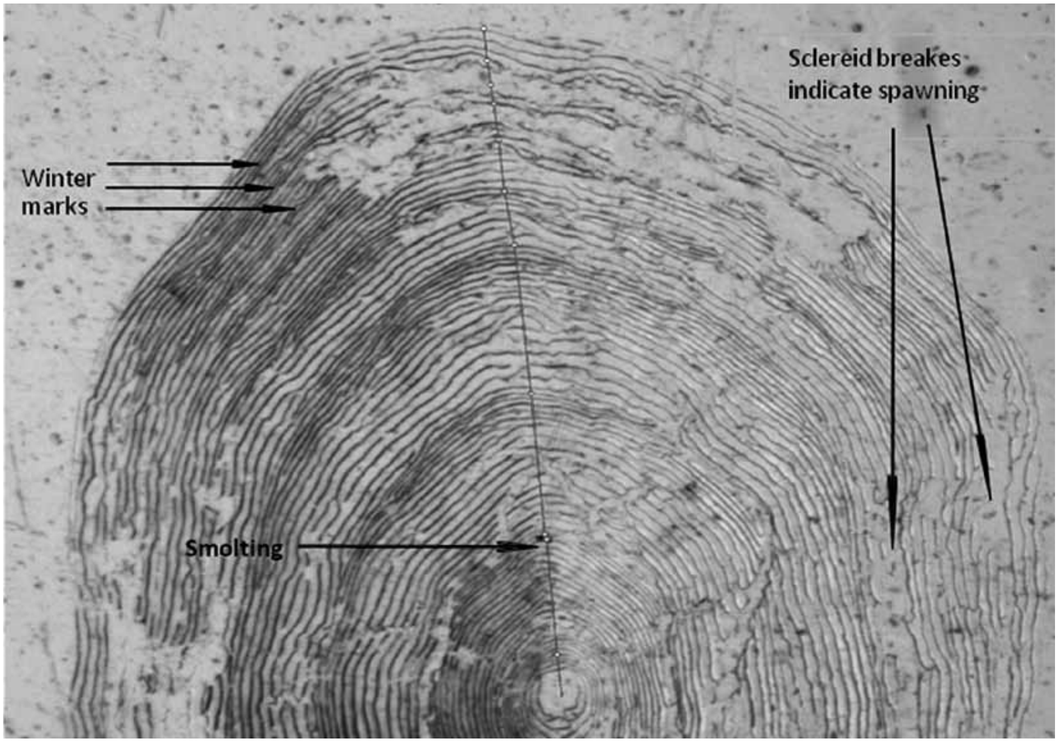

Figure 2. Scale sample of sea trout in the River Leirvogsá. The arrows points out the smolting mark, winter marks and spawning marks.

The difference in mean length in each year class between the rivers was tested separately for all year classes by independent t-test samples and to explore the difference in length increment after each sea sojourn of mature and immature sea trout from both rivers. We also used a t-test to compare the mean length between sexes after their maturation.

We used a goodness-of-fit test (G-test) (Sokal & Rohlf 1995) to compare the proportion of sexually matured trout after each sea sojourn, between the rivers. The same test was used to compare the proportion of maturation between sexes in both rivers.

RESULTS

Age and growth

On average the sea trout smolt age was higher in Grenlækur (3.32 years) than in Leirvogsá (2.81 years). In Grenlækur the highest portion of the trout migrated to sea at the age of 3 years (62.1%) and 4 years old (30.1%) but a smaller part of the run was 2 and 5 years old. Mean smolt size was 26.5 cm (SD = 4.66). In Leirvogsá most of the sea trout smolt migrated to sea at the age of 3 years (64.7%) but some smaller portions were 2 years old (27.2%) and 4 years old (8.1%) with an average smolt age of 2.81 years. Mean smolt size was 15.5 cm (SD = 3.06).

