

Marit Melby Jacobsen

A comparison of life history and biological characters between Atlantic salmon first-time and repeat spawners in two Norwegian rivers

Master's thesis in Ocean resources

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Department of Natural History



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Abstract

Iteroparity is a trade-off strategy between current and future reproduction. The risk of failure in reproduction is spread out in time if the fish can survive its first spawning and spawn again at a later point in time. The proportion of Atlantic salmon (*Salmo salar* L.) repeat spawners in a population can vary greatly among rivers and years, but information on life history and biological characters among these individuals are limited. Differences in life history and biological characters between Atlantic salmon first-time and repeat spawners were therefore studied during 1984-1987 and 2020-2021 in River Beiarelva, Northern Norway, and River Stjørdalselva, Central Norway. In total, 426 fish (≥ 880 mm) were caught by angling in the two rivers and scales were analysed.

The proportion of repeat spawners in the selected sample increased significantly from 5% to 32% in Stjørdalselva, but showed only a tendency in increase from 7% to 22% in Beiarelva between 1984-1987 and 2020-2021. Females constituted a significant higher proportion of the repeat spawners in Stjørdalselva in 2020-2021, but no statistical support was given for the observed sex frequencies in Beiarelva in the two periods nor Stjørdalselva in 1984-1987. In Beiarelva and Stjørdalselva, 13 and 19, respectively, unique life histories were found based on different combination of smolt age, sea age at first spawning and sea age at repeat spawning. Of the total life history combinations, 38% and 53% of the combinations were only found among the repeat spawners. This high amount of contribution to variation in life histories despite a low percentage of individuals in the total population, illustrates that repeat spawners can influence the population dynamics significantly since different year classes of salmon will be present during the spawning season. In Stjørdalselva, repeat spawners had on average 44 mm longer body length than first-time spawners in 2020-2021, and were on average caught earlier during the angling season compared to first-time spawners regardless of period. This difference in body length and capture date was not found in Beiarelva nor in Stjørdalselva in 1984-1987. Sea age at first spawning was lower for repeat spawners than first-time spawners in both periods and in both rivers, suggesting that repeat spawners spawn at an earlier age, at least for fish ≥ 880 mm in this sample.

Changes in management approaches and ecological factors in rivers and at sea have most likely affected the proportion of repeat spawners between 1984-1987 and 2020-2021. Future management actions to protect potential large repeat spawners may be stricter catch regulations of large salmon earlier in the angling season. However, this must be adjusted to different rivers, as capture date differed between first-time and repeat spawners in Beiarelva and Stjørdalselva.

Sammendrag

Iteroparitet er en avveiningsstrategi mellom nåværende og fremtidig reproduksjon. Risikoen for svikt i reproduksjonen er spredt over tid dersom fisken kan overleve sin første gyting og gyte igjen på et senere tidspunkt. Andelen flergangsgytere av Atlantisk laks (*Salmo salar* L.) i en bestand kan variere mye mellom elver og år, men informasjon om livshistorie og biologiske karakterer blant disse individene er begrenset. Forskjeller i livshistorie og biologiske karakterer mellom første- og flergangsgytende Atlantisk laks ble derfor studert i tidsperiodene 1984-1987 og 2020-2021 i Beiarelva i Nord-Norge og Stjørdalselva i Midt-Norge. Totalt 426 fisk (≥ 880 mm) ble fanget i sportsfiske i de to elvene, og skjellprøver ble undersøkt.

Andelen flergangsgytere i det valgte utvalget økte signifikant fra 5 % til 32 % i Stjørdalselva, men viste bare en tendens i økning fra 7 % til 22 % i Beiarelva mellom 1984-1987 og 2020-2021. Hunnfisk utgjorde en betydelig høyere andel av flergangsgyterne i Stjørdalselva i 2020-2021, men det ble ikke gitt statistisk støtte for de observerte kjønnsfrekvensene i Beiarelva i de to tidsperiodene og heller ikke i Stjørdalselva i 1984-1987. I Beiarelva og Stjørdalselva ble det funnet henholdsvis 13 og 19 unike livshistorier basert på kombinasjoner av smoltalder, sjøalder ved første gyting og sjøalder ved gjentatt gyting. Av livshistorie-kombinasjonene ble 38 % og 53 % av kombinasjonene kun funnet blant flergangsgyterne. Det høye bidraget til variasjon i livshistorier til tross for en lav andel individer i den totale populasjonen, illustrerer at flergangsgytere kan ha en signifikant påvirkning på populasjonsdynamikken siden ulike årsklasser av laks vil være til stede i gytasesongen. I Stjørdalselva var flergangsgyterne i gjennomsnitt 44 mm lengre enn førstegangsgyterne i 2020-2021, og de ble i gjennomsnitt fanget tidligere i fiskesesongen enn førstegangsgyterne uavhengig av tidsperiode. Denne forskjellen i kroppslengde og fangsttidspunkt ble ikke funnet i Beiarelva og heller ikke i Stjørdalselva i 1984-1987. Sjøalderen ved første gyting ble funnet å være lavere for flergangsgytere enn førstegangsgytere i alle tidsperioder i begge elvene, noe som tyder på at flergangsgytere gyter ved en lavere alder for fisk, i hvert all for fisk ≥ 880 mm i denne prøven.

Endringer i forvaltningstilnæringer og økologiske faktorer både i elver og til havs har mest sannsynlig påvirket andelen flergangsgytere mellom 1984-1987 og 2020-2021. Fremtidige forvaltningstiltak for å beskytte potensielle store flergangsgytere kan være strengere fangstreguleringer av stor laks tidligere i sportsfiskesesongen. Dette må imidlertid tilpasses ulike elver, da fangstdato var forskjellig mellom første- og flergangsgytere i Beiarelva og Stjørdalselva.

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1. Introduction

Atlantic salmon (*Salmo salar* L.) has historically strong cultural, social, and economic roots in the society in countries located at both sides of the North Atlantic Ocean (Aas *et al.*, 2010). One of the fascinating characteristics with Atlantic salmon is their ability to migrate between fresh and salt water, a migration pattern called diadromy (McDowall, 1997). A type of diadromy is anadromy, which involve spawning in freshwater. This applies to Atlantic salmon that spawn in freshwater, and migrate from the river to sea for increased feeding and growth opportunities (McDowall, 1997; Jonsson & Jonsson, 2011). In Norway, Atlantic salmon is valued as an angling and harvestable resource for fishers in rivers and at sea, and as a cultivable resource through aquaculture along the Norwegian coastline since the 1970s (Aarset *et al.*, 2005; Aas *et al.*, 2010).

The annual return of Atlantic salmon from the sea to Norwegian rivers for spawning has declined since 1983, and Atlantic salmon populations from central and southern Norway have faced decreased growth rates the first year in the sea (Vollset *et al.*, 2022; VRL, 2022). The biggest threats to sustainability of the Norwegian wild Atlantic salmon are salmon lice and escaped farmed salmon from the aquaculture industry (Johnsen *et al.*, 2021; Stige *et al.*, 2022; VRL, 2022). The reduction in adult individuals returning to rivers for spawning is the main reason why Atlantic salmon is listed as near threaten (NT) in the Norwegian list of threaten species (“The red list”) (Hesthagen *et al.*, 2021).

Limited resources in the environment will shape life history strategies and evolution. For salmonids, this manifests trade-offs between current and future reproduction, in terms of both offspring and adult survival (Murphy, 1968; Bordeleau *et al.*, 2020). Atlantic salmon are unlike several species of Pacific salmon (*Oncorhynchus* spp.) iteroparous (Schaffer, 1974; Crespi & Teo, 2002). Iteroparity includes several reproductive events for an individual within the lifetime, in contrast to semelparity, which is characterized by one single spawning event with consecutive death (Cole, 1954). Iteroparity is favoured when adults are long-lived and have high survival, but offspring have low survival or high variability in survival (Murphy, 1968; Schaffer, 1974). The risk of failure in reproduction will therefore be spread in time if the adult can survive its first spawning and spawn again at a later point in time. This is the opposite to semelparity where all energy and risk of failure is invested in one single reproductive event (Murphy, 1968; Stearns, 1976).

Individuals of Atlantic salmon who recover from the first spawning event and spawn for a second or more times are denoted as repeat spawners. Individuals that spawn multiple times migrate to sea between the reproductive events to feed and regain energy. This energy is used to build up the somatic body mass reserves and produce gonads, which is an energy demanding process (Jonsson & Jonsson, 2011). The recovery period in the sea between spawning events for repeat spawners is often 1 or 2 years, depending on the fish being a consecutive or alternate spawner, respectively (Persson *et al.*, 2022). The migration patterns of Atlantic salmon are well studied (Jonsson *et al.*, 1993; Aas *et al.*, 2010; Jonsson & Jonsson, 2011), but the degree of salmon that survive spawning and migrate between river and sea multiple times (repeat spawners) are less explored (Halttunen *et al.*, 2009; Halttunen *et al.*, 2013). More knowledge of Atlantic salmon repeat spawners is needed to understand their ecological role in Atlantic salmon populations, and to explain potential differences between individuals that spawn once (first-time spawners) and multiple times (repeat spawners) when it comes to biological characters such as age and growth in the rivers and at sea.

The proportion of individuals that spawn multiple times in an Atlantic salmon population are often between 1-40%, but there is a huge variation among years and rivers (Fleming, 1996; Bordeleau *et al.*, 2020; Persson *et al.*, 2022). A study of 205 050 individual Atlantic salmon from 179 rivers in Norway showed an average of 3.8% repeat spawners caught during the angling season, but the variation between rivers ranged from 0% to 26%. This study also showed that 75% of the total variation in life histories, defined as a combination of smolt age and sea age at spawning, in a population was due to the presence of repeat spawners (Persson *et al.*, 2022).

Repeat spawners may be important for populations of wild salmon in years when few first-time spawners return to the rivers for spawning (Ducharme, 1969; Halttunen, 2011; Bordeleau *et al.*, 2020). In years when smolt runs fail or many individuals die during the marine feeding, which gives subsequent low year classes of salmon, repeat spawners can act as a stabilizing factor. The occurrence of repeat spawners in such cases can lead to maintenance and variation of the genetic composition in an Atlantic salmon population (Halttunen, 2011; Bordeleau *et al.*, 2020). In River Etne, female repeat spawners contributed 43% of the female biomass and fecundity during the spawning season in 2014, when the general return of Atlantic salmon was low (Harvey *et al.*, 2022). The reproductive success of female salmon is highly connected with large body mass due to the development of gonads and eggs. Research from Canadian rivers has showed that a female repeat spawner can contribute 1.4-1.6 times more eggs during a spawning

season than first-time spawners, which shows valuable contributions to population dynamics by repeat spawners (Bordeleau *et al.*, 2020; Persson *et al.*, 2022).

Possible variation in the proportion of repeat spawners and sex ratio among the Atlantic salmon over time, may be explained by changes in environmental factors and management approaches. Environmental factors can be changes in temperature and feeding opportunities both in fresh and salt water (Hedger *et al.*, 2013; Vollset *et al.*, 2022). Differences in both marine and freshwater conditions among years and time periods might contribute to variation in post-smolt survival and number of returning spawning individuals, affecting the proportion of first-time and repeat spawners (Chaput, 2012). During recent years, fishing mortality is reduced both in the sea and rivers, and catch and release of Atlantic salmon has been increasingly used as a management tool to maintain angling when populations are declining or reduced in several countries and rivers (Post *et al.*, 2002; April *et al.*, 2021; VRL, 2022). Fishing regulations can affect the survival of Atlantic salmon differently among size classes and between the sexes (Miljødirektoratet, 2017). Specified fishing rules for female Atlantic salmon after a certain date during the angling season is a common management approach in several rivers to protect the female spawning individuals (Forseth *et al.*, 2013). Changes in selective harvest of Atlantic salmon fisheries at sea may also impact the proportion of repeat spawners (Bordeleau *et al.*, 2020). Investigations of biological characters may explain possible differences in life history between individuals that spawn once or multiple times, which may reflect environmental factors and management approaches in both the rivers and at sea.

The main aim of this master thesis was to investigate the proportion, life history and biological characters of Atlantic salmon repeat spawners in the rivers Beiarelva and Stjørdalselva during two different time periods: 1984-1987 and 2020-2021. The specific aims were to investigate if 1) the proportion of repeat spawners differed between the periods in the two rivers, 2) there were differences in sex ratio of the repeat spawners between the periods and rivers, 3) condition factor, total body length, smolt length, smolt age, sea age at first spawning, growth the first year in the sea, and capture time differed between repeat spawners and first-time spawners in each river, and 4) repeat spawners contributed to the total life histories defined as a combination of smolt age and sea age at spawning in each river. This was examined by analysing scale samples and information on the scale envelopes collected by anglers in Beiarelva and Stjørdalselva. The scale samples were investigated by scale analyses determining spawning history together with growth and age parameters for each individual fish.

2. Material and methods

The study was conducted in two river systems, River Beiarelva in Norland County and River Stjørdalselva in Trøndelag County. The number and proportion of Atlantic salmon repeat spawners was determined by analyses of scale samples collected by anglers in the two rivers. Further, differences in condition factor, total body length, smolt length, smolt age, growth first year in sea, sea age at first spawning event, and life history variation between first-time spawners and repeat spawners (second- or third-time spawners) were surveyed by scale sample analyses and information added on scale envelopes by fishers.

