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Umhverfisdeild

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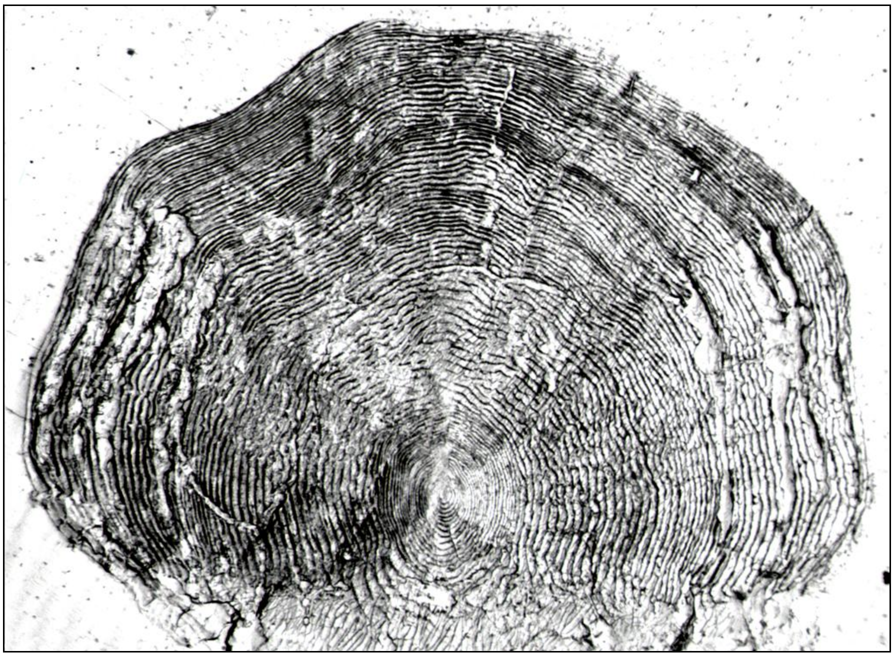

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## Yfirlýsing höfundar

*Hér með lýsi ég því yfir að ritgerð þessi er byggð á mínum eigin athugunum, er samin af mér og að hún hefur hvorki að hluta né í heild verið lögð fram áður til hærri prófgráðu.*

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Abstract

Information on repeat spawning in Atlantic salmon stocks from eight various rivers in Iceland was analyzed, using data collected by the Institute of Freshwater Fisheries in Iceland. The rivers differ in characteristics as well as location based on bedrock and geographical area. Available data from these rivers was compiled but to answer the hypothesis, data from 1989 through 2006 was utilized. From available data repeat spawning reached up to 33% of catches in Botnsá (1949) and down to no returning spawners some years in individual rivers. The average (mean) proportion of repeat spawning in individual rivers over the study period ranged from 3,0% (Norðurá) to 9,8% (Stóra-Laxá). There was significant difference of average (median) proportion previous spawners between Stóra-Laxá and Þjórsá and Stóra-Laxá and Laxá in Aðaldalur but not between the other rivers. There was only significant reduction on the proportion previous spawners with time in Laxá in Aðaldalur (p = 0,013) and nearly in Miðfjarðará (p = 0,052); but none of the other rivers. In those two rivers that are in the northeast, time (y) explained 33% of % previous spawners (x). Proportion repeat spawning when rivers were divided by bedrock type (rivers in Plio-Pleistocene vs. Tertiary) did not differ significantly (p = 0,717) but when divided up by geography (south and west versus north and east) there was a significant difference (p = 0,049). The average (mean) proportion of females amongst the previous spawners over the study period ranged from 45,1% (Stóra-Laxá) to 98,9% (Þjórsá) and of males amongst the previous spawners from 1,1% (Þjórsá) and 54,9% (Stóra-Laxá). There were significantly more females in Þjórsá, Sog, Botnsá, Norðurá and Flekkudalsá but not in Stóra-Laxá, Laxá in Aðaldalur and Miðfjarðará. Over all the study rivers the average (mean) proportion of females was 66,4% and males 33,0% with significantly more females (p = 0,001). When rivers were compaired there was significant difference of female/male proportion between Þjórsá and Laxá in Aðaldalur, Þjórsá and Stóra-Laxá and Þjórsá and Miðfjarðará. There was found difference in previous spawning between the rivers in this current study. Further studies are needed on more overall factors in the rivers and ocean connected to the life history of the salmon stocks in the rivers. Then we could possibly find the causes of variation in the trait of this vital part of the survival of Atlantic salmon stocks that repeat spawning is.

Keywords: Atlantic Salmon, *Salmo salar L.*, previous spawners, repeat spawning, Iceland, Þjórsá, Stóra-Laxá, Sog, Botnsá, Norðurá, Flekkudalsá, Laxá in Aðaldalur, Miðfjarðará, location, geography, bedrock, females, males.

# Ágrip

Endurtekin hrygning í nokkrum stofnum Atlantshafslaxins var rannsökuð í átta mismunandi ám á Íslandi með því skoða gögn frá Veiðimálastofnun. Árnar eru ólíkar að eiginleikum sem og staðsetningu út frá berggrunni og landshluta. Tiltækum gögnum frá þessum ám var safnað saman en til að svara tilgátum var notast við gögn frá 1989 til 2006. Hæsta hlutfall endurtekinnar hrygningar var 33% í Botnsá árið 1949 en mörg ár kom enginn lax aftur til hrygningar í einstökum ám. Meðaltal í hverri á fyrir sig yfir rannsóknartímann náði frá 3,0% (Norðurá) uppí 9,8% (Stóra-Laxá). Það var marktækur munur á miðgildi endurtekinnar hrygningar milli Stóru-Laxár og Þjórsár og svo Stóru-Laxár og Laxár í Aðaldal, en ekki á milli hinna ánna. Aðeins í Laxá í Aðaldal var marktæk fækkun ($p = 0,013$) á endurtekinni hrygningu með tíma og nálægt því í Miðfjarðará ($p = 0,052$). Í hinum ánum var ekki fylgni milli hlutfalls og tíma. Í þessum tveimur ám, sem eru á Norðausturlandi, útskýrði tími (y) 33% af hlutfalli endurtekinnar hrygningar (x). Það var ekki marktækur munur ($p = 0,717$) á hlutfalli endurtekinnar hrygningar út frá berggrunni (móbergssvæði vs. blágrýtissvæði) en það var hins vegar marktækur munur ($p = 0,049$) þegar ánum var skipt eftir landshlutum (suður og vestur vs. norður og austur). Meðalhlutfall hrygna á meðal fiska sem voru að koma í annað skipti til hrygningar á rannsóknartímabilinu er frá 45,1% (Stóra-Laxá) upp í 98,9% (Þjórsá) á meðan meðalhlutfall hænga var á bilinu 1,1% (Þjórsá) og 54,9% (Stóra-Laxá). Það voru marktækt fleiri hrygnur í Þjórsá, Sogi, Botnsá, Norðurá og Flekkudalsá en ekki í Stóru-Laxá, Laxá í Aðaldal og Miðfjarðará. Þegar allar ár voru teknar saman var meðaltal hrygna 66,4% og hænga 33,0% þar sem hrygnur voru marktækt fleiri ($p = 0,001$). Þegar einstakar ár voru bornar saman mátti sjá marktækan mun á hlutfalli hrygna og hænga milli Þjórsár og Laxár í Aðaldal, Þjórsár og Stóru-Laxár og Þjórsár og Miðfjarðarár. Það fannst mismunur á milli vatnsfallanna í þessarri rannsókn. Þörf er á frekari rannsóknum með yfirgripsmeiri þáttum innan ánna og sjávarins með tengingu við lífssögu laxastofnanna í ánum. Þá gætum við hugsanlega fundið betri skýringar á breytilegum eiginleikum þessa nauðsynlega þáttar, endurtekinni hrygningu, í lífsafkomu stofna Atlantshafslaxins.

Lykilorð: Atlantshafslax, *Salmo salar L.*, endurtekin hrygning, Ísland, Þjórsá, Stóra-Laxá, Sog, Botnsá, Norðurá, Flekkudalsá, Laxá í Aðaldal, Miðfjarðará, landshlutar, berggrunnur, hrygnur, hængar.

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This work is dedicated to my mum and dad that have always supported me in whatever I've done, no matter how silly it might have sounded at first. Thanks!

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# 1. Introduction

## *1.1 The Atlantic salmon*

The Atlantic salmon (Salmonidae: *Salmo salar*) is a north temperate fish species closely related to Pacific salmons, trouts, chars, graylings and whitefishes (Mills, 1989). Atlantic salmon is widely distributed both on the east and west coasts of the North Atlantic Ocean. In the west Atlantic salmon ascends rivers from the Connecticut River, USA in the south to the Ungava Bay, Canada in the north. In the eastern Atlantic it ascends rivers as far south as northern Portugal and the Bay of Biscay, to rivers as far north as the Barents Sea and White Sea areas of northern Europe (MacCrimmon & Gots, 1979). The species is also found in about 80 of Iceland's 250 rivers (Scarnecchia, 1983; Guðjónsson, 1988) as well as some rivers in Greenland (MacCrimmon & Gots, 1979).

## *1.2 General life history of anadromous Atlantic salmon*

Most stocks of Atlantic salmon are anadromous, i.e., spawn in freshwater (rivers) and migrate to saltwater (the ocean) during part or all of their adult life. A few landlocked, non-anadromous stocks occur in lakes or rivers in both North America and Europe (Mills, 1989; Guðbergsson & Antonsson, 1996). Newly-hatched anadromous Atlantic salmon remain one or more years in rivers until they undergo smoltification and migrate to the sea. As mature fish they show a precise homing to their natal river they left as smolts (Tchernavin, 1939; Carlin 1969 cited in Niemela et al., 2006a) or as previous spawners (Mills, 1989; Hansen & Jonsson, 1994). Ascent of Atlantic salmon in northern Europe usually occurs from late May through late July (*e.g.* in River Teno, Niemela, 2004a), with spawning typically occurring from the mid-October through December (Guðbergsson & Antonsson, 1996; Borgstrøm & Hansen, 1987). In some rivers spawning may not be completed until end of January (Mills, 1989). The females choose the spawning site and excavate a nest (redd) in gravel. Expulsion of eggs is followed by a male expelling milt over the eggs in the redd. The fertilized eggs are then covered with gravel by the females (Jones, 1959). In figure 1 there can be seen the main parts of the Atlantic salmon life cycle. Hatching occurs in 70-160 days depending on water temperature (Mills, 1989). The newly hatched fish (called alevins) typically remain amid the gravel and initially carry a large yolk sac for endogenous feeding. After the yolk sac has been absorbed the fish (now called fry) emerge from the gravel and starts exogenous feeding (Mills, 1989). The fish remains in the fry stage until they are about 6,5-7,0 cm long; by then the fish are called parr and have developed dark blotches along their sides known as parr marks (Mills, 1989). The parr stays in the river for 2-8 years, depending on growth rate, before smoltification and migration to the feeding areas in the ocean (Guðbergsson & Antonsson, 1996). Some male parr become sexually mature, remain in the river, and attempt to spawn, sometimes successfully, with females (Garcia-Vazquez et al., 2001). Sexually mature residual female smolts have also been reported (Power, 1969). In the ocean the salmon remains for 1-4 years and occasionally 5 years (Dymond, 1963; Niemela et al., 2006b), grow rapidly, and eventually begin sexual maturation and returns to the river for spawning (Jonsson, Hansen & Jonsson, 1991a). After spawning, salmon (now called kelts) have a high mortality rate, especially the males (Mills, 1989), but a small fraction of them returns to the sea and returns to spawn again, sometimes repeating this pattern up to 5 times (Ducharme, 1969).

### *1.3 Life history of Icelandic salmon*

In Iceland there are five species of fish in freshwater, Atlantic salmon (*Salmo* salar), stickleback (*Gasterosteus aculeatus*), Arctic char (*Salvelinus alpinus*), brown trout (*Salmo trutta*), European eel (*Anguilla anguilla*) and in the recent years the European flounder (*Platichthys flesus*) is colonizing numerous river system in the country (Jónsson, Pálsson & Jóhannsson, 2001). The salmon is very valuable in Iceland (Guðbergsson & Guðjónsson, 2005) which makes knowledge about the species important. Salmon fishery in Iceland is only allowed in freshwater and has not been allowed in the sea since 1932. Majority of rivers in Iceland only allow rod catching of salmon but two of them, Ölfusá-Hvítá and Þjórsá, allow net fishery (Institute of Freshwater Fisheries, 2004).

Main aspects of the life history of Atlantic salmon in Iceland have been described by several authors (Guðjónsson, 1978; Guðbergsson & Antonsson, 1996; Jónsson, 1983). Adult pre-spawning Icelandic salmon typically enter the rivers from late May to September (Jónsson, 1983) with the main run in July (Guðjónsson, 1978). Then they spawn from September to December (Guðjónsson, 1978). Hatching takes about 6-8 months (Guðbergsson & Antonsson, 1996). Fry emerge from the gravel till the middle of summer when the yolk sac has been absorbed (Jónsson, 1983). The majority of natural smolts in Iceland go to the sea when they are in their third to fifth year (Guðjónsson, 1978; Mills, 1989) and around 10-12 cm long (Guðbergsson & Guðjónsson, 2005). Most Icelandic salmon spend 1-2 years in the sea before maturing and returning to their native river (Guðjónsson, 1978; Guðbergsson & Antonsson, 1996), but occasionally 3 years (Guðjónsson, 1978). As discussed in the book by Guðbergsson & Antonsson (1996) the proportion of smolts returning as adult salmon to rivers in Iceland ranges from 1-30% but overall compilation has not been done systematically. Multi sea winter salmon at maturity (2SW or more) is more common in rivers in the northwest, north and in the east (Guðjónsson, 1978) but its numbers have been going down in the last years while numbers of salmon mature after one year at sea (1SW) have been more stable (Guðbergsson & Guðjónsson, 2005).

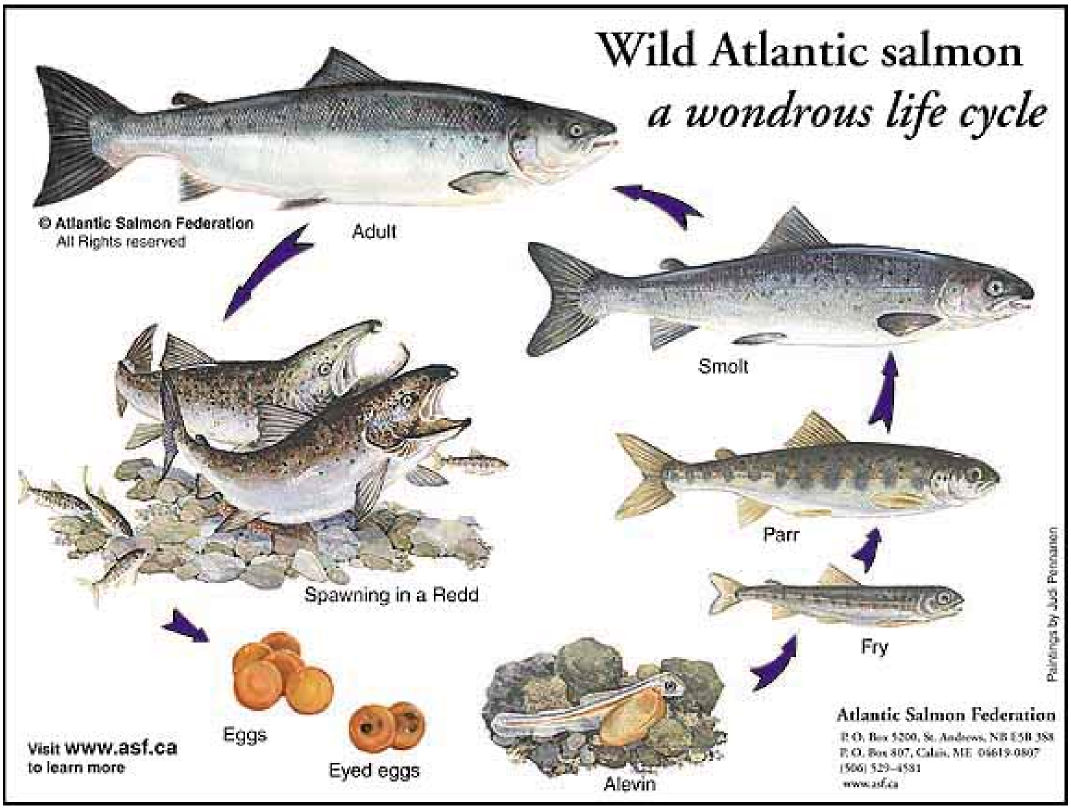


**Figure 1.** The life cycle of the wild Atlantic salmon (Atlantic Salmon Federation, 2008).

It is not fully known where the Icelandic salmon stay during the winter in the ocean, but marked salmon have been found near and in rivers in The Faroe Islands, east and west of Greenland and in rivers in Norway and Scotland (Guðjónsson, 1978; Guðbergsson & Antonsson, 1996). Recaptures of tagged salmon have shown that more salmon from the south and west coast of Iceland are found in sea fishery west of Greenland while salmon from the north and east coast is found more in the sea north of the Faroe Islands (Ísaksson, Óskarsson & Guðjónsson, 2002).