In Grenlækur the mean body length after the first growth season in fresh water was 5.3 cm, 12.8 cm after the second and 24.7 cm after the third summer, according to back-calculations (Table 1). The average body lengths of juveniles from the electrofishing survey for the same year classes were 4.8 cm, 8.5 cm and 12.6 cm, respectively. There was therefore a considerable difference in length after the third year in fresh water between these two methods, back-calculations and electrofishing, which will be discussed later. The mean length increment was 7.5 cm and 11.9 cm for the first and second years in fresh water, respectively,

Table 1. Mean body length (L-mean) with standard deviation (SD), length increment (L-incr.) and growth coefficient (G-coeff.) for two sea-trout stocks (Leirvogsá and Grenlækur). Age F-0.... is the freshwater age but S-1.... is the sea water age. N is the number of samples in each year class.

	Leirvogsá					Grenlækur				
Age	N	L - mean (cm)	SD	L - incr. (cm)	G coeff.	N	L - mean (cm)	SD	L - incr. (cm)	G coeff.
F-0	554	4.5	1.11			256	5.3	1.43		
				5.7	0.825				7.5	0.882
F-1	554	10.2	2.42			256	12.8	2.90		
				5.1	0.380				11.9	0.657
F-2	402	14.9	2.59			243	24.7	4.25		
				0.61	0.040				1.6	0.061
Smolt	553	15.5	3.06			256	26.2	4.66		
				12.1	0.577				13.0	0.411
S-1	553	27.6	4.33			250	39.5	4.86		
				11.0	0.335				10.6	0.238
S-2	452	38.6	4.43			199	50.1	4.71		
				7.7	0.182				7.1	0.133
S-3	235	46.3	4.19			102	57.2	5.26		
				5.2	0.106				4.9	0.082
S-4	96	51.5	4.47			54	62.1	5.09		
				4.4	0.082				2.4	0.036
S-5	31	55.9	4.34			19	64.5	4.16		
				2.3	0.040				4.4	0.066
S-6	12	58.2	3.88			4	68.9	4.46		
				-0.6	-0.010				0.4	0.006
S-7	2	57.6	3.33			1	69.3			
				3.8	0.064					
S-8	1	61.4								

and the run-out growth was 1.6 cm in the spring prior to emigration to the sea. In Leirvogsá the mean body length after the first growth season in fresh water was 4.5 cm, 10.2 cm after the second season and 14.9 cm after the third summer (Table 1). The mean lengths of juveniles from the electrofishing survey for the same year classes were 5.3 cm, 8.9 cm and 12.0 cm. The increase in mean length was 5.7 cm and 5.1 cm in the first two years, respectively and the run-out size was 0.6 cm in the spring.

Comparison of the mean body lengths of each year class between the rivers gave highly significant differences between all year classes in fresh water and up to the sixth year in the sea. At higher ages the number of samples was too low to test the difference. The students t-test had the highest value at the smolt stage ($t=40.5$; $P<0.001$) and after first migration to sea S-1 ($t=35.9$; $P<0.001$) but lower values were observed at both lower and higher ages.

A similar pattern was seen in trout length increment and coefficient of growth in both rivers. In the River Grenlækur the mean length increment increased after the sea migration, most at the first summer in sea (length increment 13.0 cm) but less after each repeated sea sojourn (Table 1). The coefficient of growth had the highest value ($G_L=0.882$) between the age groups 0^+ to 1^+ in fresh water and G_L was 0.657 the second year in fresh water. At the end of the first summer at sea the value of G_L was 0.411 and then the G_L was lower for each repeated migration to sea. In the River Leirvogsá the growth increased rapidly after the sea migration, most after the first summer at sea (length increment 12.1 cm) but less for each repeated sea sojourn. The coefficient of growth had the highest value ($G_L=0.825$)

between the age groups 0^+ to 1^+ in fresh water but a lower value the second year in fresh water. At the end of the first summer at sea the value of G_L increased again (G_L =0.577), but lower values of G_L were observed after each season at sea (Table 1).