2.1 Study area

2.1.1 Beiarelva

Beiarelva is located in Beiarn municipality in Nordland, Northern Norway. The watercourse flows from the glacier Svartisen in Saltfjellet mountains and ends in Beiarfjorden with an annual waterflow of 33 m³/s and a natural catchment area of 1065 km² (Jensen *et al.*, 2013; Sjørnsen *et al.*, 2018). The anadromous stretch, from the river mouth in Beiarfjorden to Høgforsen (Figure 1), is approximately 27 km long (Hellen *et al.*, 2016). The lower part of the anadromous stretch is characterized as wide with slow currents, and the river mouth and approximately 7 km upstream are affected by tidal currents (Sjørnsen *et al.*, 2018). No lakes are accessible for anadromous salmonids. The river has several tributaries with Store Gjeddåga, Trollåga and Tverråga in the upper part of the river, and Arstadelva and Eiteråga in the lower part (Figure 1). Several of the tributaries are also available for Atlantic salmon (Sjørnsen *et al.*, 2018). The tributary Store Gjeddåga was in 1981 infected by *Gyrodactylus salaris*, and Beiarelva was infected the year after, in 1982 (Jensen *et al.*, 2013). The origin of the infection was unknown (Johnsen *et al.*, 1999). The river was closed for salmon fishing from 1989 and treated with rotenone in 1994 (Hellen *et al.*, 2016). The river was free of the parasite *G. salaris* in 2001 after a successful combating of the parasite. The angling was opened again in 2001 (Johnsen *et al.*, 2008).

Beiarelva is affected by glacial water from Svartisen, which affects the water temperature. In 1993, cold glacial water from tributaries and streams connected to Svartisen was extracted over to a hydropower plant in Glomfjord. This have resulted in a higher annual water temperature and 6 m³/s lower annual water flow in Beiarelva than before the hydropower regulation (Moen, 2008; Jensen *et al.*, 2013; Sjørnsen *et al.*, 2018).

2.1.2 Fishing rules in Beiarelva

Fishing rules 1984-1987

The angling season for salmon lasted from 1 June to 15 September. There were no restrictions regarding the allowed number of fish caught during the angling season. It was allowed to fish all hours during the day (T. Martinsen, Personal communication, 7 May 2023).

Fishing rules 2020-2021

The angling season for salmon lasted from 15 June to 31 August. Allowed angling hours during each day was from 6 am in the morning until midnight. The daily bag limit was one salmon smaller than 65 cm body length, and only four salmon in total during the season per fisher. Catch and release of three fish per day was allowed, and all salmon over 65 cm was mandatory to release. It was not allowed to catch salmon with a body length smaller than 35 cm. Salmon that had stayed over the winter in the river after spawning, denoted as kelt, was not allowed to catch (Beiarelva SA, 2023; M. Selfors, Personal communication, 22 March 2023).

2.1.3 Stjørdalselva

Stjørdalselva is located in Meråker and Stjørdal municipalities, Central Norway. The watercourse flows from Sweden in the east to Stjørdal in the west and has a catchment area of 2111 km² (Arnekleiv, 1992). The anadromous stretch is denoted from the estuary next to Trondheim airport in Stjørdal to Nustadfossen in Meråker and is approximately 55 km long (Figure 2). No lakes are accessible for anadromous salmonid (Arnekleiv, 1992). Stjørdalselva has several tributaries with Forra and Sona in the lower part, and Dalåa, Kopperåa, Funna, and Torsbjørka in the upper part of the river. The tributaries Forra and Sona are also available to Atlantic salmon (Kanstad-Hanssen & Øksenberg, 2014; Arnekleiv *et al.*, 2020).

Stjørdalselva is affected by hydropower regulation, and there are three power stations located in Meråker above the anadromous stretch. The tributaries Forra and Sona are meanwhile protected areas from hydropower regulation (Arnekleiv, 1992; Kanstad-Hanssen & Øksenberg, 2014; Arnekleiv *et al.*, 2020). The river outlet of Stjørdalselva has been changed during the years in relation to the development of Trondheim Airport (Davidsen *et al.*, 2017).

2.1.4 Fishing rules in Stjørdalselva

Fishing rules 1984-1987

Specific angling rules for the years 1984-1987 was not possible to find in old protocols, but the angling season lasted from June 1 to August 31. The angling rules did to a great degree only regulate the dates for the angling season with some details as prohibition of fishing with shrimps (G. D. Fordal, Personal communication, 24 March 2023).

Fishing rules 2020-2021

The angling season lasted from June 1 to August 31. A total of six salmon was allowed to catch during the season per fisher, and the daily catch limit was one fish per day. Three of the six salmon could be larger than 65 cm. It was not allowed to catch salmon with body length smaller than 35 cm. Salmon that had stayed over the winter in the river after spawning, denoted as kelt, was not allowed to catch. Furthermore, spinners, spoons, wobbler, flies, and worms were the allowed fishing equipment. During June and July, it was allowed to fish with a maximum of two treble hooks. These were prohibited in August as well as worms due to the higher probability of damaging the caught fish. The background for this was the protection of female salmon over 65 cm during this month, which should be released back to the river alive after being caught (catch and release). It was obligatory to take scale samples of all killed salmon (SJFF, 2022; G. D. Fordal, Personal communication, 24 March 2023).

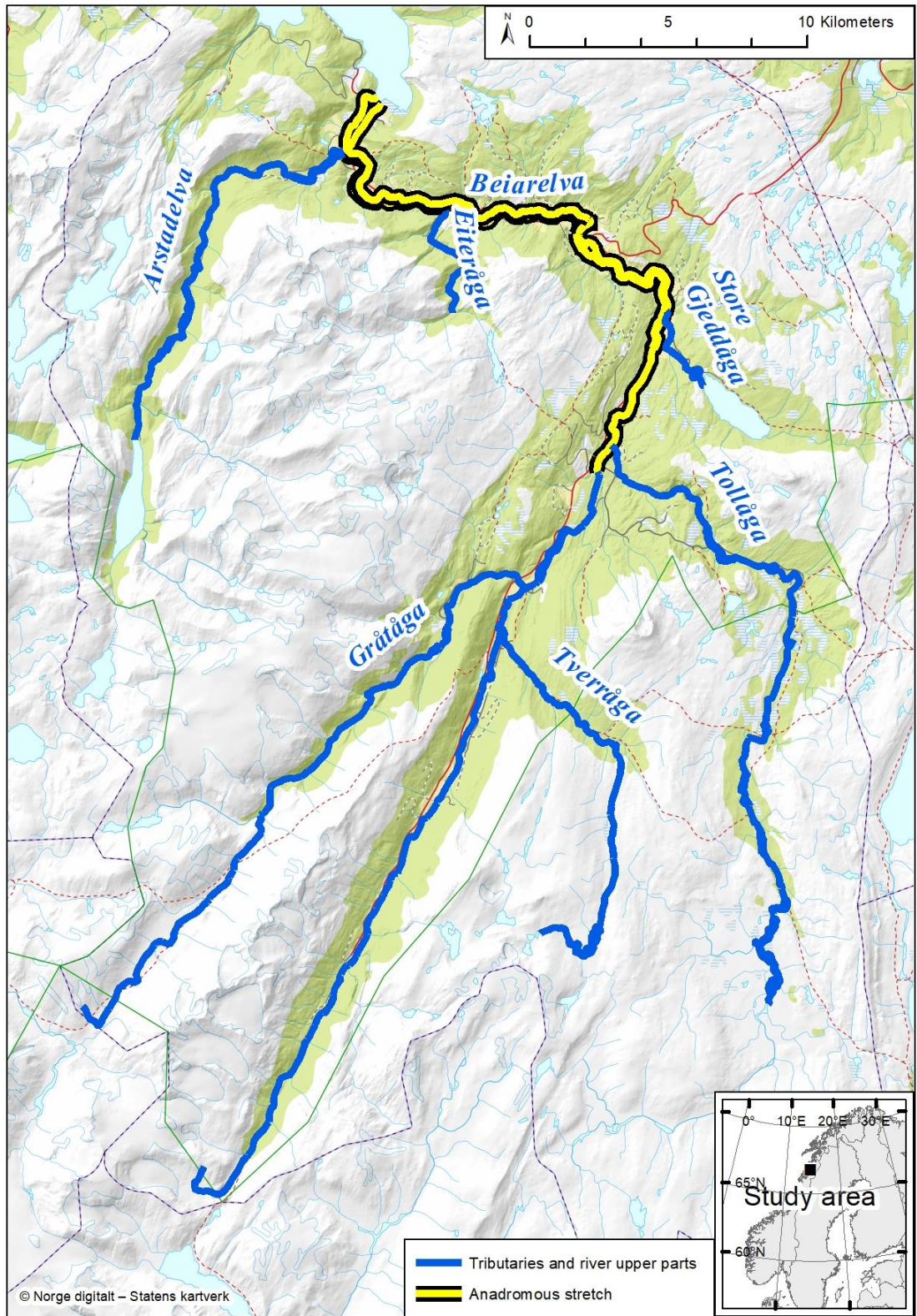


Figure 1: Map of Beiarelva with the tributaries Tverråga, Gråtåga and Tollåga in the upper part of the river and Store Gjeddåga, Eiteråga and Arstadelva in the lower part of the river. Blue color indicates the tributaries to Beiarelva and the upper parts of the main river. Yellow color represents the anadromous stretch in Beiarelva, not including anadromous stretches in the tributaries.

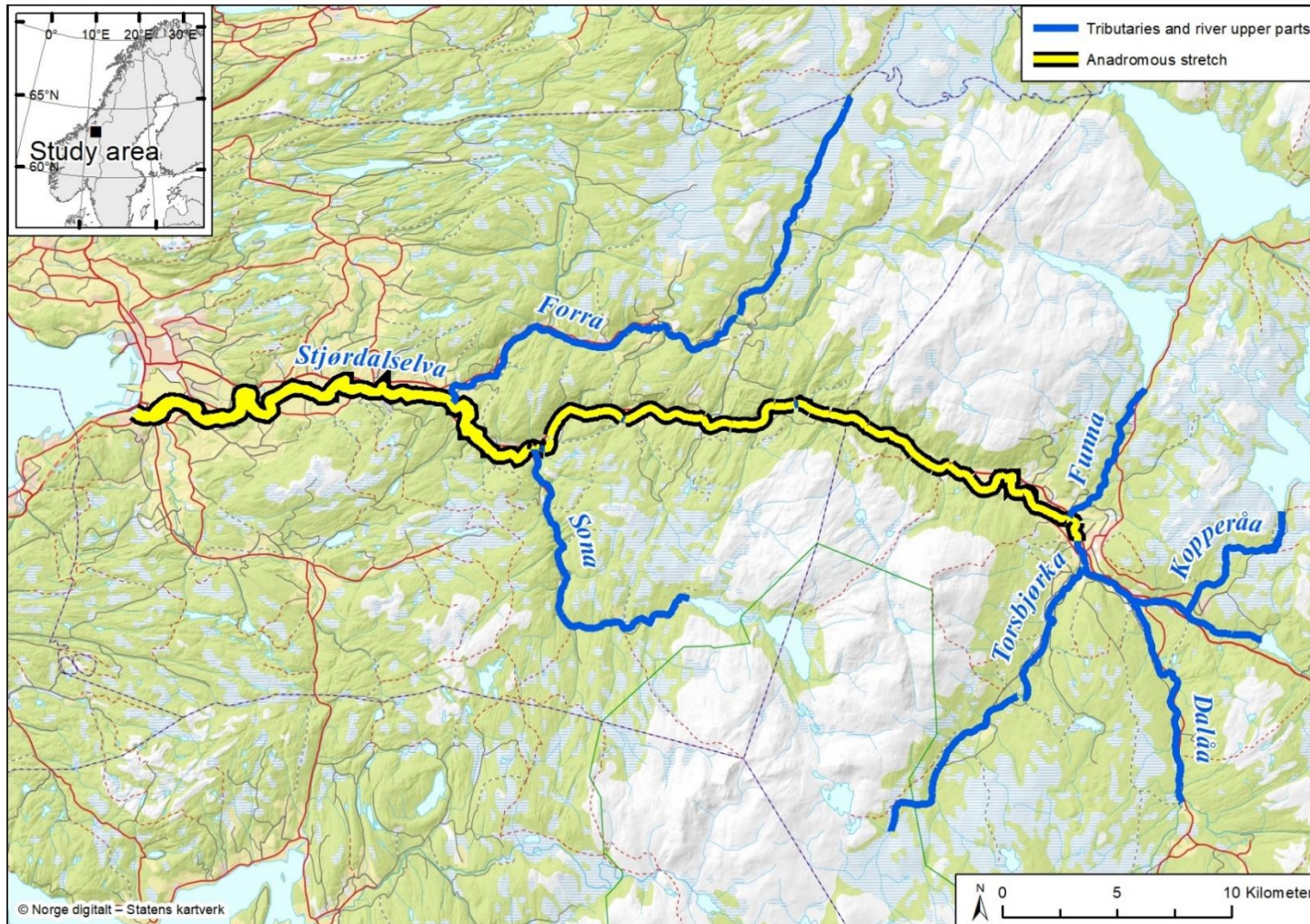


Figure 2: Map of Stjørdalselva with the tributaries Funna, Kopperåa, Torsbjørka, and Dalåa in the upper part of the river, and Forra and Sona in the lower part of the river. Blue color indicates the tributaries to Stjørdalselva and the upper parts of the main river. Yellow color represents the anadromous stretch in Stjørdalselva, not including anadromous stretches in the tributaries.

2.2 Scale analyses

2.2.1 Data sources

To describe spawning history and proportion of repeat spawners during 1984-1987 and 2020-2021, scale samples were investigated through scale analyses. Scale analyses is a tool that can be used for determining smolt age, sea age, spawning events and to back-calculate previous growth rates. The scale samples from Stjørdalselva belonged to collections of the Norwegian Veterinary Institute and the NTNU University Museum, while the samples from Beiarelva belonged to the collections at the Norwegian Institute for Nature Research (NINA).

In catch statistics, Atlantic salmon are divided into three size groups: small (< 3 kg), medium sized (3.0-6.9 kg), and large salmon (≥ 7 kg) (Statistics Norway, 2023). It is expected that the proportion of repeat spawners in each of the three groups will differ (Jonsson *et al.*, 1991a; Persson *et al.*, 2022). Due to the time frame of this master's project, and the time-consuming procedure of analysing scales, only a subsample of the available scales was analysed. A pre-study of the data set lent from NINA with already read scales of 2777 Atlantic salmon in Beiarelva during 2009-2021 (Table 1), indicated that repeat spawners were most prominent among large salmon. Due to that, only salmon with a body length ≥ 880 mm was used. This was done to get the highest possible amount of repeat spawners within the sample size regarding further statistical tests of life history and biological characters between first-time and repeat spawners.