## *1.4 Factors influencing life history of Icelandic salmon*

The evolved life histories of Icelandic salmon is strongly influenced by several major factors, including rigorous and highly variable regional climatic and weather conditions as well as distinct regional and local geological and landscape factors (Guðjónsson, 1978; Guðjónsson, 1990b). As a result of these factors, Icelandic rivers can be classified into several types with distinct geological, landscape, and hydrological differences (Guðjónsson, 1990b).

### 1.4.1 Regional effects of climate and growing season

Iceland is an island in the North Atlantic situated between 63,5° and 66,5° N latitudes and 13,5° and 24,5° W longitudes (Guðjónsson, 1978). The main part of the island is highlands over 400 m high with some peaks reaching just over 2000 m. Lowland can be found along the coast and in valleys around the country. Approx. 11 % of the country is covered with glaciers. The climate in Iceland is cool, temperate and oceanic as can be viewed from meteorological data from two locations in Iceland in table 1. Thanks to the effects of the Gulf Stream the sea and climate is relatively warmer than areas on the same latitudes lacking the Gulf Stream.

**Table 1.** Mean temperature and precipitation in Reykjavik (southwest) and in Akureyri (north) (Statistics Iceland, 2008).

| | Reykjavík | | | Akureyri | | |
|---|---|---|---|---|---|---|
| | **Year** | **January** | **July** | **Year** | **Janúar** | **Júlí** |
| **Temperature (°C)** | | | | | | |
| **Mean 2006** | 5,4 | 2,0 | 11,1 | 4,6 | 1,8 | 10,6 |
| **Mean 1961-1990** | 4,3 | -0,5 | 10,6 | 3,6 | -2,2 | 10,5 |
| **Precipitation (mm)** | | | | | | |
| **Total 2006** | 890 | 153 | 41 | 548 | 27 | 19 |
| **Mean 1961-1990** | 799 | 76 | 52 | 490 | 55 | 33 |

The greatest abundance of salmon in Iceland is found in the southern, southwest and western parts of Iceland. According to Guðjónsson (1978) there are a several good salmon rivers in the northern part but few in the West fjords (north-west) where there is little lowland and in the east and south-east where the largest glaciers are found. Atlantic salmon only thrives there where water temperatures exceed 10°C for about three months each year (Mills, 1989). In the north and northeast there is a lot of melting water that cools the rivers for longer time in the summer than in the south and southwest. Even though the water discharge is similar (see table 8 in appendix), the Atlantic salmon stocks are smaller in the northern rivers than in the southwestern rivers (Guðjónsson, 1978).

### 1.4.2 Geological factors, landscape factors and river classes

“Each stock of *S. salar* is an adaptation to local conditions and reflects past selection pressure.”(Sounders and Schom, 1985). For 77 rivers in Iceland Scarnecchia (1983) could explain much of the variation of percentages of 1SW salmon (72% for females and 62% for males) by environmental factors such as latitude, length of river, ocean temperature in June and discharge of the river in July to September. He also found that more females tended to return as a MSW, the further north their homing river was.

The Eurasian and North American plate boundaries run through Iceland, known as the North Atlantic rift. The rift is associated with volcanic and geothermal activity across the country, in an approximately northeast-southwest direction. The youngest bedrock, like hyaloclastite, is in and near the volcanic zone that’s referred to Plio-Pleistocene area; adjacent areas may consist of older and harder basalt bedrock. Such geological differences form the basis of distinct rivers types differentially influenced by a range of environmental factors, including bedrock type, how fast water flows through the river basin, and landscape vegetation (Guðjónsson, 1990b). Based on the resulting ecological conditions, Guðjónsson (1990b) has divided Iceland into 11 main areas with 4 main types (classes) of rivers: 1) spring–fed rivers in Plio-Pleistocene areas, 2) direct run-off in Plio-Pleistocene areas, 3) direct run-off in Tertiary areas, and 4) rivers originating from wetlands in heaths in Tertiary areas. These areas can be seen in figure 2 and the types of rivers are further described in the following paragraphs.

Spring-fed rivers are found in porous bedrock in the volcanic zone, such that water flows easily under the surface and comes up to the surface as springs. Run-off and temperature change little throughout the year. Conductivity is often fairly high (60-200 µS/cm). Spring fed rivers provide very stable living conditions for aquatic life. Salmon are often found in the longer spring fed rivers, particularly those that originate from lakes that elevate the temperature of the water. Examples of rivers of this type containing salmon are Sog, Laxá in Aðaldalur and partly Þjórsá.

In direct run-off rivers in Plio-Pleistocene areas, bedrock is typically very compact and water flows on the surface. These areas are easily eroded and canyons are often formed. Rivers of this type are often cold; conductivity is often 50-100 µS/cm. Habitat conditions for aquatic life, including the salmon, can change rapidly and unpredictably with weather. In southern Iceland the instability of these rivers is less than ideal for but salmon can, however be found in longer ones. Examples of rivers of this type containing salmon are Botnsá, Stóra-Laxá and Þjórsá.

In direct run-off rivers in Tertiary areas, the shorter rivers in the basalt areas are usually cold, high-gradient, low in conductivity (20–60 µS/cm), low in nutrients, and highly changeable with weather conditions. Both conductivity and aquatic productivity increase as the rivers flow longer distances through the lowlands, and if nutrients are supplied by lakes in the system. Salmon can be found in the longer rivers and lake-fed systems. Examples of rivers of this type containing salmon are Norðurá and Flekkudalsá.

In rivers originating from wetland in heaths, water flows slowly through wetlands, ponds and lakes and the conductivity is often 60-160 µS/cm and is typically high in nutrients. Rivers of this type are often important for salmon; Examples of rivers of this type containing salmon is Miðfjarðará and partly Norðurá.

Glacial rivers or rivers with glacial effects are many in Iceland but not many of them hold salmon since they are generally cold and silty. The discharge is of great variance both daily variance and seasonal variance with small discharge in the winter and larger in the summer. Example of a river with strong glacial effects is Þjórsá.

The closeness to Greenland and the Arctic causes occasional visit of drift ice that has sometimes made great impact on sea and air temperature mainly in the northwestern and northern part of Iceland (Guðjónsson, 1978). Ashes from volcanic eruptions can have effects on rivers as well (Thórarinsson, 1970).

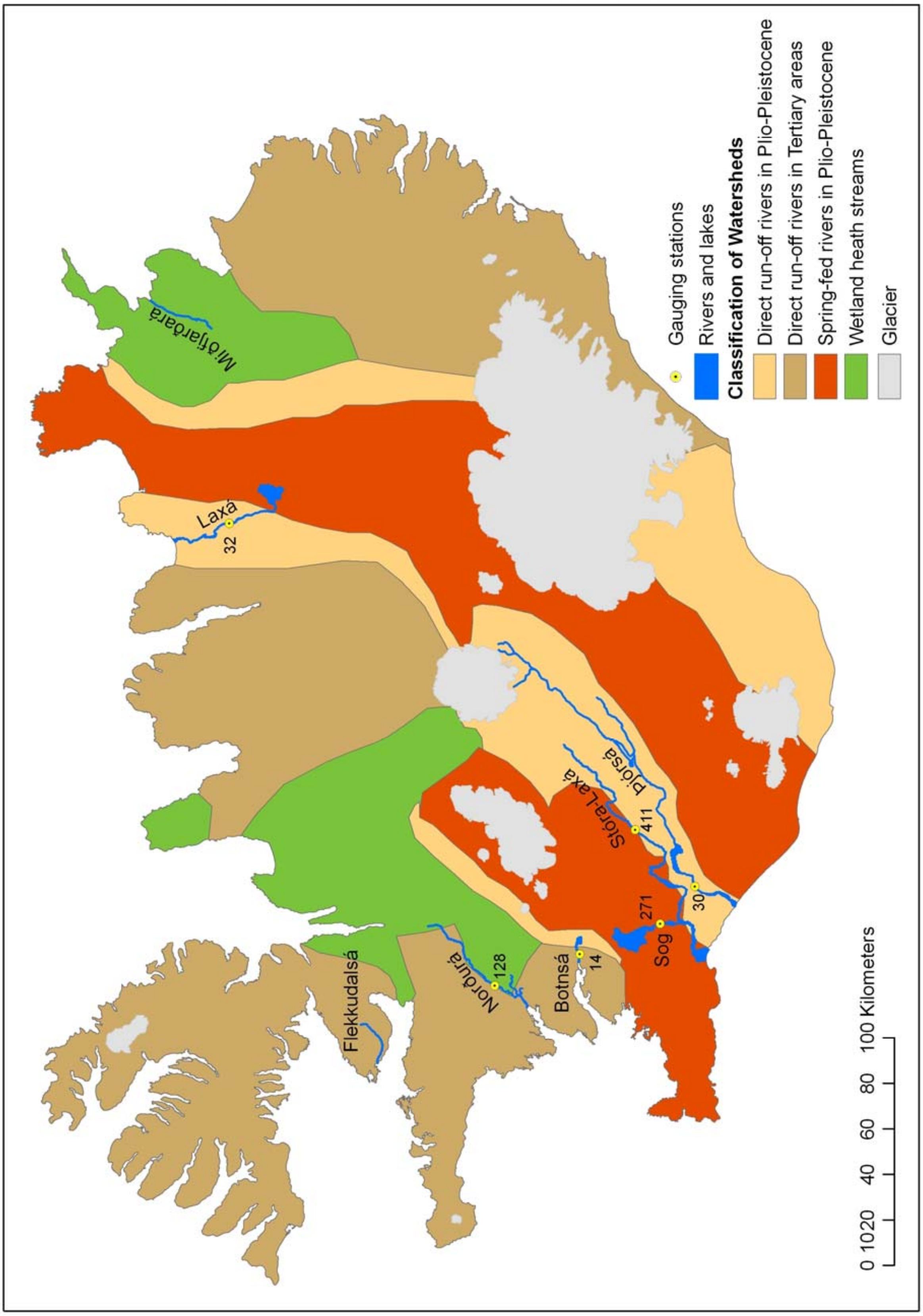


**Figure 2.** The zonal division of Iceland by bedrock characteristics (Guðjónsson, 1990b), location of the study rivers and gauging stations by location and number (Orkustofnun, 2008).

## 1.5 Repeat spawning of the Atlantic Salmon

In this chapter I consider an important and often neglected aspect of the life history of Icelandic and other salmon: the incidence of repeat spawning and its causes and consequences.

### 1.5.1 Status of knowledge

Some Atlantic salmon return more than once to a river to spawn; some fish may return five or more times (White & Medcof, 1968; Ducharme, 1969). In rivers in various countries, the proportion of previous spawners typically averages 3-6% (Mills, 1989), but has been up to 34% in a river on the west coast of Scotland (Pyefinch, 1955, cited in Dymond, 1963) and in a river in Quebec, Canada (Calderwood, 1928, cited in Dymond, 1963). Previous spawned salmon can spawn in consecutive years or in alternate (biennial) years (Niemela et al., 2006b). The length of time that the salmon spends in the sea between spawning has also been classified by Jones (1959) as: 1) short duration, *i.e.*, a few months' duration, as when a kelt goes down in spring and comes up the following autumn to spawn again; 2) long duration: *i.e.*, about 1 year, as with an entire summer and winter spent in the sea; and 3) very long duration as in a stay in the sea of about 18 months, resulting in alternate year spawning. Jonsson et al. (1991a) analyzed data from seventeen Norwegian rivers and found that the proportion of biennial spawners among previous spawners increased with size and sea-age at first maturity. In these rivers, the marine survival of kelts was 2-25%. According to Chadwick (1988), proportion of previous spawners has been decreasing over the mid last century in Newfoundland and according to Ducharme (1969) and Dymond (1963), most previous spawners among Atlantic salmon are females. The high mortality rates probably result from the great expenditure of energy when spawning. Grilse (1SW) may use 50-60% of their energy for spawning (Jonsson et al., 1991b) and older salmon may use up to 70% (Jonsson et al. 1997). The size of two 2SW salmon from the same river can vary greatly if one has spawned as a grilse but the other one hasn't (Jones, 1959), as the spawned one has presumably used the energy to spawn and survived the starvation in the river, while the other has continued to grow.

### 1.5.2 Repeat spawning in Icelandic salmon

Although repeat spawning (iteroparous) migrations have been documented for Icelandic salmon from tag recoveries (Antonsson, Þórólfur, personal comment) and scale analysis, little is known neither about the incidence and significance of repeat spawning in Icelandic salmon nor about the factors affecting it. However, numerous scale samples from rod-caught salmon has been collected by the Institute of Freshwater Fisheries in Iceland and this data provided a basis to investigate several aspects of repeat spawning.

In his book, Jónsson (1983) states that around 3-15% of spawned salmon manage to return to the ocean and might therefore survive for another spawning. A study by Guðjónsson (1978), including 10 different rivers in different parts of Iceland from 1911-1914, 1938-1939 and 1946-1965 (not data from all years from any of the rivers), showed variable percentage of previous spawners from 0-18,4% in the sampled scales. The highest proportions were in the river system Ölfusá-Hvítá in the south in 1914 (18,4%) and from 1938 to 1939 (16,8%). None of the repeat spawning in the western or south-western rivers in this study reached above 10%; only in southern and northern rivers reached above 10% repeated spawning.

Guðjónsson (1990b) suggested that fish stocks in rivers with more unstable environmental conditions have more complicated and more variable life histories than fish stocks in more stable rivers. Their greater life history variation enables them to persist in the more variable environment. In the same study he pointed out that differences also exist within river types depending on region (e.g., north versus south). In the north, the maximum flow in a river occurs, almost without exception, in spring floods due to melting of winter snow while that's not the case with rivers in the south. Rivers in the south are often spring-fed rivers that have a relatively constant flow through-out the year, while other southern rivers may have glacial effects that cause highest water flow peaks in July and August.

## *1.6 Objectives*

The objectives of this study were:

1. To compile and analyze available data on the occurrence and frequency of repeat spawning in several salmon rivers in Iceland.
2. To investigate if the incidence of repeat spawning (based on catches) has changed over the period 1989 through 2006.

3. To investigate if there is any correlation between the frequency of repeat spawning and bedrock types and/or geographical areas.
4. To investigate if there is a significant difference in the frequency of repeat spawning between males and females.
5. To discuss the significance of previous spawners for Icelandic salmon stocks and their exploitation.

From these five objectives, I established four hypotheses that were tested:

1. I hypothesize that there is a difference between average (median) proportion of previous spawners between the study rivers.
2. I hypothesize that the incidence of repeat spawning (based on catches) in the study rivers has changed over the period 1989 through 2006.
3. I hypothesize that the location of the river, i.e. bedrock type and geographical area, has an effect on the incidence of repeat spawning.
4. I hypothesize that the proportion of females and males among previous spawners is different in the study rivers and varies between rivers.