The longevity of both these sea trout stocks was similar. In the Grenlækur stock the longevity was 7.7 years for males and 8.5 years for females. The average length at these ages was 59.4 cm for males and 54.5 cm for females. The maximum number of sea sojourns was seven, shown by one trout out of 250 fish examined. The longevity of the Leirvogsá stock was 7.8 years for males and 7.3 years for females. The mean length at these ages was 48.9 cm for males and 49.3 cm for females. In the Leirvogsá one out of 553 individual examined had migrated 8 times to sea but others had migrated less frequently.

Sexual maturation

In the River Grenlækur no fish became sexually mature until after the second sea sojourn (17.0%) but 69.6% were mature after the third summer at sea (Figure 3). After five or more migrations to the sea, all the trout were sexually mature.

In the River Leirvogsá a similar pattern was seen. No sexually mature fish were found after the first sea sojourn but 2.9% after the second, 40% after the third and 85.4% after the fourth sea sojourn. After five or more emigrations to the sea, all the fish were sexually mature (Figure 3).

Even though a similar pattern was seen in both rivers the proportion of sexually mature trout differed significantly between the two rivers. Age at maturity in the Grenlækur stock was younger than in Leirvogsá, according to G-statistics (G=13.1; P=0.004).

In the River Grenlækur the males were significantly younger at sexual maturation than the females (G=10.7; P=0.029) but no difference was found in the Leirvogsá (G=2.7; P=0.260).

Size and growth after first spawning

Sea trout matured younger in Grenlækur than in Leirvogsá and were larger at maturation (Figure 4). In the Grenlækur stock a significant difference was found in mean length between sexes after first to third spawning (t=3.6, P<0.001; t=4.1, P<0.001; t=2.5, P=0.025 respectively) but this was not the case in the Leirvogsá stock (t=0.4, P=0.724; t=1.0, P=0.314, t=1.6, P=0.133 respectively).

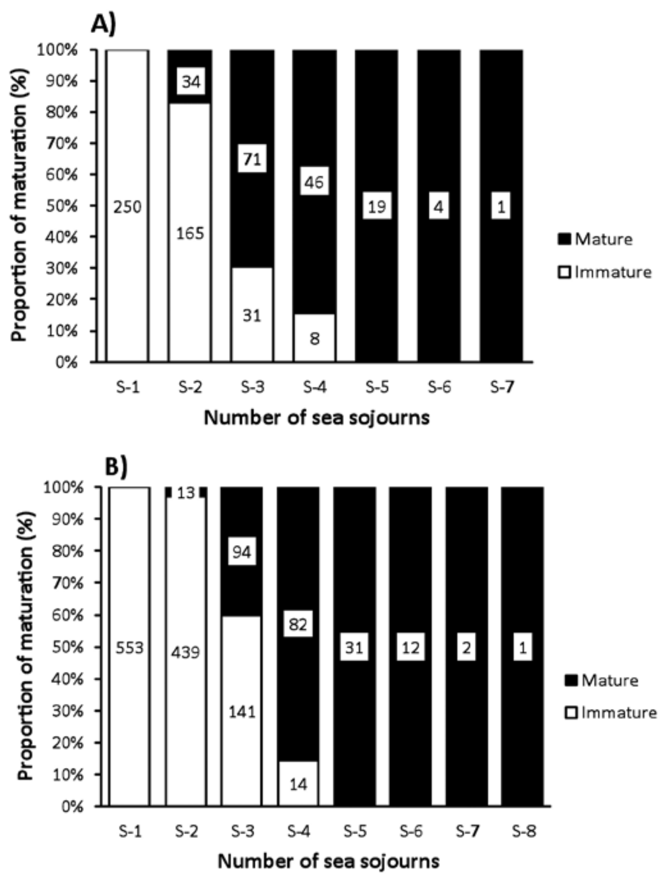

Figure 3. Proportion of sexual mature/immature sea trout in A) Grenlækur and B) Leirvogsá after a certain number of sea sojourns (S-1 to S-8). Numbers of individuals are seen within the columns.

Table 2. Comparison of the length increment (L-incr.) of sea growth, between trout which were sexually matured after third and fourth year at sea.