Table 1: Overview of scale samples of 2777 individual Atlantic salmon from Beiarelva during 2009-2021. Fish body length is divided in two length groups with total number of individuals (n) in each group, number of individuals being repeat and first-time spawners (n), and divided in number of female and male individuals (n).

Fish length	Total individuals (n)	Repeat spawner			First-time spawner		
		n	Male (n)	Female (n)	n	Male (n)	Female (n)
≥ 880 mm	709	66	25	41	644	273	371
< 880 mm	2068	65	43	22	2003	1453	550

2.2.2 Scale sampling of the fish

Scales were sampled by fishers in Beiarelva and Stjørdalselva during the angling season, which is always prior to the spawning season for Atlantic salmon. The scales should be sampled above the lateral side line between the dorsal and adipose fin (Figure 3, Norwegian Institute for Nature Research, n.d.) This area is preferable since the scales are often readable and in right shape (Figure 4A) and has low degree of replacement scales (Figure 4D), meaning they have undamaged growth pattern. Right shape of the scales means that the radius and length of the scale are proportional, giving representative length growth in the measurements. Oblong scales will give incorrect estimated growth. Replacement scales occur when the fish have got an injury and lost scales are replaced with new scales. Replacement scales do not show all the information about the life history and growth pattern of the fish since the growth information before the injury is lost with the old scale (Baglinière *et al.*, 2020).

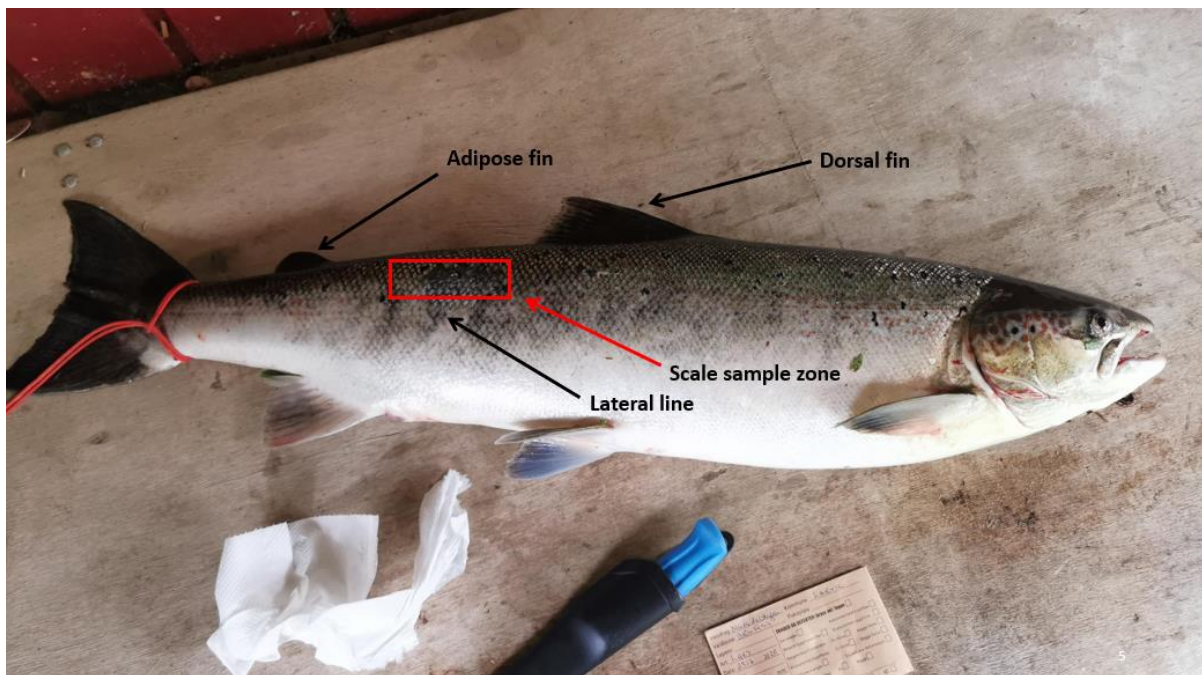


Figure 3: Illustration of scale sampling method. The photo shows an Atlantic salmon caught during the angling season in Numedalslågen, for illustration. Black arrows indicate anatomy of the fins, and the red arrow shows the scale sample zone indicated by the red rectangle (Photo: Marit Melby Jacobsen).

The preferable way to take scale samples is with use of forceps or knife to rub or nibble out scales from the skin. Before taking the scale sample, mucus should be wiped off from the skin in the scale sample area to avoid dry mucus on the scales in further analyses since this can mask the growth pattern (sclerites) (Baglinière *et al.*, 2020). The fishers themselves took the scale samples of the fish, and the method used is therefore uncertain. The fishers put the scales in an

envelope with information of length, weight, sex, date, fishing location, fishing equipment and noted as killed or caught and released.

2.2.3 Scale analyses

The scale samples were analysed at NTNU University Museum and the Norwegian Institute for Nature Research (NINA). To prepare the scales for analyses, a light microscope was used to select and sort out the readable scales with sclerites (growth pattern) from the first year in freshwater and onwards (Figure 4A). These preferable scales were pressed onto a 1 mm Lexan plate by using an iron pressing machine. Further, the scale samples from Stjørdalselva were analysed at NTNU University Museum by using a computer-controlled stereoscope with camera (Leica M165C, camera Leica MC170HD, Sankt Gallan, Switzerland), with the software LAS V4.5. The scale samples from Beiarelva were analysed at NINA on a Microfiche reader (Indus 4601-01, USA) with use of paper and ruler.

The scale analyses and back calculation of length were done after Lea-Dahls method as described in Lea (1910) and Dahl (1910). The yearly length growth was then calculated for each fish. When using this method, direct proportionality between the scale length and fish length is assumed. Until the fish is 10 cm long, the scale growth may be less than the proportional length growth of the fish, and the early juvenile length may to some degree be underestimated. Greater lengths than 10 cm is assumed to be affected by this to a smaller degree, and the method is therefore considered to be sufficient for its purpose in this thesis (Davidsen *et al.*, 2018; Sjurksen *et al.*, 2018).

The salmon were divided in three groups in terms of earlier spawning 1) no spawning marks (Figure 5B) indicating no previous spawning (first-time spawner), 2) one or two spawning marks (Figure 5A), indicating the salmon was returning to the river for a second or third spawning event (repeat spawner), and 3) unsure, indicating the growth pattern was difficult to read and it was difficult to determine if the fish had spawned before or not. In the dataset, no fish had spawned more than two previous times. The analyses were calibrated with an experienced scale reader at the NTNU University Museum.

Two datasets were produced, one for Beiarelva and one for Stjørdalselva after the scale reading. The dataset for Beiarelva was already analysed by scale readers at NINA, but only earlier spawning history was included in the 2020-2021 data set. The datafile was used as a basis for further analyses, and the 2020-2021 scales were re-read and measured due to lack of growth

calculations. The scales from 1984-1987 were only re-read for spawning marks since growth calculations were already done by the scale readers at NINA. Group 3 with individuals who had unsure spawning history are not presented in this study after preliminary analyses indicated that they did not affect the results if they were included in either group 1 or 2.

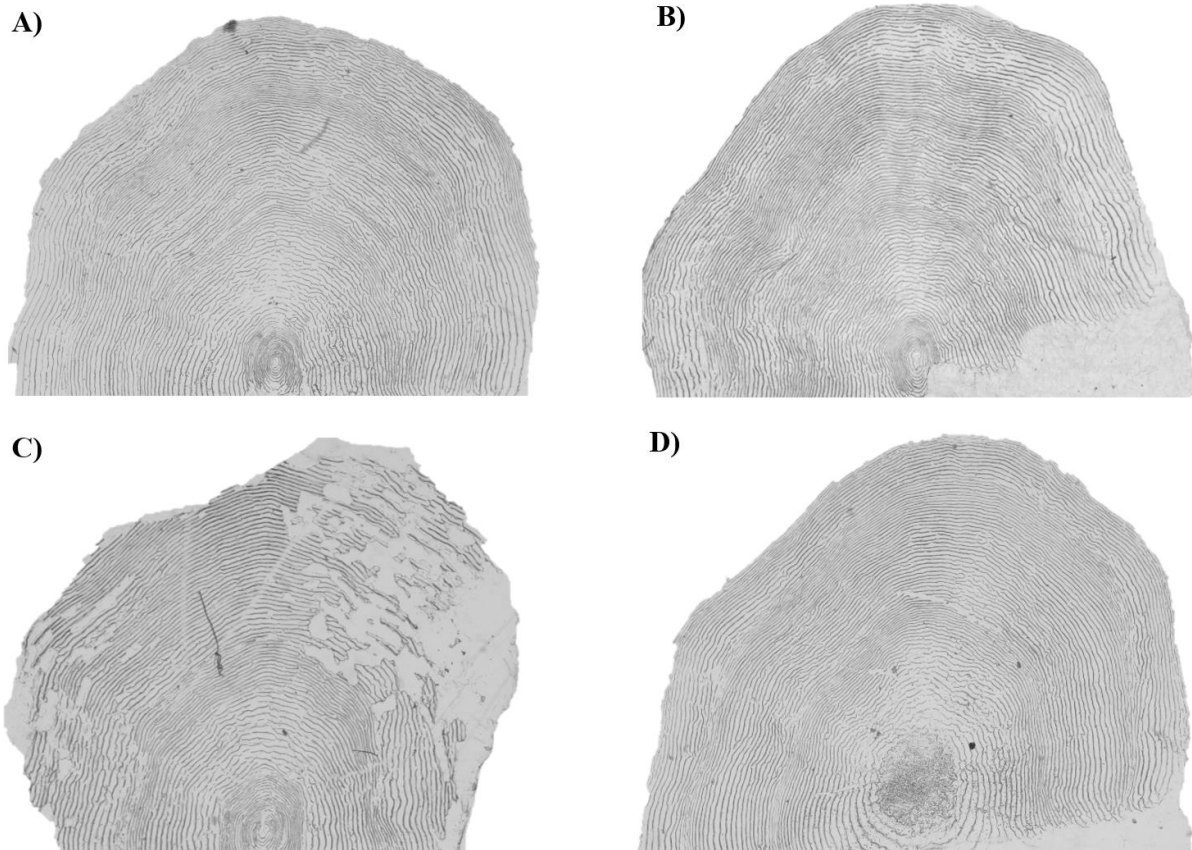


Figure 4: Scales from Atlantic salmon showing A) readable scale with the total growth pattern from the first year in freshwater and onwards, B) readable scale, but missing the first year in freshwater, C) worn scale typically from fish caught in August, and D) replacement scale without readable freshwater growth and smolt length.

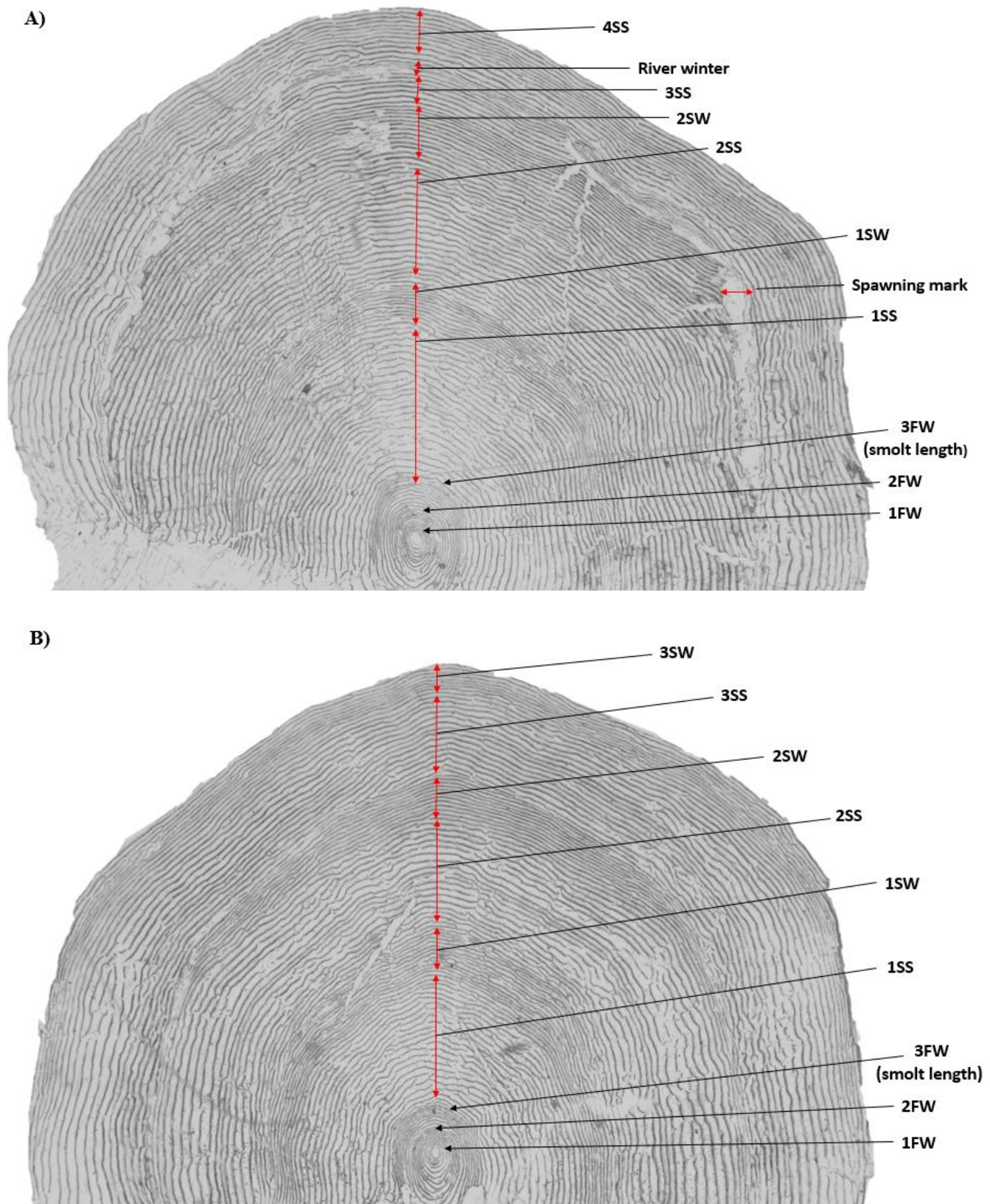


Figure 5: Scale picture of Atlantic salmon a) with spawning mark as 2SW (2-sea-winter age), and b) without spawning mark. SS = sea summer, SW = sea winter, FW = fresh water, and numbers indicate year, e.g. 1SS = first sea summer.