# 2. Study sites

My objectives and hypotheses were addressed using available data from the Institute of Freshwater Fisheries from eight rivers representing a variety of distinct regions and combinations of river types. The aim was to select rivers that could represent a range of regions and types. The selection was, however, limited by the availability of sufficient data to address objectives and evaluate hypotheses, as stated above. For that reason, the selected rivers were not evenly distributed among regions, and most were a combination of the different river types. On a regional basis, four rivers were selected from the south coast (Þjórsá, Stóra-Laxá and Sog), one river from the south west (Botnsá), two rivers from the west coast (Norðurá and Flekkudalsá), and two rivers from the north east coast (Miðfjarðará and Laxá in Aðaldalur)

## *2.1 Þjórsá*

Þjórsá is the longest river in Iceland, stretching 230 km from base to shore in the south. It is a combination of many tributaries of various origin, spring fed rivers, glacial rivers and direct run-off rivers. The drainage basin is 7530 km$^2$ and the mean annual discharge is 353m$^3$/s (see table 8 in appendix) in the gauging station Urriðafoss, located in the lower basin of the river (figure 2). Due to hydroelectric power plants in the upper part of the river, daily flow differences have mostly disappeared but floods can still occur with heavy precipitation or ablation (Jónsson, 2001). Around 105 km of the Þjórsá river are accessible for fish (see table 8 in appendix). Þjórsá holds all species of Icelandic freshwater fish. Research has showed that around 83% of the salmon were brought up in the main river but around 17% in the tributaries Kálfá and Tungnaá (Jóhannsson, Jónsson, Örnólfsdóttir, Guðjónsson & Magnúsdóttir, 2002). During the years 1996-2006, average annual salmon catch was 2317 salmon (see table 8 in appendix). As reported by Jóhannsson et al. (2002), the catch is expected to be approx. 50% of the total stock but 98% of all salmon is caught in gill nets in the main river and around 2% on rods in tributaries. Analyzis on scale sampled from 1986 to 2001 showed that 2,7% had spawned before (Jóhannsson et al., 2002).

## 2.2 Stóra-Laxá

Stóra-Laxá river in south Iceland is a direct run-off river that has the mean annual discharge of 22m$^3$/s (see table 8 in appendix) measured at the gauging station Stórhylur (figure 2). Stóra-Laxá is a 3.order tributary of the river system Hvítá-Ölfusá. Stóra-Laxá has a water basin of 512km$^2$ (see table 8 in appendix). The length of the river is 90 km, with 37 km accessible for fish (see table 8 in appendix). The river´s mouth 53 m over sea level (Jóhannsson & Guðjónsson, 2004) and the distance from mouth to sea is 64 km (see table 8 in appendix). Salmon, trout and char are caught on rods in Stóra-Laxá, with average salmon catch 310 per year (see table 8 in appendix). From 1998-2002, the average catch of trout per year was 35 and char 31 (Jóhannsson & Guðjónsson, 2004). The main river of the Hvítá-Ölfusá river system originates in the glacier Langjökull, that has had occasional glacial bursts occurring, for instance during the study period in 1980 and 1999. The consequences of glacial bursts cause the salmon to move slower up the rivers and enter later into upper tributaries, with reduced number in catch the following years (Jóhannsson & Guðjónsson, 2004). Scales have been sampled in the river continuously since 1985 (unpublished data).

## 2.3 Sog

Sog is a tributary to the river Hvítá in the south of Iceland. It originates from Lake Þingvallavatn and is the largest spring fed river in the country (Orkustofnun, Vatnsorkudeild rennslisskýrslur Ljósafoss-Ásgarður, cited in Jóhannsson, Jónsson & Magnúsdóttir, 2005). Few tributaries and creeks flow into Sog before it combines with Hvítá 25 km away from the sea and 15 m above sea level. After that it is called Ölfusá. The total length of the river is 20 km with 11 km accessible for fish (see table 8 in appendix). Average annual salmon catch was 397 from 1974-2007 (see table 8 in appendix) and, as published by Jóhannsson and Guðjónsson (2004), 33 trouts and 677 chars were caught from 1998-2002. Conductivity in the river has been measured 69-78 µS/cm (Rist, 1974; Institute of Freshwater Fisheries unpublished data cited in Jóhannsson *et al.*, 2005). In 1959, the Power Plant Steingrímsstöð was built in Sog river and the natural flow of the river changed. The natural flow was rather stable before 1959, but after it was harnessed there has been more fluctuation in the water level (Jóhannsson *et al.*, 2005).

## 2.4 Botnsá

Botnsá (in Hvalfjörður) in the southwest of Iceland is a direct run-off river with a lake in the system. The mean annual discharge is $4m^3/s$ (see table 8 in appendix) by the gauging station Stóribotn (figure 2). Its water basin covers 79 $km^2$ and the length of the river is 9 km with 3 km accessible for fish (see table 8 in appendix). The river originates from Hvalvatn lake and drops down Glymur (200m), the highest waterfall in Iceland, and flows down the valley Botnsdalur meeting four tributaries on the way to the sea (Viðarsson, 1989). Average salmon catch is 113 per year (see table 8 in appendix) but as published by Viðarsson (1989), it is known that trout spawns there as well and previously spawned salmon has been reported in the river.

## 2.5 Norðurá

Norðurá is a tributary of the glacial river Hvítá in Borgarfjörður in west of Iceland. It's origin is in a lake called Holtavörðuvatn at 325 m above sea level (Einarsson,1988). The lake holds both trout and char (Blöndal, 1975). Norðurá is a 62 km long direct run-off river with a 518 $km^2$ large water basin (see table 8 in appendix) and the whole river is accessible for fish, thanks to two salmon ladders at Glanni and Laxfoss (Einarsson,1988). There are numerous direct run-off tributaries that flow into Norðurá mainly from the west side. Spawning – and rearing habitat for salmon is generally better in the upper, as well as in some of the tributaries (Einarsson, 1988). The mouth of the river is 22 km away from the sea (see table 8 in appendix) where the river meets with Hvítá at 15 m above sea level (Rist, 1990). The gauging station Stekkur (figure 2) has a mean annual flow of 22m$^3$/s (see table 8 in appendix). Average salmon catch per year is 1634 (see table 8 in appendix). In Norðurá there has been an annual research on the salmon stocks since 1988 (*e.g.* Einarsson, 1988; Einarsson & Theódórsson, 2006) and previous spawners have been reported several times (*e.g.* Einarsson, 1988; Einarsson, 1999).

## 2.6 Flekkudalsá

The river Flekkudalsá in Fellsströnd flows through the valley Flekkudalur to the mouth of Hvammsfjörður in the northwest of Iceland (figure 2). It is a 25 km long direct run-off river of which are 20 km accessible for fish (see table 8 in appendix). The river joins the river Tunguá 1 km above its mouth and from that point to shore it´s called Kjarlaksstaðaá (Einarsson, 1987). In general, this river system is called Flekkudalsá and that name will be used in this paper. The drainage basin for Flekkudalsá is 147 km$^2$ (see table 8 in appendix) and the estimated flow during summertime 1 m$^3$/sec during (Scarnecchia 1984, cited in Einarsson 1987).

According to Einarsson (1987), juvenile habitat varies a lot within the river, but the river is well utilized by salmon where salmon habitat is favorable. The mean salmon catch is 239 per year (see table 8 in appendix). Information about angling in Flekkudalsá has been recorded in log books since 1948 and scales have been collected from the catch annually since 1989 (Einarsson, Árnason & Jónsson, 2008). According to Einarsson and Árnason (2001), salmon scales collected from 1989-2000 showed that the mean proportion of previous spawners of natural origin was 3,1% and majority (80%) were females.

## 2.7 Laxá in Aðaldalur

Laxá in Aðaldalur in the northeast of Iceland (figure 2) is a spring-fed river that originates in the lake Mývatn 277 m above sea level (Gíslason, 1991). In the river there are three hydro power stations and the flow fluctuations are negligible that can be seen on the unbroken riverbanks (Gíslason, 1991). The mean annual discharge is 42 m$^3$/s (see table 8 in appendix), measured by the gauging station Birningstaðasog (figure 2). Its water basin covers 2150 km$^2$ and the length of the river is 58 km, of which 26 km are accessible for fish (see table 8 in appendix), i.e. the stretch from the mouth in bay Skjálfandaflói to the waterfall Brúarfossar (Guðbergsson, 2004). Average salmon catch is 1609 per year (see table 8 in appendix). In Laxá there can be found salmon, trout, char and stickleback. According to Gíslason (1991), it is considered as being amongst the best salmon rivers in Iceland and the upper part sustains a world famous fishery for resident brown trout.

## *2.8 Miðfjarðará*

Miðfjarðará (in Bakkafjörður) originates from shallow water courses in about 500 m height above sea level in Miðfjarðarárdrög and from there it runs 50 km to the sea in the northeast of Iceland (Helgason, 1983). The river itself is 25 km long (see table 8 in appendix) with around 3,2 km accessible for fish (Helgason, 1983). Both salmon and char are known to run to the accessible part of the river and there is also a stock of resident char above a obstructive waterfall called Fálkafoss (Helgason, 1983). The Miðfjarðará water basin covers 139 km$^2$ and it has quite a few tributaries but the (see table 8 in appendix). Scales have been collected from the salmon catch annually since 1989 (Jónsson, Bjarni, personal comment).

# 3. Materials and Methods

## *2.1 Methods*

### 2.1.1 Importance of scales and scale reading

Scales play an important role in research on the life history of Atlantic salmon. As the fish grows circuli are added on the outside of the scales. From the closeness of these circuli and their pattern both age and growth history of the fish can be read (Bagenal & Tesch, 1978). As described by Anon (1984), wide-spaced circuli on the scale characterizes fast summer growth while narrow-spaced rings indicate slow or winter growth. From the scales, the size of the fish at different ages can be calculated, and also how many times it has spawned.

Before spawning, adult salmon changes in appearance as the bones grow bigger and a new set of breeding teeth appears (Mills, 1989). This change requires a large amount of minerals, mostly calcium (Tchernavin, 1938; Persson, P., Sundell, K., Björnsson, B. Th. & Lundqvist, H., 1998). The salmon is not feeding in this period so it has to take the minerals from other parts of the body, like the bones of the gill (Mills 1989) and the scales (Crichton, 1935, cited in Mills 1989). White and Medcof (1968) defined spawning marks as the regions in the scale where the circuli has discontinued growing. They develop first when the fish is in fresh water as parts of the scale near the edge may disappear. When the fish returns to sea and scales start growing again, the new circuli does not join the previous ones and often there is an area of scar tissue there between as can be seen in figure 3, figure 4 and figure 5.

### 2.1.2 Collection of data

*Origin of data*

As presented in table 9 in appendix and table 10 in appendix, the Institute of Freshwater Fisheries in Iceland provided the data used in the current research. Origin of the data can be seen in table 9 in appendix and table 10 in appendix.

Scales have been collected through the years by researchers, fishermen and fishing guides in the eight various rivers in concern. Much of the data used in this study existed on computers and a part was collected through personal communication. The rest was found in different form and different stage of procedure which called for special work input before it could be used in the study.

*Scale collecting*

According to Anon (1984), scales from the Atlantic salmon should be selected "3-6 rows above the lateral line and on a line extending from the anterior edge of the anal fin to the posterior edge of the dorsal fin". First the mucus should be removed from the area with a knife, the knife then cleaned and around 20 scale samples placed into a scale envelope. The envelope should dry slowly (Anon, 1984). When dry, around five scales with most of circuli whole from each individual are examined in a microscope. Earlier, the scales were put between small glass pieces but today impressions of some scales (about five) of each adult salmon are pressed onto a cellulose acetate slide so that they can be examined and read.

### 2.1.3 Scale reading

In the report from The International Council for the Exploration of the Sea (Anon, 1984) a general process how to read scales is recommended:

1. Identify the best scale.

2. Locate the beginning of the rapid sea growth phase.
3. Identify and count the annuli in the river zone
4. Identify and count the annuli and spawning marks in the sea zone.

The focus is the centre of the concentric lines in the scale. Circuli are the lines that can be seen on the surface of the scale as dark concentric lines. Band is a concentric region of the scale that is formed during a particular time of the year. A good scale should have the distance from the focus to the first circulus of less than 0,5 mm (Anon, 1984). The formation of spawning marks is described in chapter 2.1.1. To identify them is not always simple, because on some scales of previous spawners, parts of circuli have disappeared but in others complete bands have disappeared, as shown in figure 3, figure 4 and figure 5. Figure 3 shows a scale where the female salmon stayed for short time in the sea after spawning while figure 4 presents a scale from salmon that stayed a whole year in the sea after spawning before returning for a second spawn. Figure 5 shows a unique scale from a male that was returning for spawning for at least the fifth time.

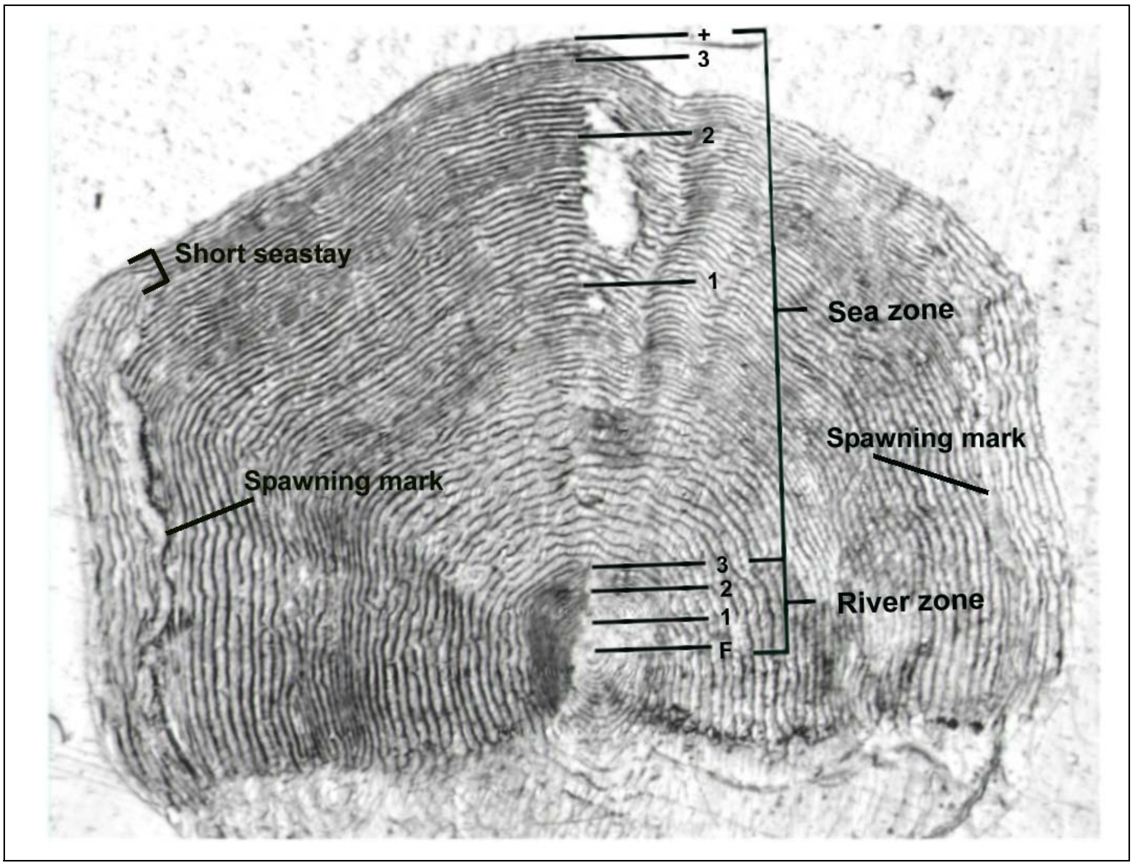


**Figure 3.** A scale from a female caught in Botnsá on the 21.07.1949. Its length was 78cm and weight 5000g. It had spent three years in freshwater and returned to the river as a 2SW, migrated to the sea next spring and stayed for a short time in the sea (short sea stay) before it came back to the river to spawn.