	Matured at 3rd year	Matured at 4th year	t - test	
	L-incr. (cm)	L-incr. (cm)	t-value	P-value
Grenlækur				
smolt - S1	13.1	12.9	0.29	0.77
S1 - S2	11.5	11.3	0.30	0.76
S2 - S3	5.4	8.8	7.09	<0.001
S3 - S4	5.0	4.4	0.98	0.33
S4 - S5	2.8	2.4	0.72	0.79
Leirvogsá				
smolt - S1	12.8	11.9	1.89	0.06
S1 - S2	11.9	11.3	1.40	0.16
S2 - S3	5.8	8.0	5.19	<0.001
S3 - S4	5.4	4.4	0.55	0.59
S4 - S5	5.4	3.3	0.60	0.55

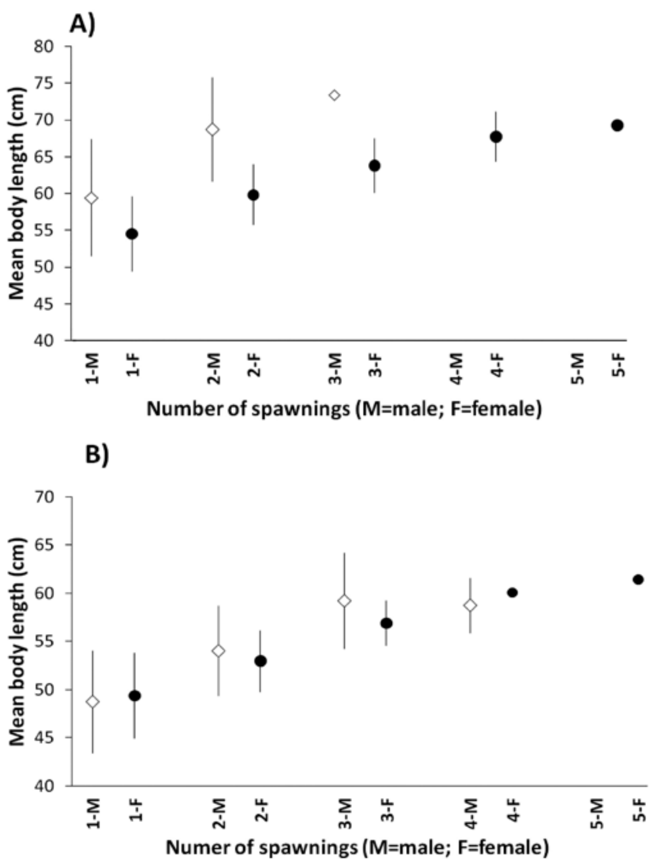

Figure 4. Mean body length after first to fifth spawning of sea trout in A) Grenlækur and B) Leirvogsá. Filled dots are females (F) and clear diamonds are males (M).

When the trout were preparing their first spawning the growth rate decreased considerably. This was seen in the length increment of the fish that were sexually mature on their third and fourth sea sojourn. By comparing the length increments of these two components no difference was found between the increments of immature trout but in the third year a highly significant difference was found between mature and immature trout (Table 2). In the following years when individuals of both age groups were mature no such difference was found. This was the case for both the Grenlækur and Leirvogsá populations.