2.3 Statistical analyses

2.3.1 Data filtration

Scale samples of 126 and 300 fish in Beiarelva and Stjørdalselva, respectively, were analysed. During the scale reading, some of the scale samples were categorized as not usable. These scale samples had replacement scales where smolt length and freshwater growth were impossible to read and were therefore excluded from the data set (Figure 4D). This was the case for two scale samples in Stjørdalselva, but none in Beiarelva. In addition, one scale sample from Stjørdalselva had remarkable differences in growth pattern, indicating that the scales originated from two different fish. This sample was therefore rejected and not used for further analyses. Some scale samples were difficult to determine as a first-time spawner or repeat spawner due to injuries in the scales where some scales could indicate that the fish was both. This was the case for 13 fish in Beiarelva and 13 in Stjørdalselva. In total, 13 fish from Beiarelva and 16 fish from Stjørdalselva were excluded from the data set because of the reasons described above. This remained in 113 scale samples from Beiarelva and 284 scale samples from Stjørdalselva for further analyses.

Among the remaining scale samples, all had information of earlier spawning history, but not all had information of every single life history trait or biological character e.g., only length was written on the scale sample envelope and not weight, and hence condition factor could not be estimated. For other scale samples, the first sea winter was hard to determine and growth during the first year in the sea could not be estimated. The sample size does therefore vary for each statistical test. In the model selection, only scale samples with information of all parameters were used (107 fish in Beiarelva and 261 fish in Stjørdalselva).

2.3.2 Calculation of condition factor and definition of biological characters

Fulton's condition factor for each individual fish was calculated using the following formula (Ricker, 1975):

$$K = \frac{100 \times \text{Weight (g)}}{\text{Length (cm)}^3}$$

where K = Fulton's condition factor.

For estimation of biological parameters, growth during the first year in the sea was defined as the first summer and winter in the sea and was measured by subtracting the first sea winter

length by the smolt length. The sea age at first spawning was defined as number of sea winters since smolt migration from the river to sea. Spawning age was for first-time spawners stated as the last sea winter that occurred in the scale. The fish would have spawned at this sea age if the individual had not been caught in angling prior to spawning. For repeat spawners, the spawning age was defined as the sea winter before the spawning mark and/or river winter that occurred in the scale.

2.3.3 Data analyses

For the statistical analyses, RStudio version 2023.03.0 (Posit team, 2023) and R version 4.2.2 (R Core Team, 2022) were used. The statistical significance level was set to $P < 0.05$. The two datasets for Beiarelva and Stjørdalselva were not merged, but used as two single datasets and analysed separately. For analyses related to period, the dataset for both Beiarelva and Stjørdalselva was split into two sub-datasets: 1984-1987 and 2020-2021.

The shapiro.test in the R “base” package was used to test the data for normality. The data were also plotted as a histogram to look for normality since the shapiro.test can be strict. The data were considered and assumed as normally distributed when the p-value output from the shapiro.test was higher than 0.05. Welch Two sample t-test was used if the normality assumption was met ($P > 0.05$), and Wilcoxon rank sum test was used if the normality was not met ($P < 0.05$). Welch two sample t-test and Wilcoxon rank sum test were used to compare the life history and biological characters between first-time and repeat spawners. The chisq.test in the R “base” package was used to test for differences in proportions of repeat spawners between 1984-1987 and 2020-2021, and to test for differences in the sex frequencies within each period.

The sample size for some groups were low. This applies for the repeat spawners in 1984-1987, which only contained 5 scale samples (individuals) in each river. The power of the statistical testing increases with sample size and difference in the mean. The probability of doing type-II mistakes, keeping the null hypothesis while it is not true, increases with low sample size (Zar, 2010). Therefore, conclusions based on statistical tests containing these individuals, must be drawn with caution due to the small sample size.

Mixed effects models were used to investigate biological characters between first-time and repeat spawners in each river, and were performed by using the general linear mixed-effects models function “glmer” within the R package “lme4” (Bates *et al.*, 2015). The response variable was set as not previous spawned or previous spawned (first-time or repeat spawner)

with sea age at first spawning (A), sex (S), growth first year in sea (G), total body length (L), smolt length (SL) and capture date in angling (D) as explanatory variables. Condition factor was left out of the modelling due to uncertainty in the measurements by anglers. Smolt length was considered a more precise measurement than smolt age for the growth in sea between individuals since the first year (age) in freshwater in some cases could be difficult to determine. Time-period was set as random factor. All numerical variables were standardized before modelling by use of the “scale” function in the R “base” package. Not all individuals had information for each explanatory variable, and in total 107 of the 113 fish were used in Beiarelva and 261 of the 284 fish in Stjørdalselva.

Collinearity (Variance inflation factors) for the models was checked using the “check.collinearity” function within the R package “performance” (Lüdecke *et al.*, 2021). The “dredge” function within the R package “MuMIn” was used for model selection and to select the best fitted models based on the Akaike’s information criterion (AIC) (Barton, 2023). When the model selection returned several models with $\Delta AIC < 2$, they were deemed to fit equally well (Burnham & Anderson, 2004). Conditional model averaging was used to calculate the parameter estimates and standard errors with inference from all models with $\Delta AIC < 4$. This since models with $\Delta AIC < 2$ have substantial support and are considered to be equally good and models with $\Delta AIC < 4$ are good, but not as good as those with $\Delta AIC < 2$ (Burnham & Anderson, 2004).

3. Results

3.1 Proportion of repeat spawners and sex frequencies

From the total of 113 fish in Beiarelva and 284 fish in Stjørdalselva, 15 (13%) and 68 (24%) individuals showed sign of earlier spawning events, respectively (Table 2).

In Beiarelva, the proportion of repeat spawners in the sample was 7% in 1984-1987 and 22% in 2020-2021, but the increase in proportion of repeat spawners between the two periods was slightly non-significant (Table 2: Chi-square test, $n = 15$, $P = 0.051$). Female fish constituted 80% of the repeat spawners in 1984-1987 and 50% of the repeat spawners in 2020-2021 (Table 2). No difference in frequency of female and male repeat spawners were found in neither of the two periods (Table 2: 1984-1987, Chi-square test, $n = 5$, $P = 0.18$; 2020-2021, Chi-square test, $n = 10$, $P = 1.0$).

In Stjørdalselva, the proportion of repeat spawners in the sample increased from 5% in 1984-1987 to 32% in 2020-2021 (Table 2: Chi-square test, $n = 68$, $P < 0.001$). Female fish constituted 80% of the repeat spawners in 1984-1987 and 71% in 2020-2021 (Table 2). Only the period 2020-2021 had a higher proportion of females than males among the repeat spawners (Table 2: 1984-1987, Chi-square test, $n = 5$, $P = 0.18$; 2020-2021, Chi-square test, $n = 63$, $P < 0.001$).

Table 2: River and year of scale samples with number of total individuals of Atlantic salmon (n) and repeat spawners (n), with percentage of repeat spawners (%), and percentage of female individuals among the repeat spawners in each period.

River	Year	Total individuals (n)	Repeat spawners (n)	Proportion repeat spawners (%)	Proportion female repeat spawners (%)
Beiarelva	1984-1987	64	5	7	80
	2020-2021	49	10	22	50
Stjørdalselva	1984-1987	92	5	5	80
	2020-2021	192	63	32	71

3.2 Life history and biological characters

3.2.1 Condition factor

Among the 113 fish in Beiarelva and 284 fish in Stjørdalselva, 108 (96%) and 283 (99%) fish had information on total body length and weight given on the scale sample envelope and hence Fulton's condition factor could be estimated for these fish. In Beiarelva, mean condition factor did not differ between first-time- and repeat spawners in neither of the two periods (Figure 6A:

Wilcoxon rank sum test, 1984-1987 $n = 63$, $P = 0.47$; 2020-2021 $n = 45$, $P = 0.53$). In 1984-1987, mean condition factor was 1.0 (SD = 0.1, range 0.7-1.2) for first-time spawners and 1.0 (SD = 0.1, range 0.9-1.2) for repeat spawners (Figure 6A). In 2020-2021, mean condition factor was 1.0 (SD = 0.1, range 0.8-1.1) for first-time spawners and 1.0 (SD = 0.2, range 0.7-1.1) for repeat spawners (Figure 6A).

In Stjørdalselva, mean condition factor did not differ between first-time- and repeat spawners in 1984-1987, but was close to being significant (Figure 6B: Wilcoxon rank sum test, 1984-1987 $n = 91$, $P = 0.054$). This indicates a possible difference in condition factor between first-time and repeat spawners, but the sample size for repeat spawners was low ($n = 5$). No difference in condition factor between first-time and repeat spawners was found in 2020-2021 (Figure 6B: Wilcoxon rank sum test, $n = 192$, $P = 0.68$). In 1984-1987, mean condition factor was 1.0 (SD = 0.1, range 0.7-1.3) for first-time spawners and 1.1 (SD = 0, range 1.1-1.1) for repeat spawners (Figure 6B). In 2020-2021, mean condition factor was 1.0 (SD = 0.2, range 0.8-1.6) for first-time spawners and 0.9 (SD = 0.3, range 0.7-1.3) for repeat spawners (Figure 6B).

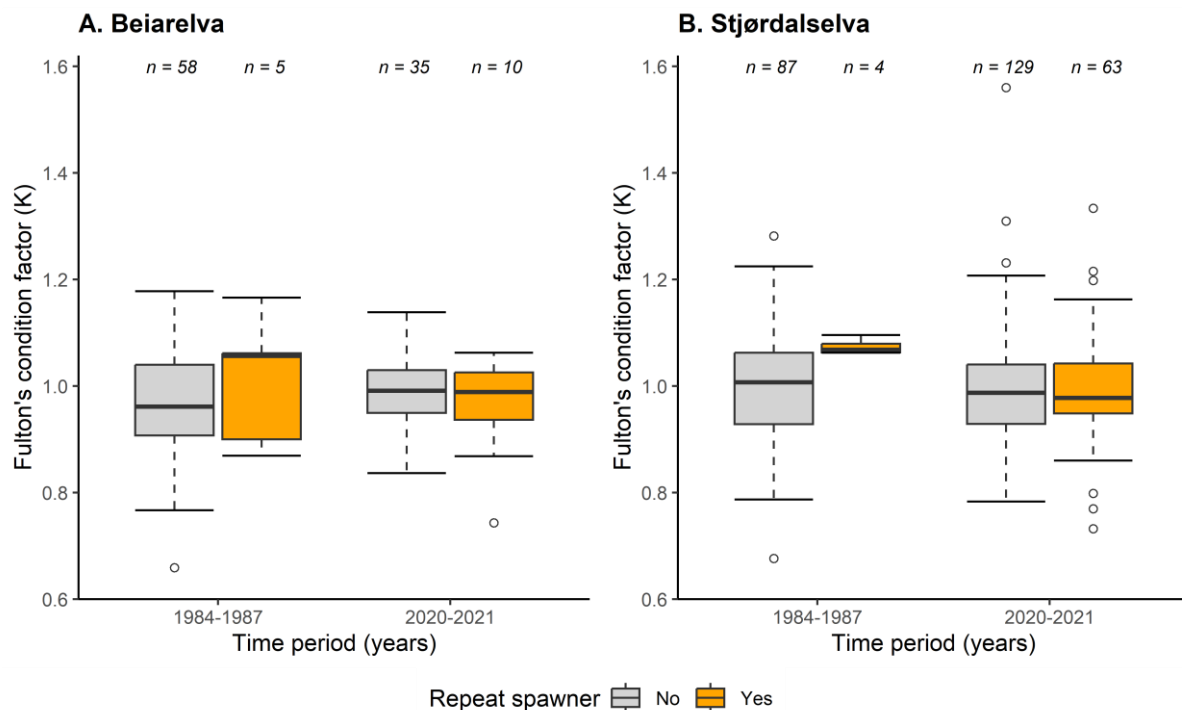


Figure 6: Fulton's condition factor (K) in the respective period for Atlantic salmon in A. Beiarelva, and B. Stjørdalselva. Grey boxes represent first-time spawners and orange boxes represent repeat spawners. The box represents 50% of the data, the horizontal line the median (bold), and whiskers the 5th and 95th percentiles. Sample size for each group is given above the respective box (n). Dots represents outliers.

3.2.2 Total body length of the fish

In Beiarelva, no difference in total body length was found between first-time and repeat spawners in neither of the two periods (Figure 7A; Wilcoxon rank sum test, 1984-1987 $n = 63$, $P = 0.37$; 2020-2021 $n = 49$, $P = 0.77$). In 1984-1987, mean total body length was 972 mm (SD = 191, range: 880-1170 mm) for first-time spawners and 944 mm (SD = 64, range 880-1030 mm) for repeat spawners. In 2020-2021, mean total body length was 964 mm (SD = 14, range: 880-1140 mm) for first-time spawners and 991 mm (SD = 127, range: 880-1200 mm) for repeat spawners (Figure 7A).