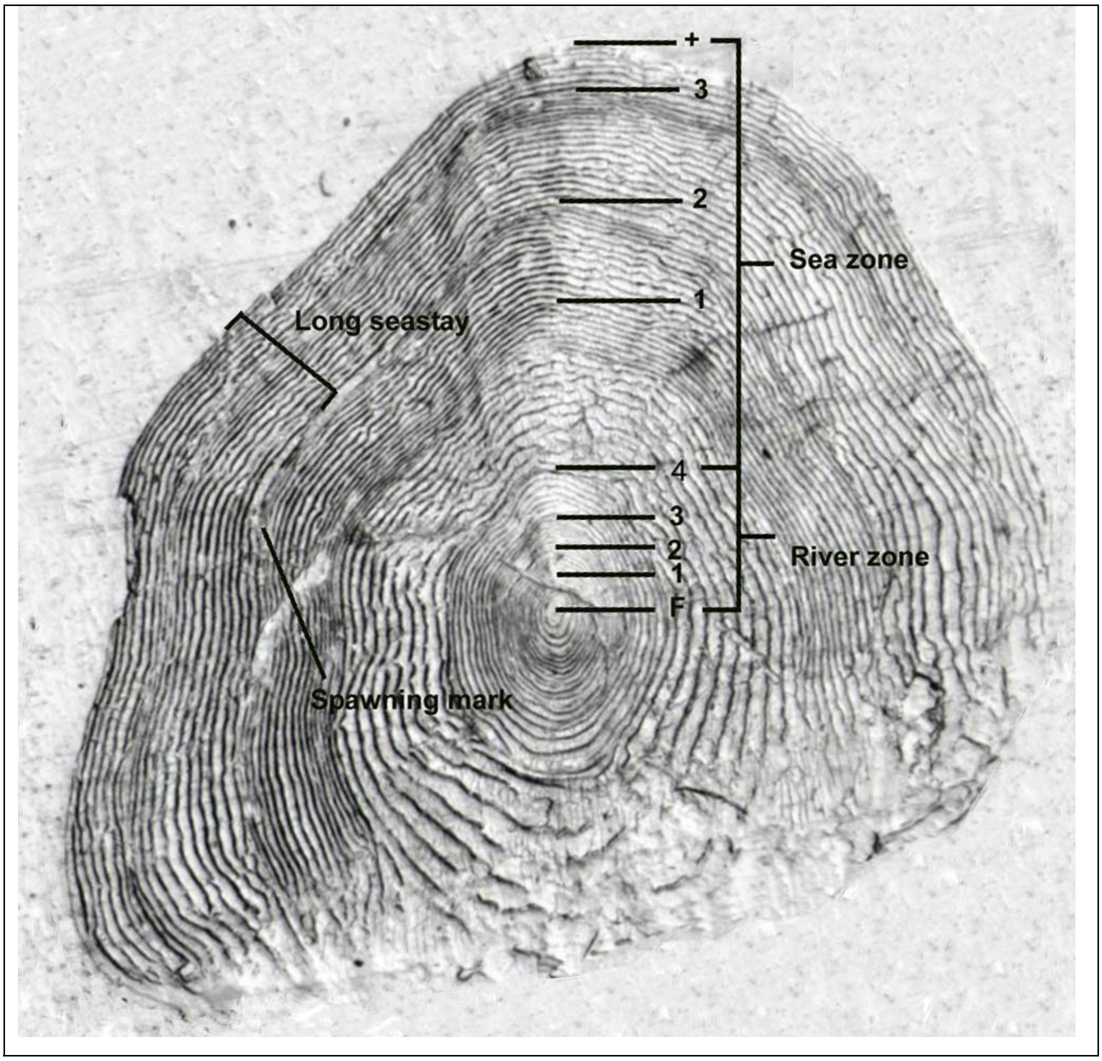


**Figure 4.** A scale sampled from a male caught in Botnsá on the 25.7.1948. Its length was 70 cm and weight 3500g. It spent four years in the river, and came to spawn as a 1SW, went out in the spring time and stayed over winter in the sea (long sea stay) before returning to spawn again in the river.

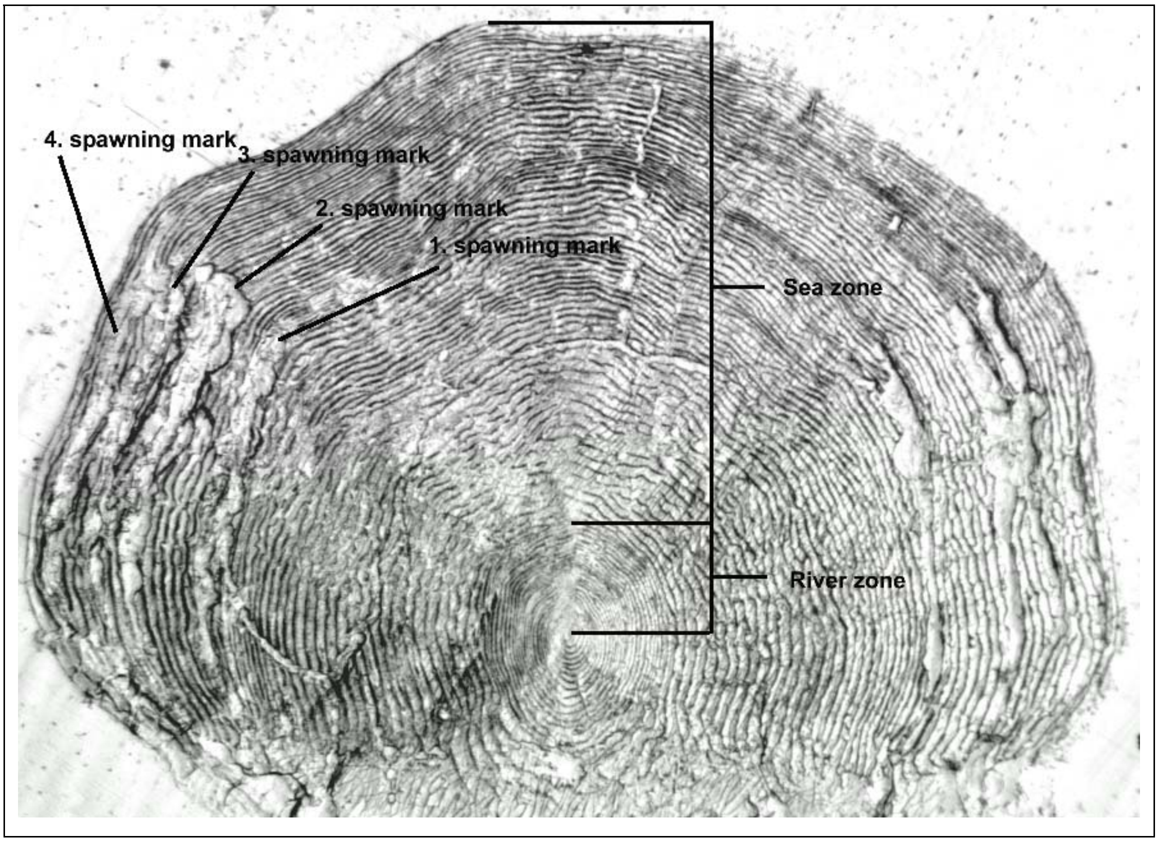


**Figure 5.** A scale sampled from a male caught in Botnsá on the 20.07.1949. Its length was 82cm and weight 5500g. When it was caught it was coming in for the fifth time to spawn. First it had come to spawn as a grilse and then at least four times after that.

### 2.1.4 Data and statistical methods

*Objective 1*

To describe data on repeat spawning as a proportion of the salmon catch in the study rivers was used box-plot in SigmaStat for the years 1989-2006 and column charts in MicrosoftExcel for all available data in the rivers including 1989-2006. Box-plots used in the study show mean for every river (dotted line), median (whole line), outliers, $25^{th}$ percentiles and $75^{th}$ percentiles and error bars that indicate the 90th and $10^{th}$ percentiles. Data available on repeat spawning varied between the study rivers. The years data was available is shown in figure 12 in appendix. Laxá in Aðaldalur and Botnsá have the oldest data reaching back to 1946 (Laxá in Aðaldalur) and 1948 (Botnsá), with large gaps in between but continuous data from 1985 (Laxá in Aðaldalur) and 1983 (Botnsá). Miðfjarðará has data from 1976 but has gaps in more recent data than the other rivers. The rivers from the south have continuous data from 1985 (Stóra-Laxá and Sog) and 1986 (Þjórsá). Available data from the rivers in the west is continuous in Norðurá from 1988 and in Flekkudalsá from 1989. Sample sizes in each river and between rivers can be seen in table 9 in appendix and table 10 in appendix. Within a year in one river, in the available data, the largest total sample size (first time and previous spawners) was 301 salmon (Laxá in Aðaldalur 1998) but the smallest was 6 salmon (Botnsá 1993).

*Hypothesis 1*

To investigate if there was significant difference between average proportion of repeat spawning between the study rivers a non-parametric test was used, one way analysis of variance on ranks called Kruskal-Wallis in SigmaStat program to test the median between the rivers. As described by Townend (2002) Kruskal-Wallis is an alternative to ANOVA that can test if there is difference between many groups when data fails requirements for ANOVA. Distributions of the values in populations need to be the same shape but not normally distributed. In Kruskal-Wallis, samples are placed in rank order and ranks related to each sample added up to give a set of sum of ranks. If the ranks are very different there is evidence that there is a difference (Townend, 2002). Then to test between which rivers there was significant difference pair-wise multiple comparisons was used, Dunn's method in SigmaStat, to find out if there was significant difference between the average (medians). Data used was from 1989 to 2006 in all rivers, apart from Miðfjarðará where 6 years were missing within the time period.

*Hypothesis 2*

To find out if incidence of repeat spawning has been changing over the period 1989 through 2006 in the study rivers regression in MicrosoftExcel was utilized which is used to define if there is linear relationship between x and y (Fowler, Cohen & Jarvis, 1998) in this case years (y) and proportion of previous spawners (x). Data was used from 1989 through 2007 from all rivers, except for Miðfjarðará there where 6 years were missing.

*Hypothesis 3*

To find out if location of a river affects the incidence of repeat spawning based on bedrock type and geographical area of the study rivers, information from figure 2 and table 8 (in appendix) was used to group the rivers together. For bedrock types Þjórsá, Stóra-Laxá, Sog, Laxá in Aðaldalur and Botnsá were classified as rivers in Plio-Pleistocene bedrock and Miðfjarðará, Norðurá and Flekkudalsá as rivers in Tertiary bedrock. In grouping rivers by geographical areas the north and east, Laxá in Aðaldalur and Miðfjarðará, became in one group and the rivers in the south and west in another group. For the statistics one way analysis of variance on ranks (Kruskal-Wallis) was used and Mann-Whitney Rank Sum Test in SigmaStat to test if there was difference between the averages (median) of the groups. Mann-Whitney is a non-parametric technique to compare the medians of unmatched samples but distributions in groups have to be similar (Fowler et al., 1998). Data used was from 1989 to 2006 in all rivers apart from Miðfjarðará where 6 years were missing.

*Hypothesis 4*

To find out if there is a difference between proportion of females and males among previous spawners in the induvidual study rivers t-test in SigmaStat was used, but if the data did not pass requirements like normal distribution Mann-Whitney rank sum test in SigmaStat was used. T-test is used when samples are small (under 30 observations) where the mean difference between two samples is divided by the standard error of the difference (Fowler et al., 1998). The Kruscal-Wallis in SigmaStat was used to see if there was difference between average (median) female or male proportion between the study rivers and Dunn's method to find out which ones. To see if there was difference in proportion of the two sexes in all the rivers combined Mann-Whitney rank sum test in SigmaStat was used. Salmon with unknown sex and years where no previous spawners came at all were taken out before running the tests. There were 144 years and 32 missing of each sex.

# 4. Results

## *4.1 Repeat spawning as a proportion of the salmon catch in the study rivers*

During the period from 1989 to 2006 the proportion of previous spawners was ranging from none at least one year in each study river (table 2) up to 25 % in Stóra-Laxá (table 2) in 1998 (figure 12 and table 9 in appendix). If the mean is compared with the median it can be seen that these numbers are quite various in the rivers. As shown in table 2 and figure 6 the mean ranges from 3,0 in Norðurá to 9,8 in Stóra-Laxá while the median ranges from 1,2 in Þjórsá to 6,0 in Stóra-Laxá. Stóra-Laxá seems to be the most different from the other rivers. Figure 6 shows how distorted the data is in most of the rivers so it is not likely to follow a normal distribution. Flekkudalsá seems to have the least distortion and is the most likely to follow a normal distribution. Looking at all available data, the highest proportion of previous spawners was found in Botnsá in 1949 where the proportion of previous spawners was 33% (figure 6).

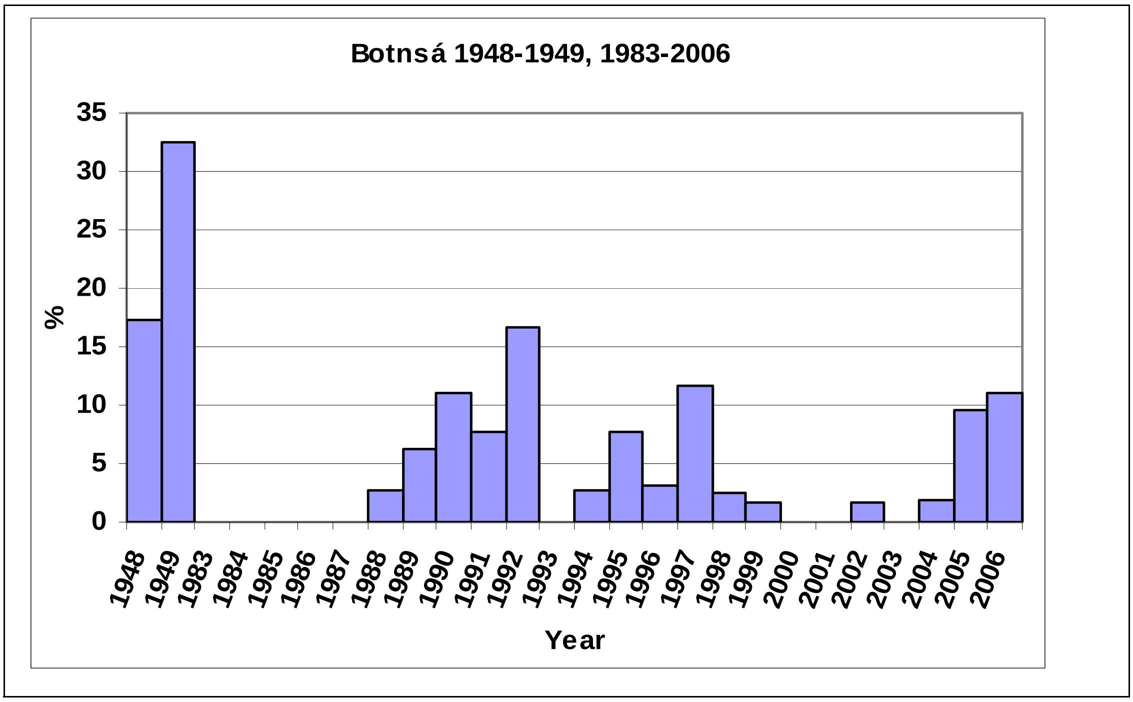


**Figure 6.** Proportion of the repeat spawning of total natural spawning in salmon samples from available data in Botnsá.