DISCUSSION

During the fresh water phase, brown trout in the River Grenlækur grew faster than the river Leirvogsá population, especially in the last year before sea migration. Therefore the sea trout smolt was considerably larger in Grenlækur and this difference continued in the sea phase and was similar after each sea sojourn. This difference in growth the last year in fresh water can probably be explained by the behaviour of the juveniles in Grenlækur which at this time leave the upper reaches of the river and migrate to lower reaches, near the estuary of the river, with more favourable feeding grounds (Jóhannsson 1992, 1993). In the lower reaches the river spreads out and is wider and deeper with lower velocity and could be defined as a lake (called Fitjarflód, see Figure 1). The prey for the young trout is mostly smaller fish (three-spined sticklebacks) instead of insect larva in the upper reaches (Jóhannsson 1992). The juveniles start to live a pelagic life and don't waste as much energy in defending their territory. In this area the juveniles of the Grenlækur stock attain a higher growth rate, while juveniles in Leirvogsá stay at the coarse river bed with its higher velocity and smaller prey for food, until they leave the river as smolts. Similar results were observed in a river near Grenlækur, the River Skaftá, where average smolt size was 25.3 cm (Jóhannsson & Einarsson 1993) and the River Úlfarsá, neighbour of the Leirvogsá river, where average smolt size was 16.0 cm (Gudjonsson 1993). Similarities in sizes of the first migrating sea trout are therefore found between rivers within the same areas. Larger smolt in the case of Grenlækur compared to Leirvogsá can not be connected to higher latitude, as was the case in Norway (L'Abée-Lund et al.1989) but is rather explained by different behaviour and fresh-water habitats.

These parr movements from upstream to downstream areas are similar to parr migrations from fresh water to brackish water, as has been registered for young trout (Landergren 2004) and for young charr (Jonsson & Antonsson 2005). In these cases the young parr seem to not tolerate full seawater salinity but benefit from a faster growth rate in a brackish environment and are larger than individuals remaining in fresh water. This is explained by more suitable prey and less competition for food and space.

The size of the trout collected by electrofishing in the River Grenlækur was smaller than those of the same age back-calculated from adult trout scales. This difference could be explained by the findings of Forseth et al. (1999) that fast-growing brown trout migrate earlier from the river nursery area to lakes than slower-growing individuals and the food consumption and the energy budgets for 2^+ migrants were more than four times higher than those of the resident 2^+ fish. Olsson and Greenberg (2011) reported that individuals of migrating brown trout had a larger body size than the same age individuals that subsequently migrated.

Jonsson et al. (1991) compared longevity with body size, growth at sea and growth in rivers of 25 populations of sea trout along the coastline of Norway. They found that longevity was positively correlated with body size but negatively correlated with growth both at sea and in rivers. Our results for the populations in Leirvogsár and Grenlækur, are in agreement of those findings for males and females separately, except regarding growth within rivers for the Grenlækur parr (both sexes). In that case the length increment during the second year in fresh water was much higher in the Grenlækur stock than in other stocks in relation to long evity. This may indicate that the juveniles in the Grenlækur population are fast-growing during the last year in fresh water, as has been noted above.

Most of the population in both stocks was still immature after the first two sea sojourns. But after the third sea sojourn 70% of the Grenlækur stock was sexually mature compared to 40% of the Leirvogsá stock. Thus the sea trout in Grenlækur were significantly younger in sea age at maturity than in Leirvogsá. This difference could be explained by the greater size of the trout in Grenlækur at the same sea age because of larger smolt. Ward & Stanley (1988) reported that age at maturity of steelhead trout (*Salmo gairdneri*) decreased with increased smolt age and assumed this held also for size.

Mean sea age at maturity has been found to be 3-4 years in the north Norwegian populations but 1-2 years in France and Spain (in Jonsson & Jonsson 2006). The two Icelandic populations studied were intermediate with 2-3 years sea age at maturity. This may be explained by environmental conditions. For example, Jonsson et al. (1991) found that sea trout from warmer rivers appear to mature younger than those from colder rivers.

The maximum number of spawning marks was similar in both the sea trout populations, five marks for the females but somewhat fewer for the males. This is similar to sea trout populations in England and Wales as four to five spawning marks were commonly observed in a study of 16 sea trout populations (Harris & Milner 2006).

The results indicated that the main difference in the life history traits of these two stocks of anadromous brown trout were reflected in the difference in habitat in these two streams. Better growth the two first years in fresh water of the Grenlækur population and movement of the parr to favourable downstream feeding grounds in fresh water the last year before smolting could explain the main differences observed in size of the individuals and probably also age at maturity between these two stocks. This indicates the importance of the freshwater environment and how it can affect the life history of different stocks.

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