In Stjørdalselva, no difference in total body length was found between first-time and repeat spawners in 1984-1987 (Figure 7B; Wilcoxon rank sum test, $n = 92$, $P = 0.64$). However, in 2020-2021 repeat spawners were on average 44 mm longer than first-time spawners (Figure 7B; Wilcoxon rank sum test, $n = 192$, $P < 0.001$). In 1984-1987, mean total body length was 994 mm (SD = 57, range 890-1320) for first-time spawners and 1010 mm (SD = 21, range 970-1080 mm) for repeat spawners. In 2020-2021, mean total body length was 961 mm (SD = 35, range: 880-1210 mm) for first-time spawners and 1005 mm (SD = 14, range: 880-1200 mm) for repeat spawners (Figure 7B).

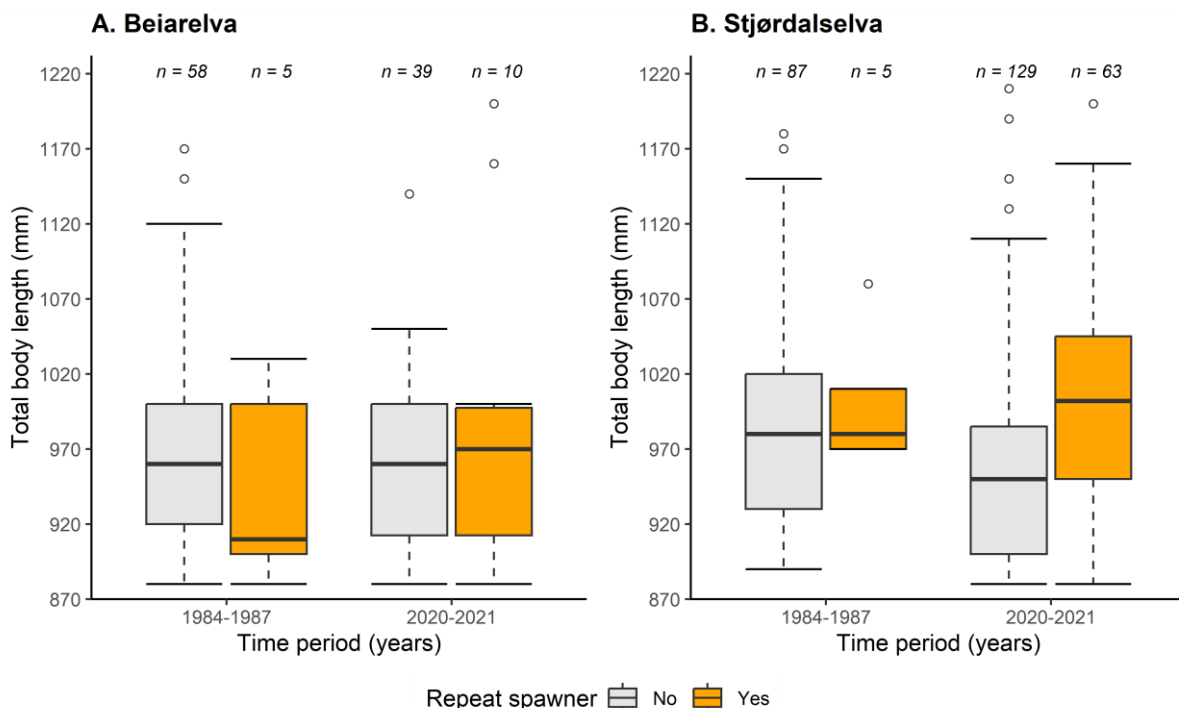


Figure 7: Total body length of the Atlantic salmon in the respective period in A. Beiarelva, and B. Stjørdalselva. Grey boxes represent first-time spawners and orange boxes represent repeat spawners. The box represents 50% of the data, the horizontal line the median (bold), and whiskers the 5th and 95th percentiles. Sample size for each group is given above the respective box (n). Dots represents outliers.

3.2.3 Smolt length

The smolt length could be determined for 110 fish (97%) in Beiarelva and 284 fish (100%) in Stjørdalselva. The smolt length ranged from 107-200 mm in Beiarelva and 82-229 mm in Stjørdalselva.

In Beiarelva, no difference in smolt length between first-time and repeat spawners was found in neither of the two periods (Figure 8A; Welch two sample t-test, 1984-1987 $n = 63$, $P = 0.78$; 2020-2021 $n = 47$, $P = 0.74$). However, the mean smolt length for first-time spawners was 158 mm (SD = 24, range 107-200 mm) in 1984-1987 and 150 mm (SD = 13, range 118-191 mm) in 2020-2021, which was a decrease in smolt length between 1984-1987 and 2020-2021 (Welch two sample t-test, $n = 95$, $P = 0.041$). Repeat spawners had a mean smolt length of 153 mm (SD = 36, range 114-199 mm) in 1984-1987 and 148 mm (SD = 7, range 128-172 mm) in 2020-2021, which was not different between the two periods (Welch two sample t-test, $n = 15$, $P = 0.79$).

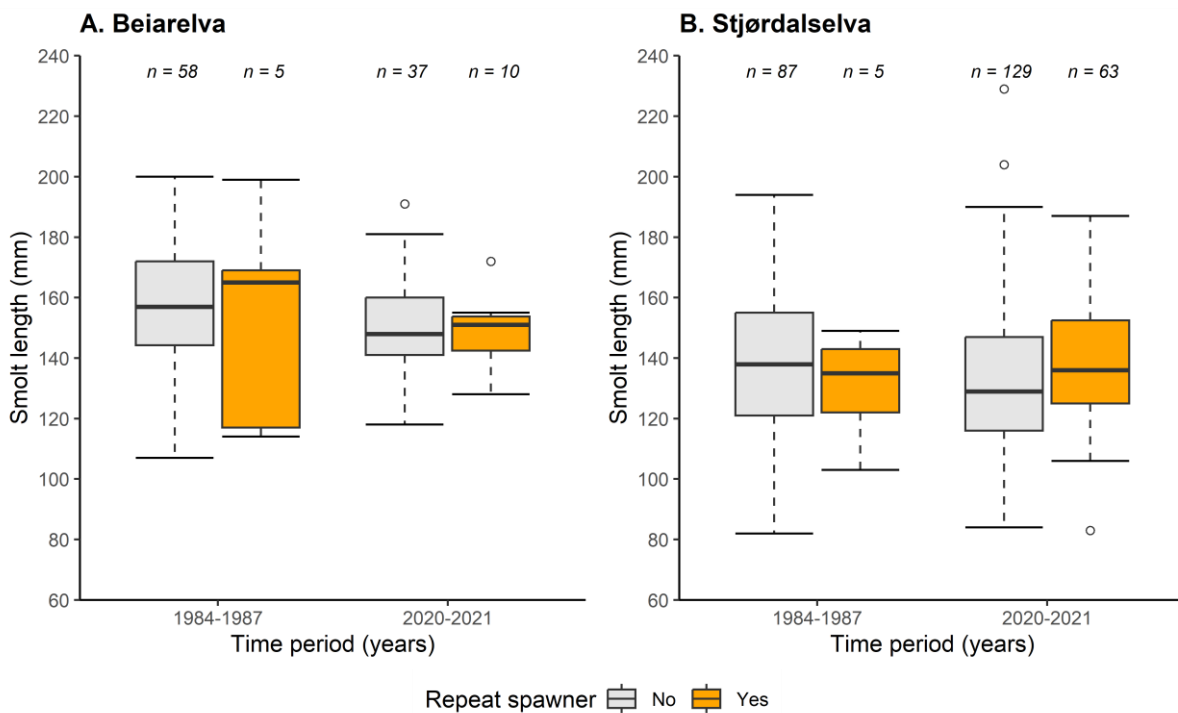


Figure 8: Smolt length (mm) for Atlantic salmon in the respective period in A. Beiarelva and B. Stjørdalselva. Grey boxes represent first-time spawners and orange boxes represent repeat spawners. The box represents 50% of the data, the horizontal line the median (bold), and whiskers the 5th and 95th percentiles. Sample size for each group is given above the respective box (n). Dots represents outliers.

In Stjørdalselva, no difference in smolt length was found between first-time and repeat spawners in neither of the two periods (Figure 8B; Welch two sample t-test 1984-1987, $n = 284$, $P = 0.37$; 2020-2021 $n = 192$, $P = 0.11$). The mean smolt length for first-time spawners was 139 mm (SD = 19, range 82-194 mm) in 1984-1987 and 132 mm (SD = 5.7, range 84-229 mm) in 2020-2021. Repeat spawners had a mean smolt length of 130 mm (SD = 9, range 103-149 mm) in 1984-1987 and 138 mm (SD = 0.7, range 83-187 mm) in 2020-2021. The decrease in smolt length for first-time spawners between 1984-1987 and 2020-2021 was close to being significant (Welch two sample t-test, $n = 216$, $P = 0.054$). No difference in smolt length for repeat spawners was found between 1984-1987 and 2020-2021 (Welch two sample t-test, $n = 68$, $P = 0.43$).

3.2.4 Smolt age

The smolt age could be determined for all fish in Beiarelva and Stjørdalselva. The smolt age at seawards migration ranged from 3-6 years in Beiarelva (Figure 9A, B) and 2-5 years in Stjørdalselva (Figure 9C, D), including both periods.

In Beiarelva, no difference in smolt age was found between first-time and repeat spawners in neither of the two periods (Figure 9A, B; Wilcoxon rank sum test, 1984-1987 $n = 64$, $P = 0.39$; 2020-2021 $n = 49$, $P = 0.37$). In 1984-1987, mean smolt age for first-time spawners was 4.3 years (SD = 0.7, range 3-6 years) and 4.6 years (SD = 0.7, range 3-6 years) for repeat spawners (Figure 3). In 2020-2021, mean smolt age for first-time spawners was 4.3 years (SD = 0.8, range 3-6 years) and 4.6 years (SD = 0.8, range 3-6 years) for repeat-spawners (Figure 3).

In Stjørdalselva, no difference in smolt age between first-time and repeat spawners was found in neither of the two periods (Figure 9C, D; Wilcoxon rank sum test, 1984-1987 $n = 92$, $P = 0.32$; 2020-2021 $n = 192$, $P = 0.59$). In 1984-1987, mean smolt age for first-time spawners was 3.4 years (SD = 0.6, range 2-5 years) and 3.2 years (SD = 0.6, range 3-4 years) for repeat spawners. In 2020-2021, mean smolt age for first-time spawners was 3.1 years (SD = 0.5, range 2-4 years) and 3.1 years (SD = 0.6, range 2-4 years) for repeat spawners. No difference in smolt age for repeat spawners was found between the periods (Figure 9; Wilcoxon rank sum test, $n = 68$ $P = 0.80$), but a lower smolt age in 2020-2021 compared to 1984-1987 was supported for first-time spawners (Figure 9; Wilcoxon rank sum test, $n = 216$, $P < 0.001$).

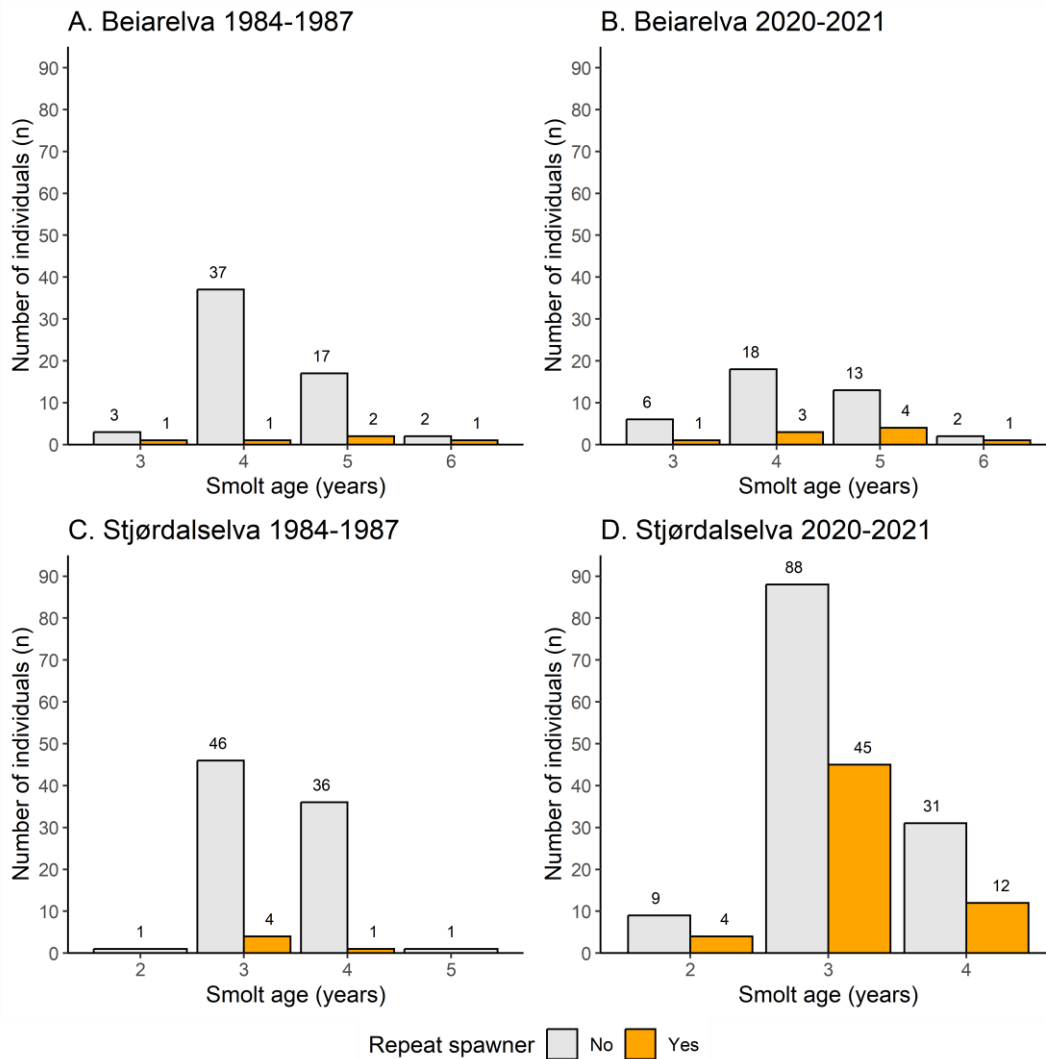


Figure 9: Smolt age composition for Atlantic salmon in Beiarelva during A. 1984-1987 and B. 2020-2021, and in Stjørdalselva during C. 1984-1987 and D. 2020-2021. Grey colour represents first-time spawners and orange colour represents repeat spawners. Sample size for each group is given above the respective bar (*n*).