**Table 2.** Statistics for the proportion of the repeat spawning in the study rivers from 1989-2006.

| River | N (years) | Mean | Max | Min | Median | Std Dev | C.I. of Mean |
|---|---|---|---|---|---|---|---|
| Þjórsá | 18 | 3,4 | 13,6 | 0,0 | 1,2 | 4,6 | 2,3 |
| Stóra-Laxá | 18 | 9,8 | 25,0 | 0,0 | 6,0 | 7,7 | 3,8 |
| Sog | 18 | 6,6 | 20,0 | 0,0 | 5,1 | 5,8 | 2,9 |
| Botnsá | 18 | 5,3 | 16,7 | 0,0 | 2,9 | 5,1 | 2,5 |
| Norðurá | 18 | 3,0 | 7,5 | 0,0 | 2,4 | 2,1 | 1,0 |
| Flekkudalsá | 18 | 5,8 | 14,0 | 0,0 | 5,3 | 4,3 | 2,2 |
| Laxá in Aðaldalur | 18 | 3,6 | 23,5 | 0,0 | 1,5 | 5,8 | 2,9 |
| Miðfjarðará | 18 | 3,8 | 12,5 | 0,0 | 2,1 | 3,7 | 2,4 |

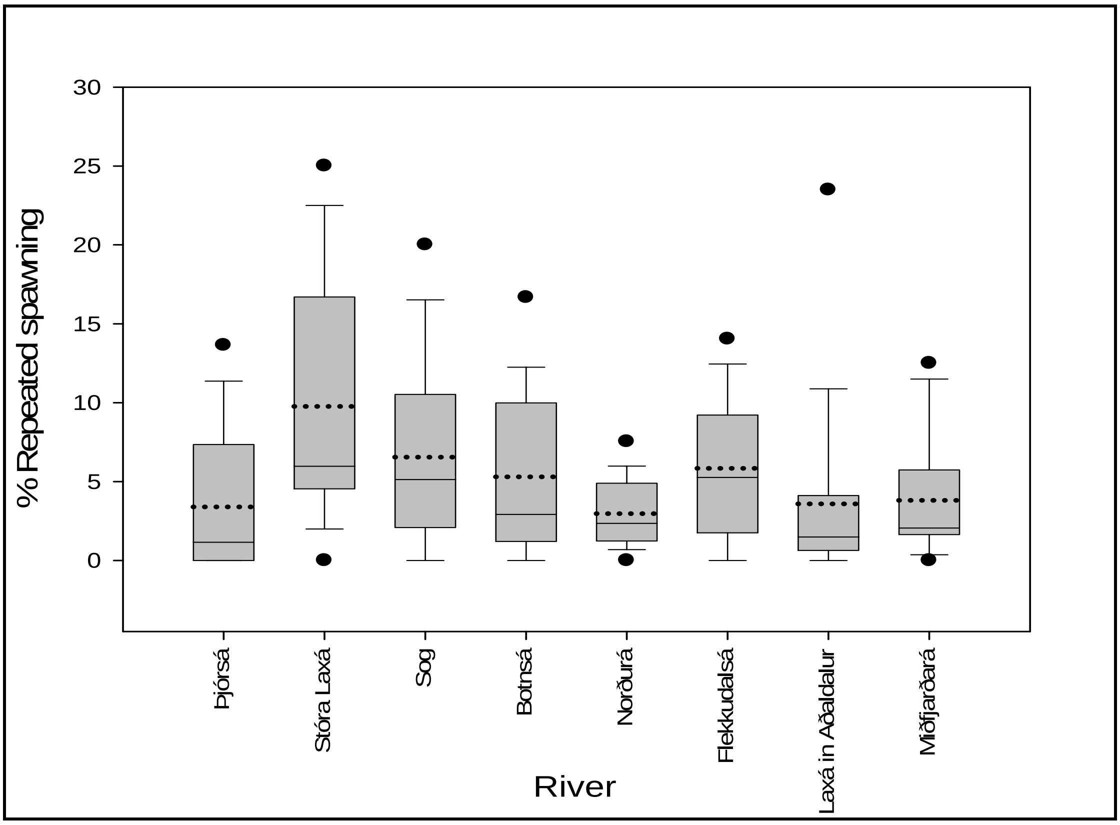


**Figure 7.** Box-plot of the repeat spawning in the study rivers from 1989-2006.

## *4.2 Average proportion of repeat spawning in the study rivers*

Following hypothesis was tested:

- There is no difference between average proportions of previous spawners between the study rivers ($H_0$).
- There is difference between average proportions of previous spawners between the study rivers ($H_1$).

As shown in figure 7 the average (median) proportion of previous spawners is quite various between the rivers, from 1,16 (Þjórsá) to 5,97 (Stóra-Laxá). When testing significant difference between the average (median) proportions repeat spawners between two individual study rivers the results were that most of the rivers had no significant difference between them. However there was significant difference between Stóra-Laxá and Þjórsá (q = 3,41) and Stóra-Laxá and Laxá in Aðaldalur (q = 3,36), then $H_0$ is therefore rejected and $H_1$ accepted.

## *4.3 Proportion of repeat spawning in the study rivers with time*

Following hypothesis were tested:

- The incidence of repeat spawning (based on catches) has not changed over the period 1989 through 2006 in individual rivers ($H_0$).
- The incidence of repeat spawning (based on catches) has changed over the period 1989 through 2006 ($H_1$).

As there can be seen in table 3 there is not significant change of proportion repeat spawning over the study period in Þjórsá (p=0,580), Stóra-Laxá (p=0,974), Sog (p=0,214), Botnsá (0,267), Norðurá (p=0,858) and Flekkudalsá (p=0,229). In Miðfjarðará it is not significant but very close (p=0,052). There is significant change of the proportion in Laxá in Aðaldalur (p = 0,013). The $r^2$ supports that y (time) explains very little of the x (proportion of repeat spawning) or from 0 to 9 % in most of the rivers. However in both of the rivers in the north, Laxá in Aðaldalur and Miðfjarðará, the $r^2$ is 33%, so 33% of the difference of x (proportion repeat spawning) can be explained by y (time). There has not been changes in incidence of repeat spawning in all rivers but Laxá in Aðaldalur therefore $H_0$ is accepted and $H_1$ rejected in those rivers. There has been reduction in repeat spawning over time in Laxá in Aðaldalur so there $H_0$ is rejected and $H_1$ accepted. In figure 8 can be seen regression line in Laxá in Aðaldalur where it was significant and Miðfjarðará where it was close to being significant.

**Table 3.** Regression of the proportion repeat spawning where x is the year and y is the proportion of repeat spawning.

| Location | Equation | R-square (%) | P-value for x variable |
|---|---|---|---|
| Þjórsá | y = -12x + 243,11 | 2,000 | 0,580 |
| Stóra-Laxá | y = 0,012x – 14,118 | 0,007 | 0,974 |
| Sog | y = -0,3342x + 647,08 | 9,000 | 0,214 |
| Botnsá | y = -0,263x + 530,65 | 8,000 | 0,267 |
| Norðurá | y = 0,0179x - 32,827 | 0,000 | 0,858 |
| Flekkudalsá | y = 0,2426x - 478,76 | 9,000 | 0,229 |
| Laxá in Aðaldalur | y = -0,6149x+1231,9 | 33,000 | 0,013 |
| Miðfjarðará | y = -0,3707x + 744,68 | 33,000 | 0,052 |

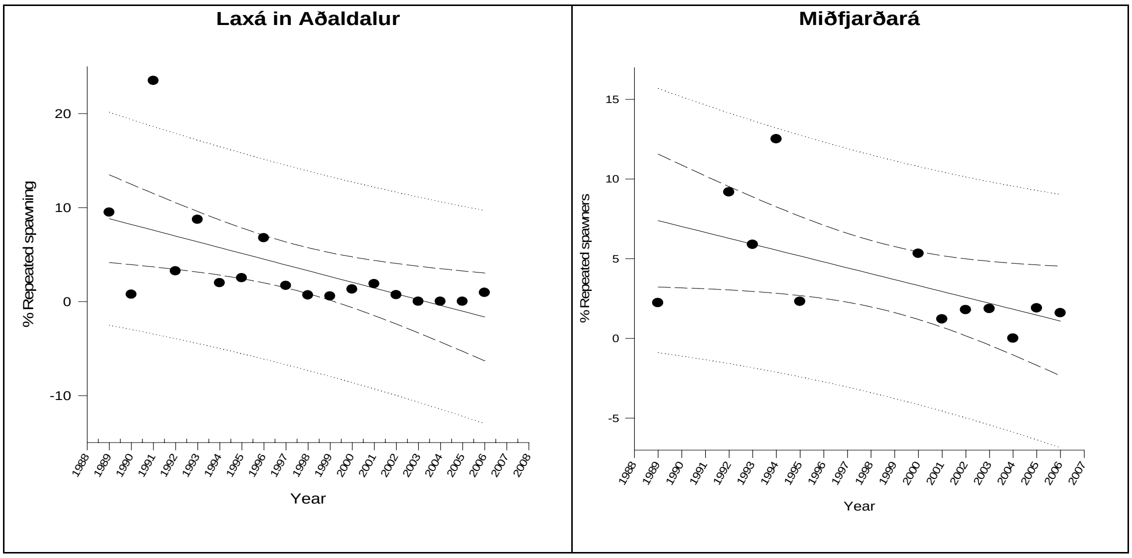

**Figure 8.** Regression lines of proportion of repeat spawning in Laxá in Aðaldalur and Miðfjarðará from 1989-2006.

## 4.4 Incidence of repeat spawning based on bedrock type and geographical area

*Variability based on bedrock type*

The following hypothesis were tested:

- Location of a river based on bedrock type does not affect the incidence of repeat spawning ($H_0$).
- Location of a river based on bedrock type affect the incidence of repeat spawning ($H_1$).

When the rivers were divided in two groups depending on bedrock, one group with rivers in Plio-Pleistocene bedrock and another with rivers originating in areas with Tertiary bedrock there was no significant difference between the groups (p = 0,717). Location of a river based on bedrock type does not affect the incidence of repeat spawning therefore the $H_0$ is accepted and $H_1$ rejected.

*Variability based on geographical area*

The following hypothesis were tested:

- Location of a river based on geographical does not affect the incidence of repeat spawning ($H_0$).
- Location of a river based on geographical area affects the incidence of repeat spawning ($H_1$).

When the rivers were divided in two groups depending on geographical areas, north and east versus south and west there appeared to be significant difference ($p = 0{,}049$) with Kruskal-Wallis. When tested with Mann-Whitney Rank Sum Test there was not significant difference ($p = 0{,}05$). If the results from Kruskal-Wallis test are used there is significant difference between rivers in the east and north and rivers from the south and west then $H_0$ is rejected and $H_1$ accepted. When using the Mann-Whitney Sum test $H_0$ is accepted and $H_1$ is rejected.

## *4.5 Proportion of female and male salmon amongst previous spawners in the study rivers*

The mean proportion of previous spawned females in all the study rivers gets as low as 45,1% in Stóra-Laxá (table 4) but median proportion gets down to 50% in the same river (table 4). The highest proportion of females is in Þjórsá where the mean is 98,5% and median is 100%. Most of the rivers have some years with only males arriving but two of the rivers have different minimum proportion numbers, Þjórsá (88,9%) and Norðurá (33,3%). As seen in figure 9 the data is distorted in Sog, Botnsá, Laxá in Aðaldalur and especially in Þjórsá where most values are the same. In the other rivers it is not as evident.

**Table 4.** Females amongst previous spawners in the study rivers from 1989-2006.

| River | Mean | Max | Min | Median | Std Dev | C.I. of Mean |
|---|---|---|---|---|---|---|
| Þjórsá | 98,9 | 100,0 | 88,9 | 100,0 | 3,5 | 2,5 |
| Stóra-Laxá | 45,1 | 100,0 | 0,0 | 50,0 | 35,7 | 18,3 |
| Sog | 70,2 | 100,0 | 0,0 | 100,0 | 41,4 | 23,9 |
| Botnsá | 69,0 | 100,0 | 0,0 | 90,0 | 38,7 | 22,4 |
| Norðurá | 76,6 | 100,0 | 33,3 | 75,0 | 21,1 | 10,9 |
| Flekkudalsá | 75,4 | 100,0 | 0,0 | 81,7 | 28,4 | 15,1 |
| Laxá in Aðaldalur | 46,6 | 100,0 | 0,0 | 60,0 | 37,2 | 21,5 |
| Miðfjarðará | 52,2 | 100,0 | 0,0 | 50,0 | 35,9 | 25,7 |

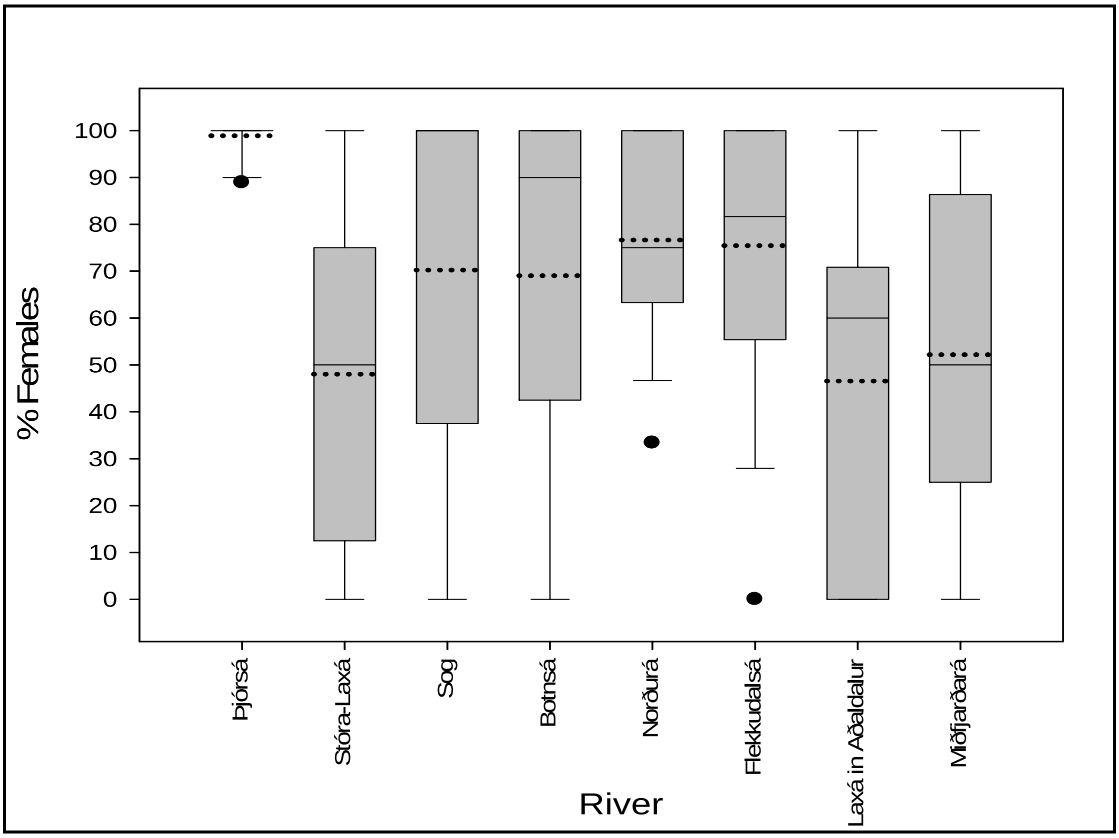


**Figure 9.** Box-plot of proportion of females amongst the previous spawners in the study rivers from 1989-2006.

In table 5 and figure 10 is presented the mean proportion of previous spawned males in the study rivers. It ranges from 1,1% in Þjórsá to 54,9% in Stóra-Laxá while the median from 0,0 in Þjórsá and Sog to 50% in Stóra-Laxá and Miðfjarðará. All of the rivers have some years where no males are arriving (table 5). Þjórsá differs from the other rivers with almost all the values in the same place (figure 10) and in all of the rivers except Miðfjarðará the values have distorted distribution (figure 10).

**Table 5.** Males amongst the previous spawners in the study rivers from 1989-2006.

| River | Mean | Max | Min | Median | Std Dev | C.I. of Mean |
|---|---|---|---|---|---|---|
| Þjórsá | 1,1 | 11,1 | 0,0 | 0,0 | 3,5 | 2,5 |
| Stóra-Laxá | 54,9 | 100,0 | 0,0 | 50,0 | 37,5 | 19,3 |
| Sog | 21,8 | 100,0 | 0,0 | 0,0 | 42,4 | 24,5 |
| Botnsá | 31,0 | 100,0 | 0,0 | 10,0 | 38,7 | 22,4 |
| Norðurá | 23,4 | 66,7 | 0,0 | 25,0 | 21,1 | 10,9 |
| Flekkudalsá | 24,6 | 100,0 | 0,0 | 18,3 | 28,4 | 15,1 |
| Laxá in Aðaldalur | 53,4 | 100,0 | 0,0 | 40,0 | 37,2 | 21,5 |
| Miðfjarðará | 47,8 | 100,0 | 0,0 | 50,0 | 35,9 | 25,7 |

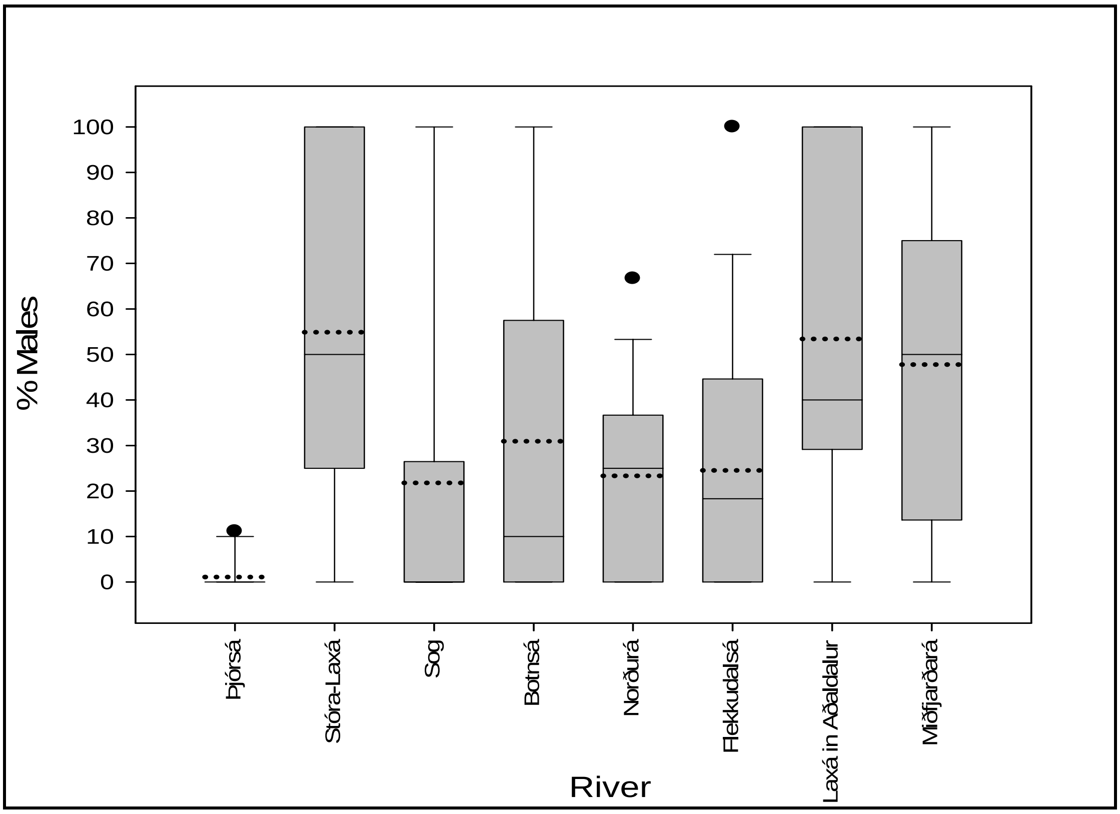


**Figure 10.** Box-plot of proportion of males amongst the previous spawners in the study rivers from 1989-2006.

*Females and males within each river*

The following hypothesis were tested:

- There is no difference between proportion of females and males among previous spawners in each study river ($H_0$).
- There is a difference between proportion of females and males among previous spawners in each study river ($H_1$).

As introduced in table 6 there is significant difference between numbers of females and males in Þjórsá (p = 0,001), Sog (p = 0,032), Botnsá (p = 0,015), Norðurá (p = 0,001) and Flekkudalsá (p = 0,001) so with these rivers $H_0$ is rejected and $H_1$ is accepted.

There is not significant difference between numbers of females and males in Stóra-Laxá (p = 0,452), Laxá in Aðaldalur (p = 0,631) and Miðfjarðará (p = 0,789). $H_0$ is therefore accepted and $H_1$ is rejected. It should be kept in mind that the power of the performed test is below the desired power (0,8) in Stóra-Laxá (0,05), Botnsá (0,639), Laxá in Aðaldalur (0,05) and Miðfjarðará (0,05). Then it is more likely that difference is not detected when one actually exists. That could be the case for Stóra-Laxá, Laxá in Aðaldalur and Miðfjarðará.

**Table 6.** Comparation of the proportion females and males amongst previous spawners in the individual study rivers.

| River | N (years) for each group | Missing N (years) for each group | Test | P-value | Power of the performed test |
|---|---|---|---|---|---|
| Þjórsá | 18 | 8 | Mann-Whitney | 0,001 | |
| Stóra-Laxá | 18 | 1 | t-test | 0,452 | 0,050 |
| Sog | 18 | 4 | Mann-Whitney | 0,032 | |
| Botnsá | 18 | 4 | t-test | 0,015 | 0,639 |
| Norðurá | 18 | 1 | t-test | 0,001 | 1,000 |
| Flekkudalsá | 18 | 2 | t-test | 0,001 | 0,999 |
| Laxá in Aðaldalur | 18 | 4 | t-test | 0,631 | 0,050 |
| Miðfjarðará | 18 | 8 | t-test | 0,789 | 0,050 |
| All rivers | 144 | 32 | Mann-Whitney | 0,001 | |

*Females and males in all the rivers*

When all numbers of males and females in the study rivers are pooled together the mean proportion of females is 66,4% (table 7) and males 33,0% (table 7). The median is quite different or from 72,1% females (table 7) and 25,0% males (table 7). In figure 11 can be seen that the distribution is distorted.

**Table 7.** Total previously spawned females and males in the study rivers from 1989-2006.

| Sex | Mean | Max | Min | Median | Std Dev | C.I.of Mean |
|---|---|---|---|---|---|---|
| Females | 66,4 | 100 | 0 | 72,1 | 35,3 | 6,6 |
| Males | 33,0 | 100 | 0 | 25,0 | 36,2 | 6,8 |

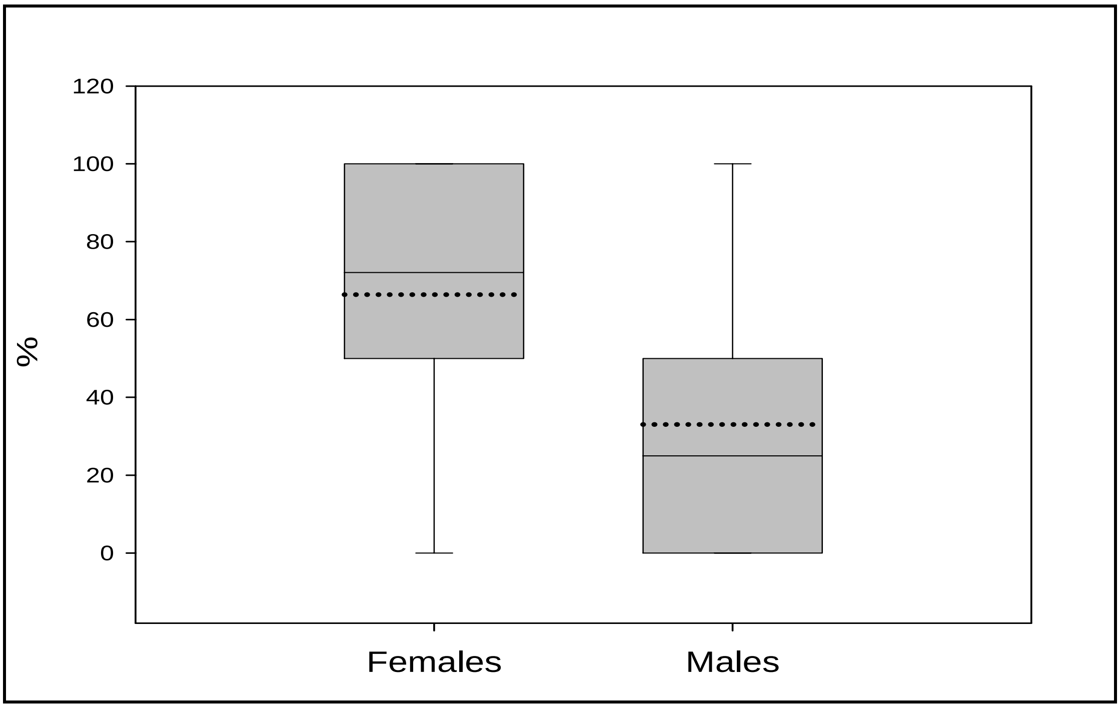


**Figure 11.** Box-plot of the total proportion of females and males amongst the previous spawners in the study rivers from 1989-2006.

The following hypothesis were tested:

- There is no difference between proportion of females and males among previous spawners in all study rivers ($H_0$).
- There is a difference between proportion of females and males among previous spawners in all study rivers ($H_1$).

There was significant difference ($p = 0,001$) between the proportion (median of all rivers used) of females and males when all river were tested together table 6. $H_0$ is therefore rejected and $H_1$ accepted.

*Difference in proportion of females and males between the rivers*

The following hypothesis were tested:

- There is no difference between the proportions of sexes between the study rivers ($H_0$).
- There is difference between the proportions of sexes between the study rivers ($H_1$).

When the rivers were compared with each other there was not significant difference between the majorities of them. There was significant difference between Þjórsá and Laxá in Aðaldalur ($q = 3,720$), Þjórsá and Stóra-Laxá ($q = 3,811$) and Þjórsá and

Miðfjarðará (q = 3,209). There is difference between some of the study rivers so $H_0$ is rejected and $H_1$ accepted.

# 5. Discussion

## *5.1 Repeat spawning in the study rivers*

In Iceland few studies are present on previous spawners so these results are important addition to the knowledge of them nationally and worldwide. The proportion of repeat spawning in the study rivers seems to be similar to other countries according to Mills (1989) and Jonsson et al. (1991a), but slightly lower than found in French rivers from 1987-1996 where the percent of previous spawners ranged from 0,5-3% (unpublised data, cited in Bardonnet & Baglinière, 2000). In this study, the southern river Stóra-Laxá stands out with the highest average (mean) proportion 9,0%. Many years within the older data was missing so it can’t be compared to the other rivers in the study. However, it is an important finding that one river reaches up to 33% repeat spawning in a single year (1949), which is close to the highest proportion of previous spawners in scale samples that the author could find in references from Scotland and Canada (Pyefinch, 1955 cited in Dymond, 1963; Calderwood, 1928 cited in Dymond, 1963; Moore, Chaput & Pickard, 1995). Also, some quite unique individuals were seen in the data, as the one seen in figure 5 with extraordinary life history as it was coming for the fifth time to spawn when caught. It is not known that an Icelandic salmon has spawned that many times before, but spawning for a fourth time has been reported from a salmon that was caught in Elliðaár River in 1992. It had been tagged as a parr in 1988 and when caught it was a 69 cm long salmon that weight 3000 g, with three spawning marks coming for the fourth spawning (Antonsson, Þórólfur, personal comment).

For further examination of the older data it would be interesting to compare the available catching data of previous spawners with other factors, like climatic and oceanic conditions. Such comparisons have been done previously by e.g. Scarnecchia, Ísaksson and White (1989) that studied many rivers in Iceland. They found that there was more variation of salmon catching (yields) in rivers with more variable environment. Especially in rivers in the northeast where there is more variation in summer and spring temperature when the smolts are moving to the sea.

More recent studies by Niemela et al. (2004b) show, that in River Teno in Finland there was significant positive relationship between mean sea temperatures in July in the year of smoltification and numbers of 1SW and MSW the following years. They did not, however, find any relationships like that in another finnish river, River Näätämöjoki, they also studied. By combining environmental factors there should be a possibility to test if rougher conditions in the sea or river would lead to fewer returning spawners and better conditions would lead to more previous spawners. This could further be combined to older data and together these could perhaps give a better picture of the life history of the salmon.

The highest proportion of repeat spawners was found in Stóra-Laxá, which was the only river that showed significant difference of average (median) with some of the other rivers. Stóra-Laxá and Þjórsá are located in the same geographical area (figure 2) so there are probably other factors than the conditions in the sea that are causing the difference. Stóra-Laxá is a direct run-off river while Þjórsá is a direct run-off river (mainly) with tributaries of various origins, as spring-fed origin and considerable glacial effects. The rivers have different behavior and annual water discharge (353$m^3$/s and 22$m^3$/s), as seen in table 8 in appendix. Jonsson, Hansen and Jonsson (1991a) found that in rivers smaller than 12$m^3s^{-1}$ salmon that had gained sexually mature after only one winter at sea was more than 70% of the population, whereas salmon that had taken two or three sea-winters to mature was more common in larger rivers. The flow in Þjórsá is probably more stable than Stóra-Laxá nowadays due to the hydro power plants, but it is likely that the strong glacial effect in Þjórsá has had great impact on the salmon stocks in the river. Obstacles on the way up the river, river type, temperature and visibility could have an effect on the life history of the stocks. It would, however, be needed to test more possible control factors within the rivers to find out what factor it is that has the most effect on the repeat spawning. Cunjak et al (1998, cited in Bardonnet & Baglinière, 2000) connected good survival of previous spawners in some rivers to the amount and variability of suitable winter habitats in the river system, like pools, lakes or river channels. These should be factors to consider for testing.

There was also a significant difference in the average (median) proportion of previous spawners between Stóra-Laxá and Laxá in Aðaldalur. These rivers are in different parts of the country (south and northeast), one is a direct run-off river (Stóra-Laxá) and the other (Laxá in Aðaldalur) is spring-fed with lake in the river system. The water discharge of Laxá in Aðaldalur is closer in amount to Stóra-Laxá (42 $m^3/s$ (see table 8 in appendix)) than to Þjórsá. According to Guðjónsson (1978), there is more cooling of the rivers in the north and northeast than in the rivers in the south. One would assume that Laxá in Aðaldalur, with more stable river environment and a lake providing nutrition to the river would make it easier for the salmon to recover and return again for spawning. On the other hand there could be more competition with energetic first time spawners, that would make it less possible for the previous spawned salmon to be successful if they returned, and therefore less important in their life history to return. As mentioned before, the conditions in the ocean and/or the type of river could be affecting the proportion of previous spawners.

Why there was not found significant difference between any of the other rivers could be because there *is* no difference between them but it could also be because there was not an adequate or enough data or some unknown influencing factor in the scale sampling or reading that could be affecting the results.

## 5.2 Repeat spawning in the study rivers over time

In Iceland, there has been a reduction in large salmon, 2SW or older, over the last decades due to unknown causes (Guðbergsson & Guðjónsson, 2005). As previous spawners are usually larger than 1SW salmon, we can assume that if there has been a reduction in numbers of large salmon the same would apply to previous spawners. It’s known that there is higher exploitation rate on the larger salmon partly, explained by the fact that they generally arrive earlier and stay for a longer time in the river during the fishing period (Guðbergsson & Guðjónsson, 2005). This fact has not been studied in relation to previous spawners, since they might not have the same arrival time. A study made by Moore, Chaput and Pickard (1995), in the Miramichi River in Canada, found that previous spawners that had spawned as 1SW were more abundant in June and July while previous spawners of 2SW maiden fish were more abundant in September and October. This pattern was not looked at in the current study.

When tested for significant changes of the proportion of repeat spawning with time within the data sets, only Laxá in Aðaldalur showed significant reduction. Miðfjarðará showed a trend in the same direction. Similar trend was shown in Newfoundland, where the percentage of previous spawners decreased to less than 5% of the commercial fisheries in the 1970´s, from 15-20% in the 1930´s (Chadwick, 1988). Studies from the Teno River in Finland over thirty more recent years (1972-

2003) have shown an increase in the proportion of previous spawners, even though numbers of 4SW salmon have decreased (Niemela et al., 2004b). The rivers with or close to significant negative correlation are both located in the northeast Iceland. In those rivers, only 33% of the proportion repeated spawners could be explained by the time period, and time explained very little in the other rivers and that was not significant. The explanation why there was a significant (and almost significant) reduction in the rivers in the northeast and not in the other rivers in the study might thus lie in some factors at sea or other environmental factors. Global warming could possibly be having an impact, as salmon from the north and east coast is known to travel to the ocean north of Faroe Islands, and salmon from the south and west coast to the west of Greenland. According to the Arctic Climate Impact Assessment (ACIA, 2004), the average temperature in the Arctic in the last decades has increased twice as much as in the rest of the world. It is known that fish species are moving their habitat boundaries further north (ACIA, 2004) so prey species of the Atlantic salmon could be disappearing, or other competitive fish species might be overtaking some habitats or food. There could be a difference in the degree of what is happening in different areas in the ocean. When we have more knowledge about where different salmon stocks stay in the ocean it will be easier to relate different factors and marine life studies to the return of the salmon to the rivers.