3.2.5 Growth during the first year at sea

Growth during the first year at sea could be determined for 111 fish (98%) in Beiarelva and 271 fish (95%) in Stjørdalselva. In Beiarelva, no difference in growth during the first year at sea was found between first-time and repeat spawners in neither of the two periods (Figure 10A; Wilcoxon rank sum test, 1984-1987 $n = 64$, $P = 0.89$; 2020-2021 $n = 47$, $P = 0.54$). In 1984-1987, mean growth during the first year at sea was 323 mm (SD = 26, range 231-520 mm) for first-time spawners and 324 mm (SD = 19, range = 268-413 mm) for repeat spawners. In 2020-2021, mean growth the first year at sea was 311 mm (SD = 8, range 238-455 mm) for first-time spawners and 317 mm (SD = 66, range 263-347 mm) for repeat spawners.

In Stjørdalselva, no difference in growth during the first year at sea was found between first-time and repeat spawners in neither of the two periods (Figure 10B; Wilcoxon rank sum test, 1984-1987 $n = 91$, $P = 0.93$; 2020-2021 $n = 180$, $P = 0.78$). In 1984-1987, mean growth during the first year at sea was 363 mm (SD = 19, range 269-501 mm) for first-time spawners and 360 mm (SD = 7, range 338-378 mm) for repeat spawners. In 2020-2021, mean growth during the first year at sea was 319 mm (SD = 6, range 186 – 500 mm) for first-time spawners and 318 mm (SD = 73, range 235-462 mm) for repeat spawners.

Mean growth during the first year at sea for the Atlantic salmon, independent of being a first-time or repeat spawner, was 363 mm (SD = 19, range 269 – 501 mm) in 1987-1987 and 318 mm (SD = 6, range 186-500 mm) in 2020-2021, which gives 45 mm decreased growth between the periods (Figure 10B; Welch two sample t-test, $n = 271$, $P = 0.036$).

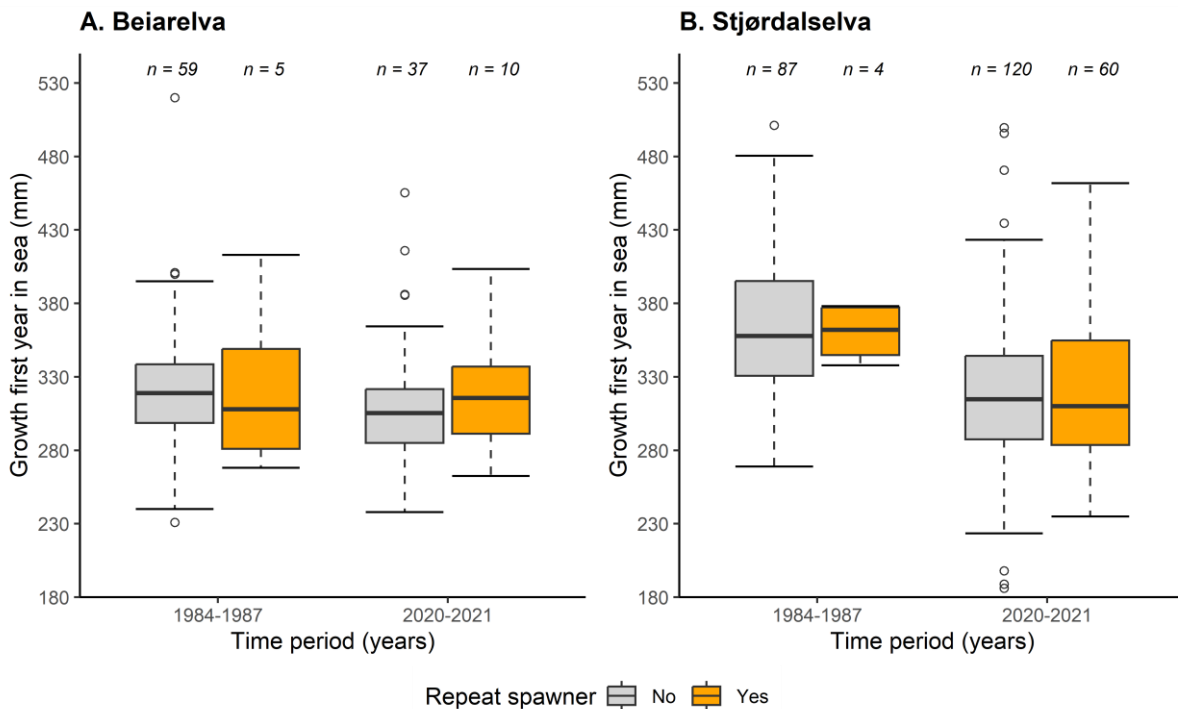


Figure 10: Growth first year in sea (mm) for Atlantic salmon in the respective period in A. Beiarelva and B. Stjørdalselva. Grey boxes represent first-time spawners and orange boxes represent repeat spawners. The box represents 50% of the data, the horizontal line the median (bold), and whiskers the 5th and 95th percentiles. Sample size for each group is given above the respective box (n). Dots represents outliers.

3.2.6 Sea age at first spawning

The sea age at first spawning could be determined for all fish in Beiarelva and Stjørdalselva. The sea age at first spawning event ranged from 2-3 sea winters in Beiarelva in 1984-1987 and

2020-2021 (Figure 11A, B). In Stjørdalselva, sea age at first spawning event ranged from 2-5 sea winters in 1984-1987 and 1-5 sea winters in 2020-2021 (Figure 11C, D).

In Beiarelva, mean sea age at first spawning event differed between first-time and repeat spawners in both periods (Figure 11A, B; Wilcoxon rank sum test, 1984-1987 $n = 64$, $P = 0.002$; 2020-2021 $n = 49$, $P < 0.001$). In 1984-1987, mean sea age at first spawning event was 2.7 years ($SD = 1$, range 2-3 years) for first-time spawners and 2.0 years ($SD = 0$, range 2 years) for repeat spawners. In 2020-2021, mean sea age at first spawning event was 2.8 years ($SD = 1$, range 2-3 years) for first-time spawners and 2.0 ($SD = 0$, range 2 years) for repeat spawners.

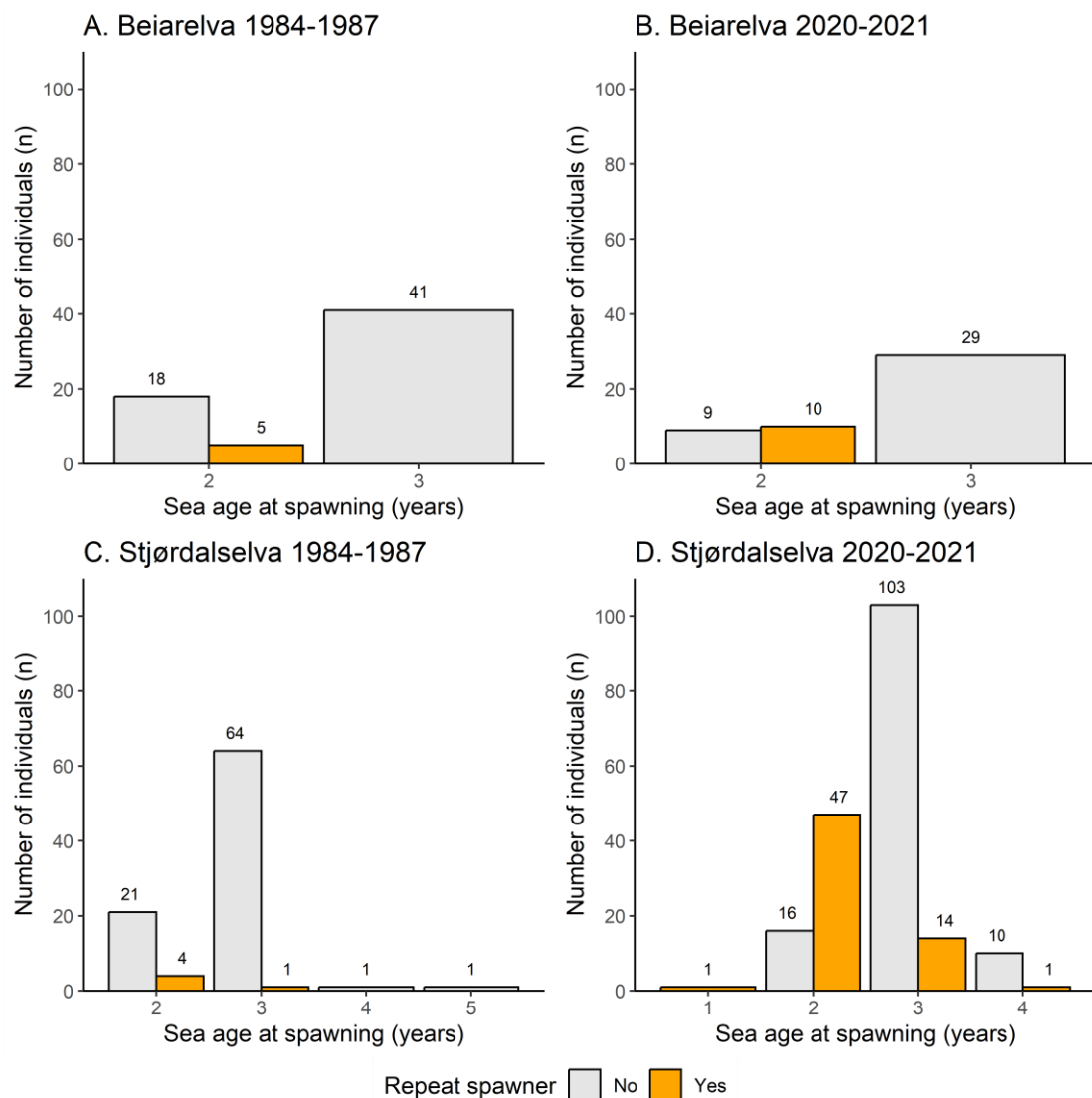


Figure 11: Sea age at spawning (years) for Atlantic salmon in Beiarelva during A. 1984-1987 and B. 2020-2021, and in Stjørdalselva during C. 1984-1987 and D. 2020-2021. Grey colour represents first-time spawners and orange colour repeat spawners. Sample size for each group is given above the respective bar (n).

In Stjørdalselva, mean sea age at first spawning event differed between first-time and repeat spawners in both periods (Figure 11 C, D; Wilcoxon rank sum test, 1984-1987 $n = 92$, $P = 0.007$; 2020-2021 $n = 192$, $P < 0.001$). In 1984-1987, mean sea age at first spawning event was 2.8 years ($SD = 0.5$, range 2-5 years) for first-time spawners and 2.2 years ($SD = 0.5$, range 2-3 years) for repeat spawners. In 2020-2021, mean sea age at spawning was 3.0 years ($SD = 0.5$, range 2-4 years) for first-time spawners and 2.3 ($SD = 0$, range 1-3 years) for repeat spawners.

3.2.7 Life history variation: Combination of smolt age and sea age

In Beiarelva and Stjørdalselva, the life history variation for first-time and repeat spawners was described based on the combination of smolt age, sea age at first spawning and sea age at repeat spawning. Across all individuals, 13 and 19 unique life history combinations were identified in Beiarelva (Figure 12A) and Stjørdalselva (Figure 12B), respectively, including both periods.

Among the life histories in Beiarelva, 38% were found only within the repeat spawners, despite the mean proportion of repeat spawners in total was 13% during the two periods. The most frequent life history type found among first-time spawners was a smolt age of 4-5 years and sea age of 3-4 years (Figure 12A). The most frequent life history type found among repeat spawners was a smolt age of 4-6 years and a sea age of 2 years before the first spawning event took place. All the repeat spawners stayed one year in the sea between the spawning events and were consecutive spawners (Figure 12A).

Among the life histories in Stjørdalselva, 53% were found only within the repeat spawners, despite the mean proportion of repeat spawners in total was 24% during the two periods. The most frequent life history type found among first-time spawners was a smolt age of 3-4 years and sea age of 3 years (Figure 12B). The most frequent life history type found among repeat spawners was a smolt age of 3-4 years and a sea age of 2 years before the first spawning event took place. The repeat spawners stayed mainly one year in the sea between the spawning events and were consecutive spawners (95%), while some individuals stayed two years in the sea and were alternate spawners (5%) (Figure 12B).

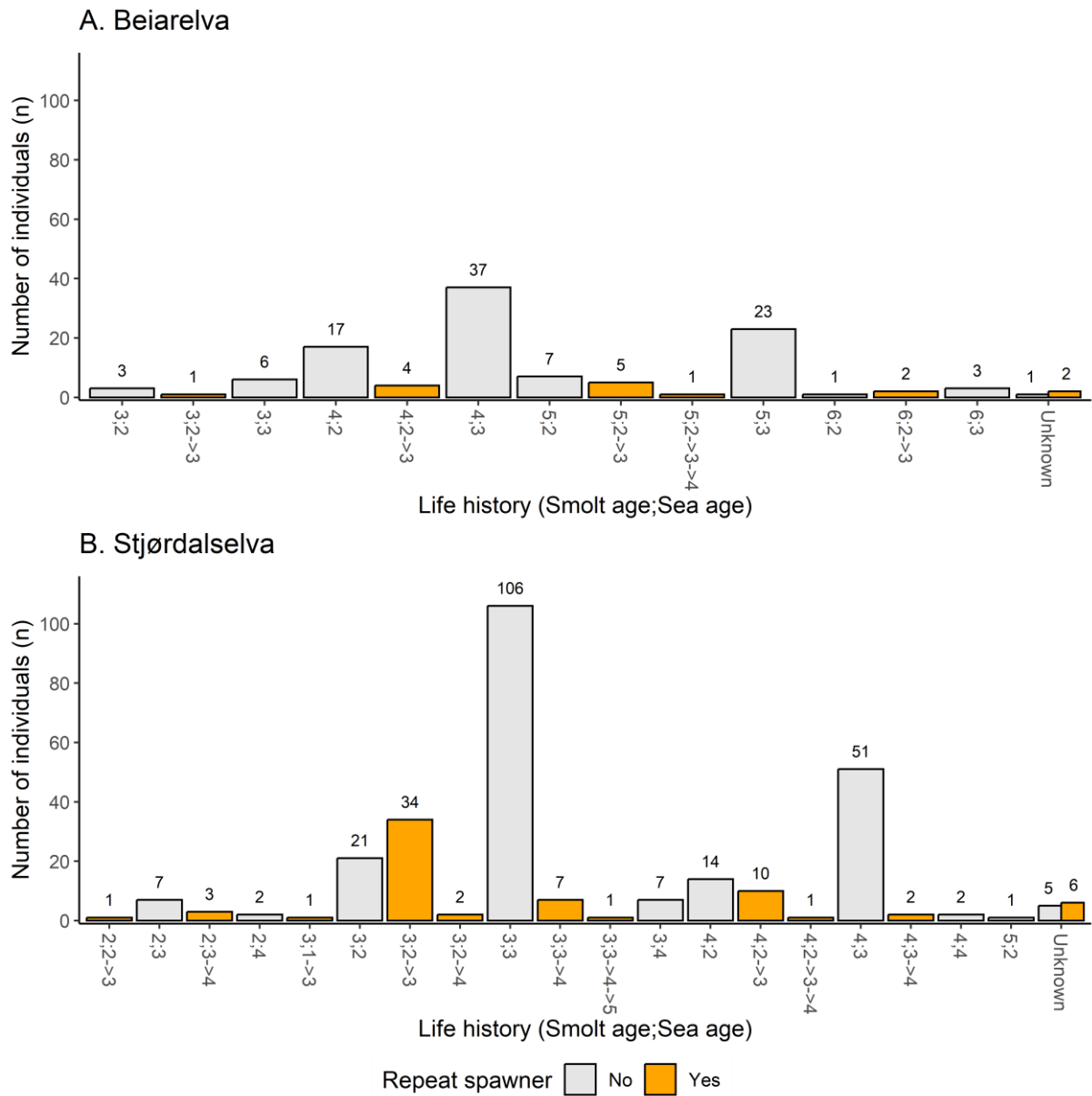


Figure 12: Life history composition of smolt age, sea age at first spawning and sea age at repeat spawning (->) for Atlantic salmon in A. Beiarelva and B. Stjørdalselva including both periods. Grey and orange bars represent first-time spawners and repeat spawners, respectively. Sample size for each group is given above the respective bar (*n*).

3.2.8 Capture date

Capture date was given for 112 fish (99%) in Beiarelva, and 284 fish (99%) in Stjørdalselva.

In Beiarelva, no difference in capture date during the angling season was found between first-time and repeat spawners including both period (Figure 13A; Wilcoxon rank sum test, $n = 112$, $P = 0.76$). The capture date ranged from June 16 to September 28, and the mean capture date was July 27 for both first-time and repeat spawners (Figure 13A).

In Stjørdalselva, repeat spawners was found to be caught earlier during the angling season than first-time spawners regardless of period (Figure 13B; Wilcoxon rank sum test, $n = 282$, $P = 0.014$). The capture date ranged from June 1 to August 31 and the mean capture date for repeat spawners was June 27 and July 4 for first-time spawners (Figure 13B).

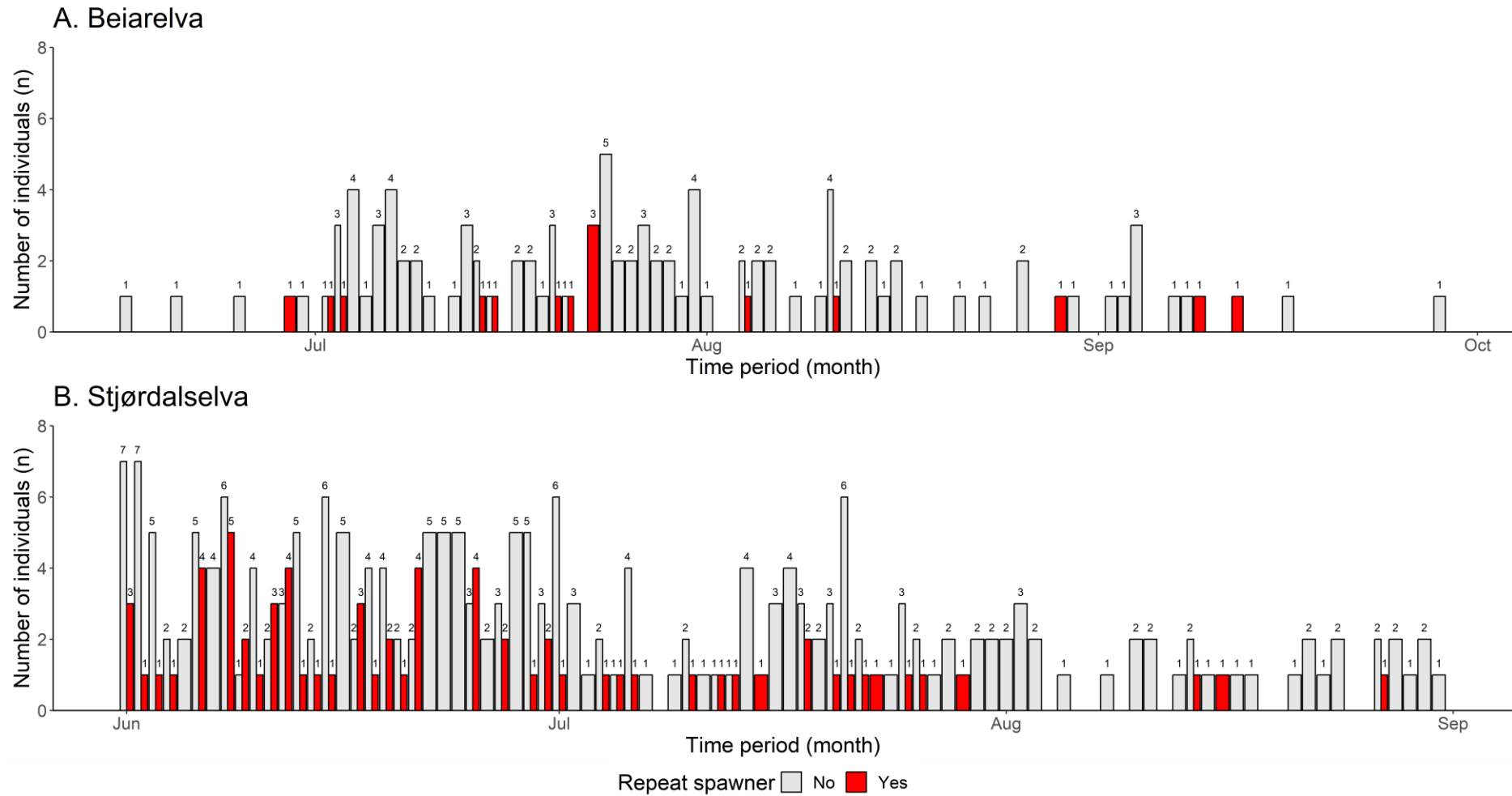


Figure 13: Capture date of Atlantic salmon in A. Beiarelva and B. Stjørdalselva during the angling season (June – September) including both time periods. Month notation indicates the first day in the month. Red bars show repeat spawners and grey bars show first-time spawners. Sample size for each group is given above the respective bar (*n*).

3.3 Characters affecting individuals being first-time versus repeat spawners

3.3.1 Beiarelva

The influence of biological characters on the Atlantic salmon individuals being either a first-time or repeat spawner was surveyed using general linear effects models. In the modelling, 107 fish were included, of which 15 fish were repeat spawners and 92 fish were first-time spawners. In Beiarelva, model selection found 14 fitted models (Δ AIC < 4, Table 5) where nine fitted equally well (Δ AIC < 2, Table 5) with the combination of sea age at first spawning event, sex, growth first year in the sea, smolt length, total body length, and capture date.

Sea age at first spawning event was included in all nine well-fitted models (Δ AIC < 2, Table 5), and hence seen as the best predictor for being either a first-time spawner or repeat spawner. However, the conditional average model showed an extreme standard error for the estimated sea age at first spawning even after the parameter was scaled (Appendix 2). The estimated intercept was not significant ($P > 0.05$), and the standard error was high (Appendix 2). The sea age at first spawning event and intercept were therefore rejected from the conditional average model figure (Figure 14). The conditional average model showed no significant relationship between the estimated parameters and spawning strategy ($P > 0.05$).

Further, the parameters included in the model selection were sex, growth first year in the sea, smolt length, total body length and capture date, and 16 fitted models were found in Beiarelva (Δ AIC < 4). Six equally well-fitted models (Δ AIC < 2, Table 5) were identified, all including sex, growth first year in the sea, smolt length, and date. The model selection included a zero model as one of the best models, meaning that neither of the models were good. The conditional average model showed no relationship between the estimated parameters and spawning strategy ($P > 0.05$), and all standard errors exceeded the estimate for all parameters (Figure 15, Appendix 2). The conditional average model was therefore rejected.

Table 5: Model selection of mixed effects for influence of sea age at first spawning event (A), sex (S), growth first year in the sea (G), smolt length (SL), total body length (L), and capture date (D) on the individuals being first-time spawner versus repeat spawner in Beiarelva. Each model is ranked with decreasing Δ AIC, with supported models noted with grey background (Δ AIC < 2).

Model	df	AIC	Δ AIC	AIC weights
[A, S, L, SL, G]	7	49.23	0.00	0.15
[A, L, SL, G]	6	49.45	0.22	0.13
[A, D, L, G]	6	49.63	0.40	0.12
[A, L, G]	5	49.66	0.43	0.12
[A, S, L, G]	6	50.08	1.85	0.10
[A, S, L, SL, G]	7	50.38	1.15	0.08
[A, D, S, L, SL, G]	8	50.60	1.37	0.07
[A, D, S, L, G]	7	50.63	1.40	0.07
[A, S, L, SL]	6	51.58	2.35	0.05
[A, S, SL]	5	51.98	2.75	0.04
[A, S, L]	5	52.04	2.81	0.04
[A, L]	4	52.80	3.57	0.02

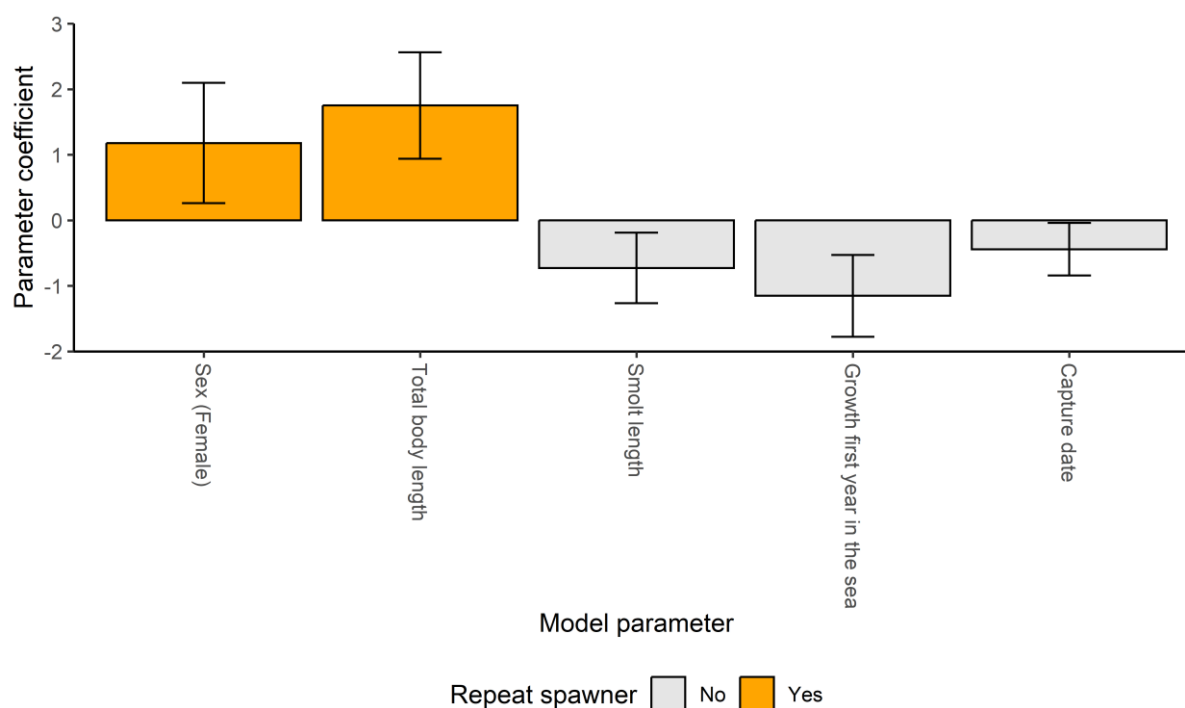


Figure 14: Conditional average model summary for the mixed effects models (Δ AIC < 4) for the parameters sex (S), growth first year in the sea (G), smolt length (SL), total body length (L), and capture date (D) on Atlantic salmon individuals being first-time spawner versus repeat spawner in Beiarelva. Intercept ($P > 0.05$) and age at first spawning (A) are left out.