According to Guðbergsson (2008b), the number of 2SW fish has been decreasing in Laxá in Aðaldalur from 1979 due to of unknown factors, but their numbers in the river have generally been higher than 1SW. Due to the fact that large salmon is decreasing in numbers, the exploition rate got higher and possible overfishing occurred (Guðbergsson, Guðni, personal comment). The higher the exploitation rate is and the less salmon that over winters in the river, the less the possibilities for the salmon to survive to another spawning.

## *5.3 Repeat spawning based on location of the river*

Guðjónsson (1990b) divided the rivers in Iceland accordin to bedrock type in their drainage areas. He noted that that spring-fed rivers in the Plio-Pleistocene areas (as Sog and Laxá in Aðaldalur) and direct run-off rivers in the same areas (Þjórsá, Stóra-Laxá and Botnsá) are known for being high in conductivity, because of easily eroded bedrock, and these are often cold. According to Guðjónsson (1990a), rivers that are high in conductivity are more fertile than rivers low in conductivity, and are more likely to have salmon as the dominant species. Spring-fed rivers are often stable while direct run-off rivers are more unstable and can be difficult habitats. The direct run-off rivers in the Tertiary areas (as Norðurá, Flekkudalsá and Miðfjarðará) are often low in conductivity and nutrients but as they flow longer distances and if wetland and lakes are added to the system conductivity and nutrients increase. Most of the rivers in the study are mainly direct run-off rivers apart from Sog and Laxá in Aðaldalur. The rivers have quite different conductivity as seen in table 8 in appendix, that ranges from 44 µS/cm (Flekkudalsá) to 157 µS/cm (Laxá in Aðaldalur) which is very high but the second highest number is 83 µS/cm. The two lowest are rivers on the Tertiary area without a lake in the river system. Miðfjarðará has its conductivity value missing. When tested on the bases of bedrock type, there was not significant difference between the average (median) proportions of previous spawners between the groups. There might be other factors that have stronger effects than the bedrock, as the type and length of the river, different lakes, water discharge, wetland, steepness or other environmental conditions.

When the rivers were divided by geography there was a significant difference found on the average (median) proportion of previous spawners. The difference was between the two rivers in the northeast, that grouped together, and the rest that pooled together. Earlier studies by Antonsson (1998) and Scarnecchia and partners (1989) have also shown that there is a difference in salmon catches between rivers, when they are divided by geography. Antonsson (1998) was investigating the connection between environmental factors in the sea and salmon catch in two rivers, one in the south and one in the northeast while Scarnecchia et al. (1989) was looking at 59 rivers from all over the country.

## *5.4 Female and male salmon amongst previous spawners in the study rivers*

There was a significantly higher proportion of females than males among previous spawners, when all the study rivers were tested together, which supports earlier research from Ducharme (1969), Dymond (1963) and Baglinière and Porcher (1994). In the rivers in the west (Norðurá and Flekkudalsá), southwest (Botnsá) and the southern rivers Þjórsá and Sog, the proportion of females was significantly higher than the males. However, the northern rivers (Laxá in Aðaldalur and Miðfjarðará) and the southern river Stóra-Laxá did not give significant difference or only so with too little power of the test so the results were not reliable. Þjórsá was the only river that seemed to have significant difference in proportions of females and males with other rivers (Stóra-Laxá, Laxá in Aðaldalur and Miðfjarðará).

The reason why there are more females than males amongst the previous spawners is not quite clear. Neither is it clear why there is so much difference between rivers in the same area as there is between Þjórsá and Stóra-Laxá. Both of the sexes loose similar amount of energy during the spawning period, as was shown in studies by Jonsson et al. (1991a) and Jonsson et al. (1997). According to Fleming (1998), females fight for around 5-6 days over their territory, until they have finished nesting. Males can be reproductively active for over a month and fight over mating opportunities during that time (Webb & Hawkins, 1989) against other males. During that time they often get wounds that can become infected by fungus and these can kill them quickly (Baglinière & Porcher, 1994, cited in Bardonnet & Baglinière, 2000). So it can be assumed that more wounds in longer period of fighting can cause more deaths among the males than the females in the river.

Stóra-Laxá was the only river where the mean was higher for the males than females, which is interesting since that was also the river where the proportion of previous spawners was the highest which could perhaps be explained by the over winter conditions in the river as discussed in chapter 5.1.

## *5.5 The significance of previous spawners for Icelandic salmon stocks*

The data used in this study was sampled by many different people and scales were read by several people under the supervision of Institute of Freshwater Fisheries. Sample sizes were very variable, and are probably in most cases collected randomly but might in some years not be as randomly sampled as preferred. With increasing knowledge and better instructiosn from the Institute of Freshwater Fisheries one will assume that data collection has improved with time, even though this is hard to test. To see if the proportion of the sample sizes is describing the salmon stocks in the river or if larger salmon were rather sampled than smaller it would be necessary to compare the sampling with fishing log books. As White and Medcof (1968) noted, reading spawning marks from scales of salmon with known age is not always a reliable method to tell the exact age of a salmon. It tells us though the minimum of times the salmon has spawned. Even with skilled scale readers, important information of the life cycle can be lost from the scales due to scale erosion. It can be said that parts of the sampling might include some uncertainty of significance.

Variability in the environment should be selecting salmon with life history that will survive and can increase reproductive effort in difficult years. There are many factors that can affect salmon distribution, life history and abundance in Iceland, i.e. location, environment, discharge, temperature and how and where from the water comes into the river system etc. As studied by Moore, Chaput and Pickard (1995), the high increase of proportion of previous spawners amongst the 2SW fish was the result of reduced fisheries exploitation. It is known that exploitation rate of angling in Iceland is higher than in many salmon rivers in other countries (Einarsson & Guðbergsson, 2003), which can certainly effect possibilities for salmon to survive for another spawning.

Previous spawners are a small proportion of salmon stocks worldwide, as well as in Iceland, but they can play an important role in the survival of the species and the survival of individual stocks in some areas. According to Chadwick (1988) previous spawners are important because they mitigate the effects of variation in sea survival and if sea survival of 1SW salmon is low then previous spawners can offset small egg deposition. In the Miramichi River in Canada, 40% of the total egg depositions to the river have been contributed by previous spawners in some years (Moore et al., 1995). Saunders and Schom (1985) suggest that the diverse life history of salmon is the mechanism that enables small populations to persist and maintain genetic diversity, by givng the possibility for genetic contribution of one year-class over more years and therefore reduce the risk of inbreeding. With this variability in life-history, the salmon is also maximizing survival and population stability (Klementsen et al, 2003). Repeat spawning both lengthens the period of successful fishing and increases the value of the resource, but makes management more complicated (Niemela et al., 2006a) as more year classes are contributing to the fisheries. According to Chadwick (1988), the effect of decreased repeat spawning is less secure egg production, if there are some variations in sea survival.

The current study answered basic questions about previous spawners in few various salmon rivers in Iceland. During the study, other questions and ideas rose on the matter. It would be interesting to gather more climatic and oceanic data, both within the river and in the ocean, to analyse what factors can explain the difference in the proportion of previous spawners and also the difference in the proportion of females and males. Studies on when the previous spawners are returning to the river, how long they stay in the sea before returning to spawning and where they are staying remain a field for further studies.

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# Appendix

**Table 8.** Basic information about the study rivers.

| River | Water basin ($km^2$)[1] | Length (km)[1] | Accessible for fish | Gauging station[9] | Conduct-ivity (µS/cm)[3] | Geographical region | Type of river[1] | Distance from sea (km)[1] | Mean annual discharge $m^3$/s (no. of years (period)) | Average salmon catch per year 1974-2007 |
|---|---|---|---|---|---|---|---|---|---|---|
| Þjórsá | 7530 | 230 | 105[15] | 030 - Urriðafoss | 83 | S | D+J+L | 0 | 353 (36) [2] | 2317[5] |
| Botnsá | 79 | 9 | 3[11] | 014 - Stóribotn | 64 | SW | D+S | 0 | 4 (18(1967-1985)) [2] | 113[4] |
| Norðurá | 518 | 62 | 62[12] | 128 - Stekkur | 48 | W | D | 22 | 22 (35) [2] | 1634[4] |
| Stóra-Laxá | 512 | 90 | 37[16] | 411 - Stórhylur | 53 | S | D | 64 | 18 (5) [2] | 310[4] |
| Sog | 1200 | 20 | 11[10] | 271 -Ásgarður | 75 | S | L+S | 25 | 108 (34) [2] | 397[4] |
| Laxá in Aðaldalur | 2150 | 58 | 26[13] | 32 – Birningsstaða-sog | 157 | NE | L+S | 0 | 42 (47(1951-1998)[7] | 1609[4] |
| Flekkudalsá | 147 | 25 | 20[14] | | 44 | W | D | 0 | 1[8] | 239[4] |
| Miðfjarðará | 300 | 25 | 3,2[6] | | | NE | D | 0 | | 139[4] |

River type is explained with the following acronyms: D: Direct run-off river, L: Spring fed river, J: Glacial river and S: Lake on the river system.

[1]Rist, 1990.

[2]Þórarinsson, Óðinn (personal comment).

[3]Unpublished data.

[4]Guðbergsson, 2008a.

[5] Mean salmon catch in the drainage basin of Þjórsá 1996-2006 (Jóhannsson, 2007).

[6]Helgason, 1983.

[7]Þórarinsson, Óðinn (personal comment).

[8]Scarnecchia, 1984 cited in Einarsson, 1986.

[9]Orkustofnun, 2008.

[10]Jóhannsson & Guðjónsson, 2004.

[11] Einarsson, Sigurður Már cited in Hauksdóttir, 1999.

Zimsen, Kristinn. cited in Hauksdóttir, 1999.

Einarsson, Sigurður Már (personal comment) cited in Hauksdóttir, 1999.

[12] Valdemarsson, Sigurjón (personal comment) cited in Hauksdóttir, 1999.

[13] Einarsson, Sigurður Már cited in Hauksdóttir, 1999.

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[14] Einarsson, Sigurður Már cited in Hauksdóttir, 1999.

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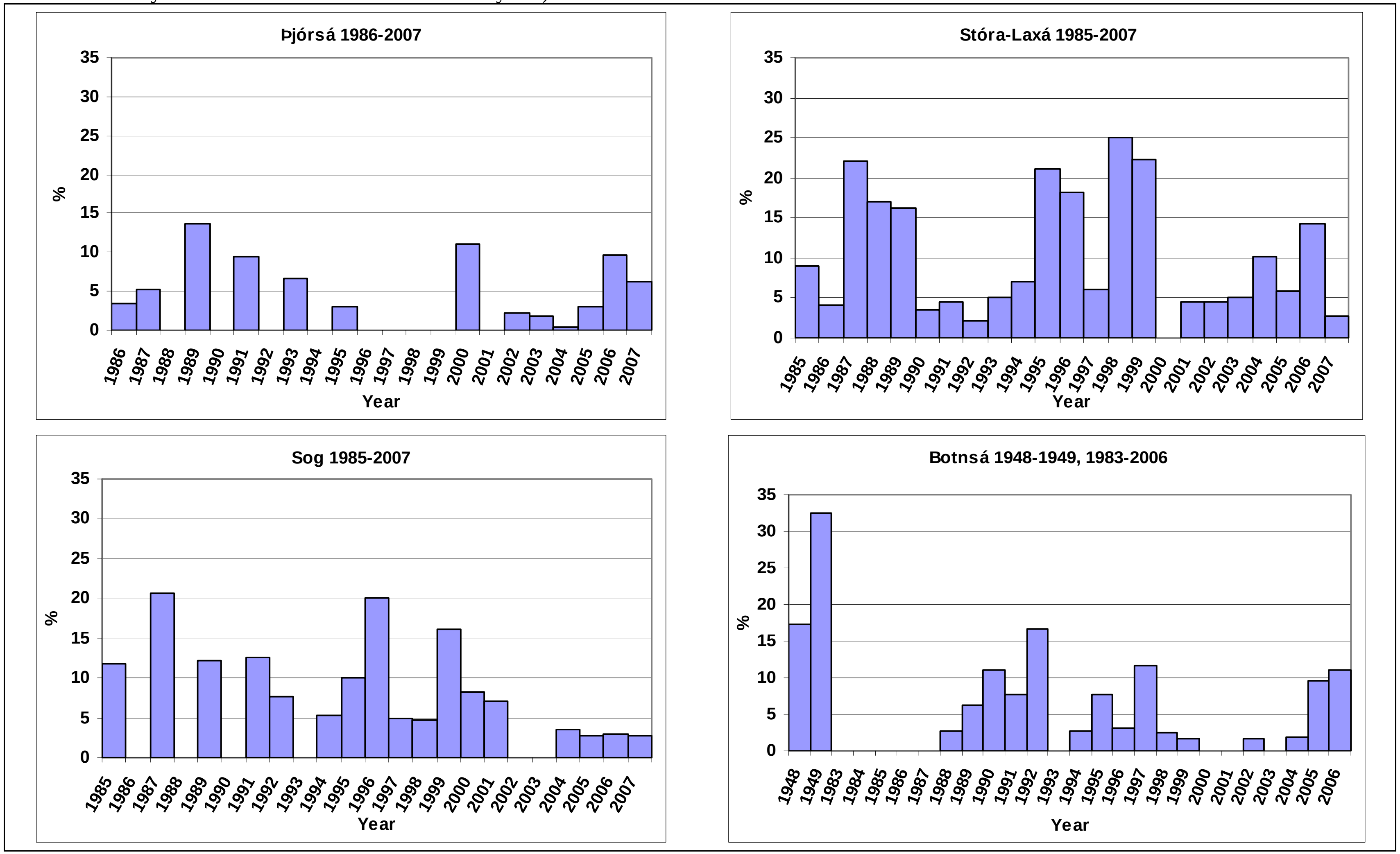
[15] Einarsson, Sigurður Már cited in Hauksdóttir, 1999.

Jóhannsson, M. & Guðjónsson, S. (1989) cited in Hauksdóttir, 1999.

Jóhannsson, Magnús (personal comment) cited in Hauksdóttir, 1999.

[16]Jóhannsson, Magnús (personal comment) cited in Hauksdóttir, 1999.

**Figure 12.** Proportion of previous spawners of total natural spawners in salmon samples from available data in various years in the study rivers (references: Table 9 for the years 1989-2006 and table 10 for other years).



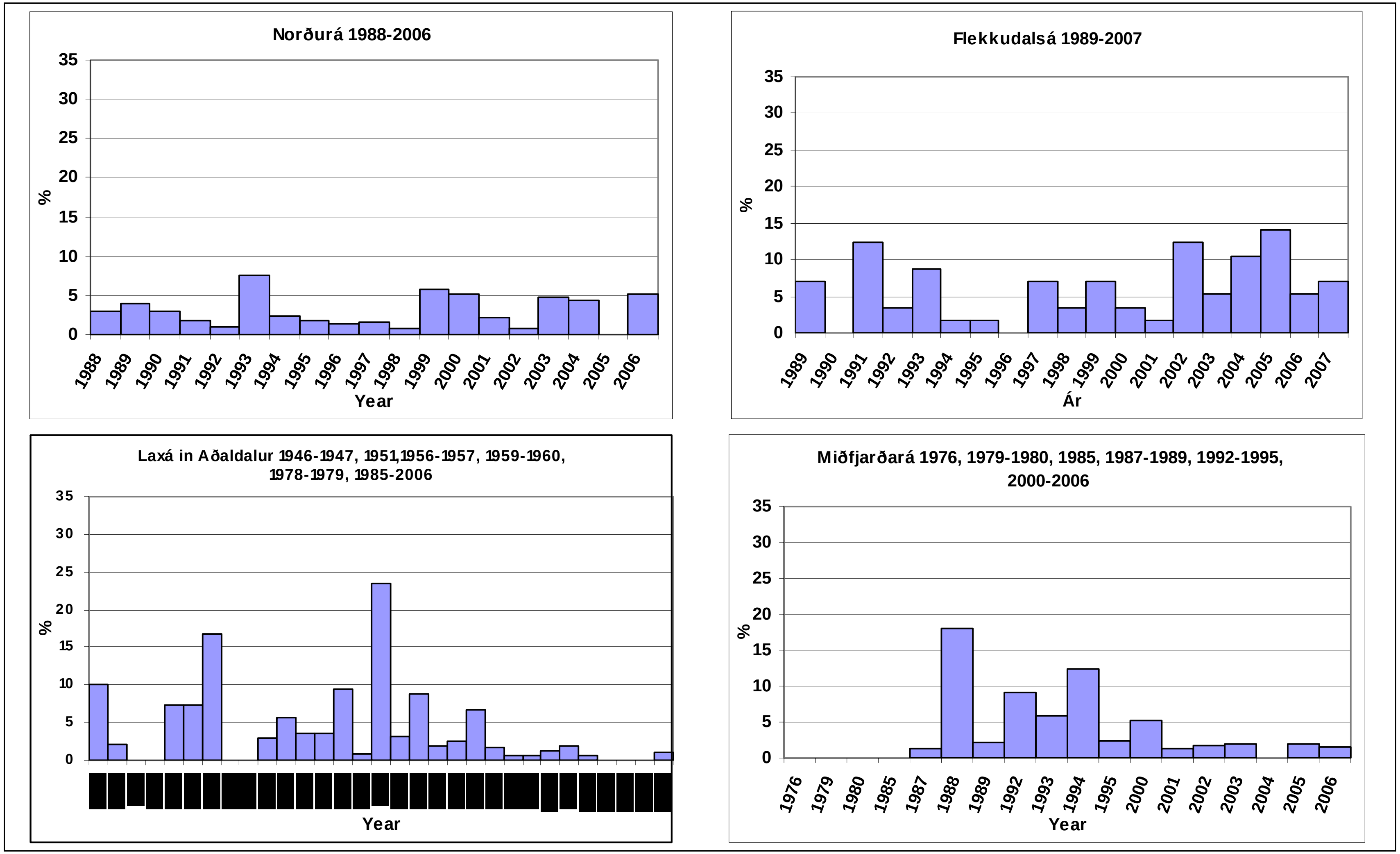

Norðurá 1988-2006
35
30
25
20
15
10
5
0
%
1988 1989 1990 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006
Year
Flekkudalsá 1989-2007
35
30
25
20
15
10
5
0
%
1989 1990 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007
Ár
Laxá in Aðaldalur 1946-1947, 1951,1956-1957, 1959-1960,
1978-1979, 1985-2006
35
30
25
20
15
10
5
0
%
[redacted]
Year
Miðfjarðará 1976, 1979-1980, 1985, 1987-1989, 1992-1995,
2000-2006
35
30
25
20
15
10
5
0
%
1976 1979 1980 1985 1987 1988 1989 1992 1993 1994 1995 2000 2001 2002 2003 2004 2005 2006
Year

**Table 9.** Data from the study rivers from 1989-2006 and references.

| River | Year | First time spawn. | Previous spawners | Total | % pre. spawn. | References |
|---|---|---|---|---|---|---|
| Þjórsá | 1989 | 57 | 9 | 66 | 13,6 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 1990 | 18 | 0 | 18 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 1991 | 48 | 5 | 53 | 9,4 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 1992 | 14 | 0 | 14 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 1993 | 28 | 2 | 30 | 6,7 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 1994 | 46 | 0 | 46 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 1995 | 64 | 2 | 66 | 3,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 1996 | 25 | 0 | 25 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 1997 | 13 | 0 | 13 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 1998 | 59 | 0 | 59 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 1999 | 25 | 0 | 25 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 2000 | 8 | 1 | 9 | 11,1 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 2001 | 23 | 0 | 23 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 2002 | 88 | 2 | 90 | 2,2 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 2003 | 108 | 2 | 110 | 1,8 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 2004 | 200 | 1 | 201 | 0,5 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 2005 | 220 | 7 | 227 | 3,1 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Þjórsá | 2006 | 93 | 10 | 103 | 9,7 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 1989 | 62 | 12 | 74 | 16,2 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 1990 | 27 | 1 | 28 | 3,6 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 1991 | 42 | 2 | 44 | 4,5 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 1992 | 44 | 1 | 45 | 2,2 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 1993 | 37 | 2 | 39 | 5,1 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 1994 | 40 | 3 | 43 | 7,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 1995 | 15 | 4 | 19 | 21,1 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 1996 | 18 | 4 | 22 | 18,2 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 1997 | 31 | 2 | 33 | 6,1 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |

| River | Year | First time spawn. | Previous spawners | Total | % pre. spawn. | References |
|---|---|---|---|---|---|---|
| Stóra-Laxá | 1998 | 18 | 6 | 24 | 25,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 1999 | 14 | 4 | 18 | 22,2 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 2000 | 13 | 0 | 13 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 2001 | 21 | 1 | 22 | 4,5 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 2002 | 21 | 1 | 22 | 4,5 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 2003 | 37 | 2 | 39 | 5,1 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 2004 | 35 | 4 | 39 | 10,3 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 2005 | 32 | 2 | 34 | 5,9 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 2006 | 24 | 4 | 28 | 14,3 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1989 | 33 | 4 | 29 | 12,1 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1990 | 9 | 0 | 9 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1991 | 24 | 3 | 21 | 12,5 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1992 | 13 | 1 | 12 | 7,7 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1993 | 13 | 0 | 13 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1994 | 19 | 1 | 18 | 5,3 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1995 | 30 | 3 | 27 | 10,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1996 | 10 | 2 | 8 | 20,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1997 | 40 | 2 | 38 | 5,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1998 | 43 | 2 | 41 | 4,7 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1999 | 31 | 5 | 26 | 16,1 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 2000 | 12 | 1 | 11 | 8,3 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 2001 | 14 | 1 | 13 | 7,1 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 2002 | 15 | 0 | 15 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 2003 | 37 | 0 | 37 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 2004 | 29 | 1 | 28 | 3,4 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 2005 | 36 | 1 | 35 | 2,8 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 2006 | 34 | 1 | 33 | 2,9 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Botnsá | 1989 | 30 | 2 | 32 | 6,3 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |

| River | Year | First time spawn. | Previous spawners | Total | % pre. spawn. | References |
|---|---|---|---|---|---|---|
| Botnsá | 1990 | 24 | 3 | 27 | 11,1 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Botnsá | 1991 | 12 | 1 | 13 | 7,7 | Viðarsson & Guðjónsson, 1992. |
| Botnsá | 1992 | 25 | 5 | 30 | 16,7 | Viðarsson & Guðjónsson, 1993. |
| Botnsá | 1993 | 6 | 0 | 6 | 0,0 | Viðarsson & Guðjónsson, 1994. |
| Botnsá | 1994 | 37 | 1 | 38 | 2,6 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Botnsá | 1995 | 24 | 2 | 26 | 7,7 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Botnsá | 1996 | 30 | 1 | 31 | 3,2 | Guðbergsson, Guðni (personal comment). |
| Botnsá | 1997 | 15 | 2 | 17 | 11,8 | Guðbergsson, Guðni (personal comment). |
| Botnsá | 1998 | 38 | 1 | 39 | 2,6 | Guðbergsson, Guðni (personal comment). |
| Botnsá | 1999 | 59 | 1 | 60 | 1,7 | Guðbergsson, Guðni (personal comment). |
| Botnsá | 2000 | 79 | 0 | 79 | 0,0 | Unpublished data from Institute of Freshwater Fisheries. |
| Botnsá | 2001 | 44 | 0 | 44 | 0,0 | Unpublished data from Institute of Freshwater Fisheries. |
| Botnsá | 2002 | 61 | 1 | 62 | 1,6 | Unpublished data from Institute of Freshwater Fisheries. |
| Botnsá | 2003 | 63 | 0 | 63 | 0,0 | Harðarson, Högni (personal comment). |
| Botnsá | 2004 | 52 | 1 | 53 | 1,9 | Harðarson, Högni (personal comment). |
| Botnsá | 2005 | 47 | 5 | 52 | 9,6 | Harðarson, Högni (personal comment). |
| Botnsá | 2006 | 40 | 5 | 45 | 11,1 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Norðurá | 1989 | 254 | 10 | 244 | 3,9 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 1990 | 200 | 6 | 194 | 3,0 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 1991 | 226 | 4 | 222 | 1,8 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 1992 | 188 | 2 | 186 | 1,1 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 1993 | 146 | 11 | 135 | 7,5 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 1994 | 242 | 6 | 236 | 2,5 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 1995 | 224 | 4 | 220 | 1,8 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 1996 | 232 | 3 | 229 | 1,3 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 1997 | 187 | 3 | 184 | 1,6 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 1998 | 130 | 1 | 129 | 0,8 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 1999 | 172 | 10 | 162 | 5,8 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |

| River | Year | First time spawn. | Previous spawners | Total | % pre. spawn. | References |
|---|---|---|---|---|---|---|
| Norðurá | 2000 | 58 | 3 | 55 | 5,2 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 2001 | 135 | 3 | 132 | 2,2 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 2002 | 129 | 1 | 128 | 0,8 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 2003 | 124 | 6 | 118 | 4,8 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 2004 | 114 | 5 | 109 | 4,4 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 2005 | 165 | 0 | 165 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Norðurá | 2006 | 196 | 10 | 186 | 5,1 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 1989 | 57 | 4 | 53 | 7,0 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 1990 | 78 | 0 | 78 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 1991 | 130 | 7 | 123 | 12,3 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 1992 | 83 | 2 | 81 | 3,5 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 1993 | 129 | 5 | 124 | 8,8 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 1994 | 52 | 1 | 51 | 1,8 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 1995 | 40 | 1 | 39 | 1,8 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 1996 | 93 | 0 | 93 | 0,0 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 1997 | 107 | 4 | 103 | 7,0 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 1998 | 159 | 2 | 157 | 3,5 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 1999 | 49 | 4 | 45 | 7,0 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 2000 | 50 | 2 | 48 | 3,5 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 2001 | 59 | 1 | 58 | 1,8 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 2002 | 116 | 7 | 109 | 12,3 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 2003 | 138 | 3 | 135 | 5,3 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 2004 | 122 | 6 | 116 | 10,5 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 2005 | 113 | 8 | 105 | 14,0 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Flekkudalsá | 2006 | 70 | 3 | 67 | 5,3 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Laxá in Aðaldalur | 1989 | 116 | 11 | 127 | 9,5 | Tómasson, 1991. |
| Laxá in Aðaldalur | 1990 | 134 | 1 | 135 | 0,7 | Tómasson, 1991. |

| River | Year | First time spawn. | Previous spawners | Total | % pre. spawn. | References |
|---|---|---|---|---|---|---|
| Laxá in Aðaldalur | 1991 | 132 | 31 | 163 | 23,5 | Tómasson, 1991. |
| Laxá in Aðaldalur | 1992 | 247 | 8 | 255 | 3,2 | Guðbergsson, 1993. |
| Laxá in Aðaldalur | 1993 | 195 | 17 | 212 | 8,7 | Guðbergsson, 1994. |
| Laxá in Aðaldalur | 1994 | 254 | 5 | 259 | 2,0 | Guðbergsson, 1995. |
| Laxá in Aðaldalur | 1995 | 280 | 7 | 287 | 2,5 | Guðbergsson, 1996. |
| Laxá in Aðaldalur | 1996 | 222 | 15 | 237 | 6,8 | Guðbergsson & Tómasson, 1997. |
| Laxá in Aðaldalur | 1997 | 178 | 3 | 181 | 1,7 | Guðbergsson, 1998. |
| Laxá in Aðaldalur | 1998 | 299 | 2 | 301 | 0,7 | Guðbergsson, 1999. |
| Laxá in Aðaldalur | 1999 | 181 | 1 | 182 | 0,6 | Guðbergsson, 2000. |
| Laxá in Aðaldalur | 2000 | 154 | 2 | 156 | 1,3 | Guðbergsson, 2002. |
| Laxá in Aðaldalur | 2001 | 107 | 2 | 109 | 1,9 | Guðbergsson, 2002. |
| Laxá in Aðaldalur | 2002 | 145 | 1 | 146 | 0,7 | Guðbergsson, 2003. |
| Laxá in Aðaldalur | 2003 | 144 | 0 | 144 | 0,0 | Guðbergsson, 2005. |
| Laxá in Aðaldalur | 2004 | 94 | 0 | 94 | 0,0 | Guðbergsson, 2005. |
| Laxá in Aðaldalur | 2005 | 115 | 0 | 115 | 0,0 | Guðbergsson, 2006. |
| Laxá in Aðaldalur | 2006 | 106 | 1 | 107 | 0,9 | Guðbergsson, 2007. |
| Miðfjarðará | 1989 | 132 | 3 | 135 | 2,2 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Miðfjarðará | 1992 | 109 | 11 | 120 | 9,2 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Miðfjarðará | 1993 | 96 | 6 | 102 | 5,9 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Miðfjarðará | 1994 | 28 | 4 | 32 | 12,5 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Miðfjarðará | 1995 | 127 | 3 | 130 | 2,3 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Miðfjarðará | 2000 | 89 | 5 | 94 | 5,3 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Miðfjarðará | 2001 | 82 | 1 | 83 | 1,2 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |

| River | Year | First time spawn. | Previous spawners | Total | % pre. spawn. | References |
|---|---|---|---|---|---|---|
| Miðfjarðará | 2002 | 110 | 2 | 112 | 1,8 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Miðfjarðará | 2003 | 53 | 1 | 54 | 1,9 | Harðarson, Högni (personal comment). |
| Miðfjarðará | 2004 | 126 | 0 | 126 | 0,0 | Harðarson, Högni (personal comment). |
| Miðfjarðará | 2005 | 155 | 3 | 158 | 1,9 | Njarðardóttir, Eydís (personal comment). |
| Miðfjarðará | 2006 | 62 | 1 | 63 | 1,6 | Unpublished data from Institute of Freshwater Fisheries. |

**Table 10.** Available data (not included in testing hypothesis) from the study rivers from various years and its references.

| River | Year | Reference |
|---|---|---|
| Þjórsá | 1986-1988, 2007 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Stóra-Laxá | 1985-1988, 2007 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Sog | 1985-1988, 2007 | Unpublished data from Institute of Freshwater Fisheries in Selfoss. |
| Botnsá | 1948-1949 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Botnsá | 1983 | Kristjánsson, Jón (personal comment) |
| Botnsá | 1984 | Garðarson, Finnur (personal comment). |
| Botnsá | 1985 | Tómasson,1987. |
| Botnsá | 1986 | Tómasson, 1987; Guðbergsson, Guðni (personal comment). |
| Botnsá | 1987 | Guðbergsson, Guðni (personal comment). |
| Botnsá | 1988 | Guðbergsson, Guðni (personal comment); Unpublished data from Institute of Freshwater Fisheries. |
| Norðurá | 1988 | Unpublished data from Institute of Freshwater Fisheries in Hvanneyri. |
| Laxá in Aðaldalur | 1946-1947, 1951,1956-1957,1959-1960, 1978-1979, 2007 | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |
| Laxá in Aðaldalur | 1985-1990, 1946-1947, 1951, 1956-1957, 1959-1960 | Unpublished data from Institute of Freshwater Fisheries in Sauðárkrókur. |
| Laxá in Aðaldalur | 1987 | Tómasson, 1988. |
| Laxá in Aðaldalur | 1988 | Tómasson, 1989. |
| Miðfjarðará | 1976, 1979-1980, 1985, 1987-1988, | Unpublished data from Institute of Freshwater Fisheries in Reykjavík. |