Table 6: Model selection of mixed effects for influence of sex (S), growth first year in the sea (G), smolt length (SL), total body length (L), and capture date (D) on the individuals being first-time spawner versus repeat spawner in Beiarelva. Each model is ranked with decreasing Δ AIC, with supported models noted with grey background (Δ AIC < 2).

Model	df	AIC	Δ AIC	AIC weights
[Null]	2	86.76	0.00	0.21
[G]	3	88.44	1.68	0.09
[D]	3	88.44	1.68	0.09
[S]	3	88.49	1.73	0.09
[SL]	3	88.52	1.76	0.08
[L]	4	88.62	1.86	0.04
[A, G]	4	90.11	3.35	0.04
[S, SL]	4	90.13	3.37	0.04
[D, SL]	4	90.13	3.37	0.04
[SL, G]	4	90.19	3.43	0.04
[D, S]	4	90.24	3.48	0.04
[D, L]	4	90.28	3.52	0.04
[S, G]	4	90.30	3.54	0.04
[L, G]	4	90.35	3.59	0.03
[L, SL]	4	90.35	3.59	0.03
[S, L]	4	90.39	3.63	0.03

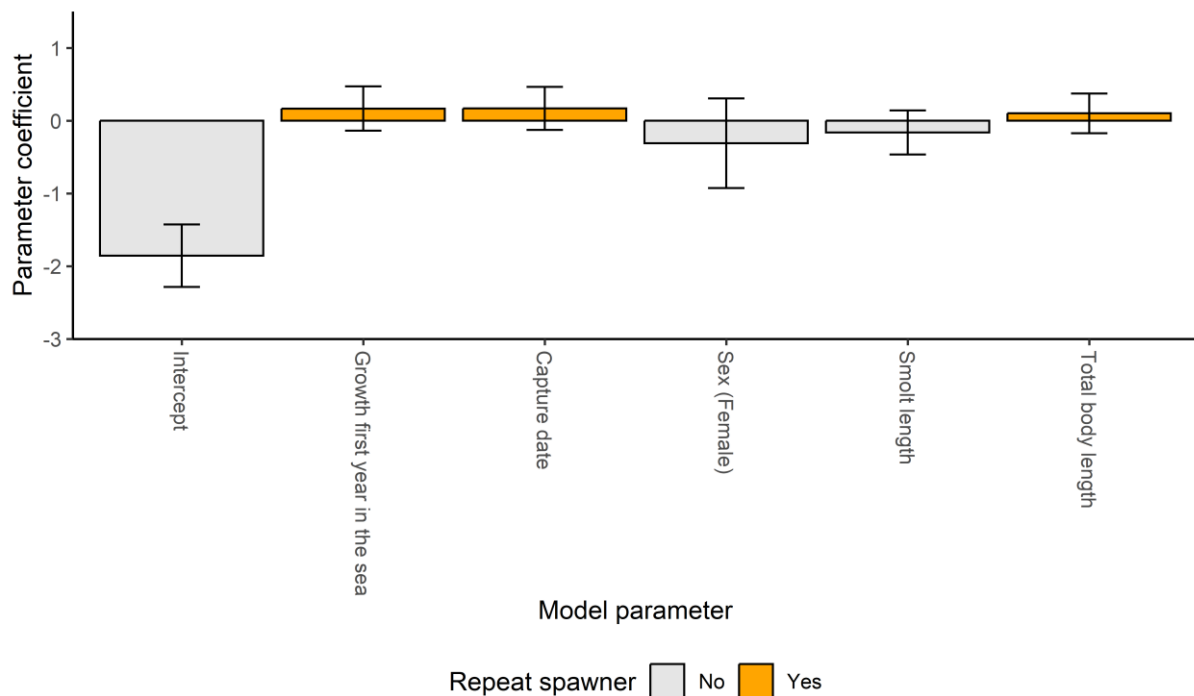


Figure 15: Conditional average model summary for the mixed effects models (Δ AIC < 4) for the parameters sex (S), growth first year in the sea (G), smolt length (SL), total body length (L), and capture date (D) on Atlantic salmon individuals being first-time spawner versus repeat spawner in Beiarelva.

3.2.2 Stjørdalselva

In the model for Stjørdalselva, 261 fish were included, of which 59 fish were repeat spawners and 202 fish were first-time spawners. In Stjørdalselva, model selection found four fitted models ($\Delta \text{AIC} < 4$, Table 6) where all four fitted equally well ($\Delta \text{AIC} < 2$, Table 6) with the combination of sea age at first spawning event, sex, growth first year in the sea, smolt length, total body length, and capture date. Sea age at first spawning, sex, total body length, and growth first year in the sea were included in all well-fitted models ($\Delta \text{AIC} < 2$, Table 6), and hence seen as the best predictors for an individual being either first-time spawner or repeat spawner.

The conditional average model (Figure 16, Appendix 2) showed a relationship for female and total body length in direction of repeat spawners, indicating that females had a higher probability of becoming a repeat spawner than males and increasing body length gave higher probability of being a repeat spawner ($P < 0.05$). Sea age at first spawning and growth first year in the sea showed a relationship for first-time spawners, indicating that increasing sea age at first spawning and growth the first year in the sea gave higher probability of being a first-time spawner ($P < 0.05$).

Table 6: Model selection of mixed effects for influence of sea age at first spawning event (A), sex (S), growth first year in the sea (G), smolt length (SL), total body length (L), and capture date (D) on the individuals being first-time spawner versus repeat spawner in Stjørdalselva. Each model is ranked with decreasing ΔAIC , with supported models noted with grey background ($\Delta \text{AIC} < 2$).

Model	df	AIC	ΔAIC	AIC weights
[A, S, L, SL, G]	7	112.13	0.00	0.36
[A, S, L, G]	6	112.57	0.44	0.29
[A, D, S, L, SL, G]	8	113.50	1.36	0.18
[A, D, S, L, G]	7	113.64	1.51	0.17

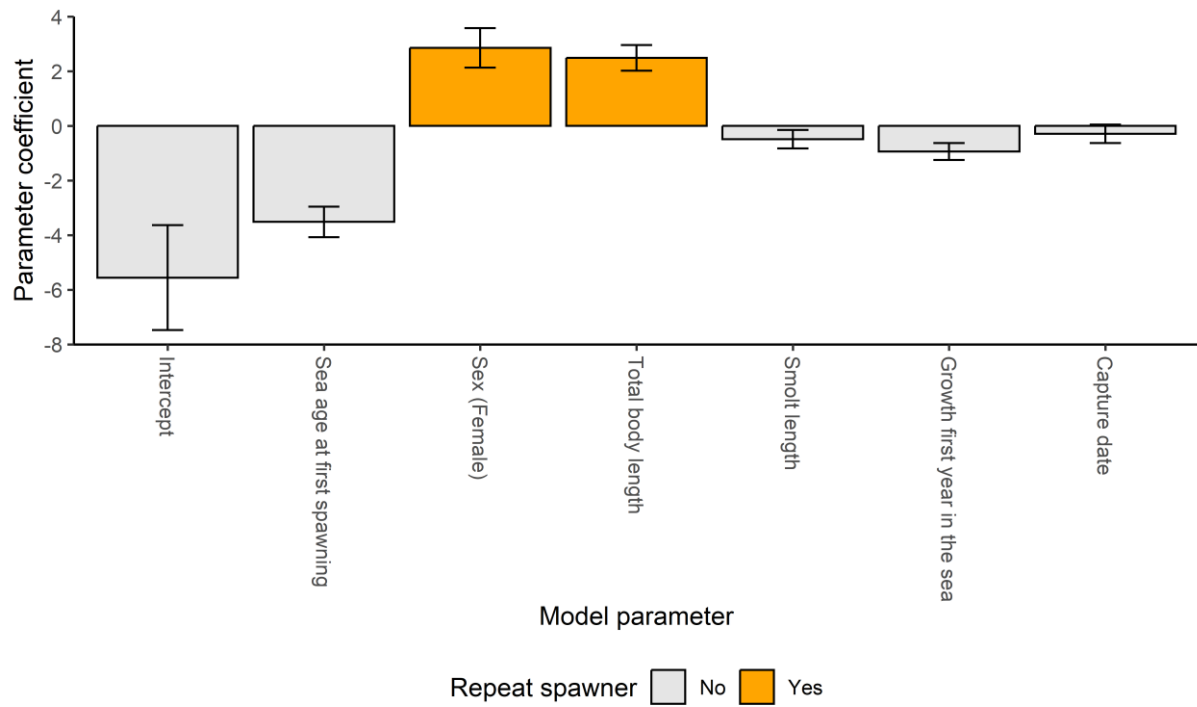


Figure 16: Conditional average model summary for the mixed effects models ($\Delta AIC < 4$) for the parameters sea age at first spawning event (A), sex (S), growth first year in the sea (G), smolt length (SL), total body length (L), and capture date (D) on the individuals being first-time spawner versus repeat spawner in Stjørdalselva.

4. Discussion

Life history and biological characters between first-time and repeat spawners larger or equal to 880 mm in River Beiarelva and River Stjørdalselva were investigated during two periods. The proportion of repeat spawners increased significantly from 1984-1987 to 2020-2021 in Stjørdalselva, but showed only a tendency in increase between the periods in Beiarelva. Females constituted a significant higher proportion of the repeat spawners in Stjørdalselva in 2020-2021, but the observed sex frequencies did not differ in Beiarelva in the two periods nor Stjørdalselva in 1984-1987. Despite constituting only 13-24% of the total populations in the studied rivers, repeat spawners contributed to great life history variation among the Atlantic salmon in each river. No difference in smolt age at seawards migration was found between first-time and repeat spawners, but a shorter sea phase before the first spawning event for repeat spawners than first-time spawners was found in both rivers.

The proportion of repeat spawners across the rivers ranged from 5-7% in 1984-1987 to 22-32% in 2020-2021. The increase in proportion of repeat spawners was statistically significant in Stjørdalselva, and close to being significant in Beiarelva. The general increase in proportions of repeat spawners in the two rivers is similar to the findings by Bordeleau et al. (2020) who found an increase in iteroparity among northern and mid-latitudinal populations of Atlantic salmon in Canada between 1971-1993 and 1993-2017. The proportion of repeat spawners in 2020-2021 was higher in Stjørdalselva (32%) in central Norway compared to Beiarelva (22%) in northern Norway. This is in accordance with Persson et al. (2022) who found lower proportions of repeat spawners in the north compared to the south in Norway, most likely explained by environmental factors in freshwater and at sea.

The total estimated proportions of repeat spawners may have been underestimated in both periods in Beiarelva and Stjørdalselva. Halttunen (2011) showed a higher proportion of repeat spawners caught in the Altafjord compared to the recapture of the same fish in the rivers by anglers. This shows that the estimated proportions of repeat spawners in the rivers can be underestimated due to less willingness to bite for repeat spawners compared to first-time spawners. However, the willingness to bite is likely to be the same in both periods and therefore not affecting the increase in proportion of repeat spawners. On the other hand, the proportions of repeat spawners may have been overestimated since only fish ≥ 880 mm were included in this thesis. The proportion of repeat spawners would most likely be lower if individuals from all length classes were included, as shown by the pre-study of the scale samples from Beiarelva in this thesis.

Even though the repeat spawners on average only constituted 13% in Beiarelva and 24% in Stjørdalselva of the individuals included in the study in the two periods, they contributed with 38% and 53% of the life history variation, respectively. The large contribution of previous spawners to life history variation is supported by previous studies (Erkinaro *et al.*, 2019; Persson *et al.*, 2022). However, the contributions to life history variation by repeat spawners was lower in this thesis compared to previous studies that found repeat spawners to contribute up to 76% of the life history variation (Erkinaro *et al.*, 2019; Persson *et al.*, 2022). The total number of different life history combinations were 13 and 19 in Beiarelva and Stjørdalselva, respectively, compared to up to 141 different life history combinations in previous studies (Niemelä *et al.*, 2006a; Erkinaro *et al.*, 2019; Persson *et al.*, 2022). The higher contribution to life history variation in previous studies are expected since the study by Erkinaro *et al.* (2019) is from the large and complex River Teno system, and Persson *et al.* (2020) that covered a broad geographical area with 179 rivers. The high amount of contribution to life histories in comparison with low percentage of individuals in the total population, illustrates that repeat spawners can influence the population dynamics since different year classes of salmon will be present during the spawning season and most likely will contribute to genetic variation in the offspring (Erkinaro *et al.*, 2019; Persson *et al.*, 2022). However, many of the life histories did only occur in some individuals, which is similar to previous findings (Erkinaro *et al.*, 2019; Persson *et al.*, 2022). All repeat spawners were consecutive spawners in Beiarelva. Stjørdalselva had a mix of consecutive and alternate repeat spawners. The finding of only consecutive spawners in Beiarelva does not correspond to earlier findings where northern populations more often are alternate spawners than central populations in Norway (Jonsson *et al.*, 1991a; Persson *et al.*, 2022), but this can have been affected by the low sample size of repeat spawners in Beiarelva.

Females constituted a significant higher proportion of the repeat spawners in Stjørdalselva in 2020-2021, but no statistical support was given for the observed sex frequencies in Beiarelva in the two periods nor Stjørdalselva in 1984-1987. Modelling of the data from Stjørdalselva showed stronger influence on females becoming repeat spawners than males. Higher proportions of female repeat spawners may arise from the trade-off between current and future reproduction (Murphy, 1968; Bordeleau *et al.*, 2020). Persson *et al.* (2022) found that male first-time spawners that had stayed two years in sea before the first spawning event, had reduced body mass compared to female first-time spawners of the same age. This may indicate a higher investment in current reproduction by males and subsequent lower energy left for surviving to

a next spawning compared to females (Persson *et al.*, 2022). On the other hand, previous research found equal investment in current reproduction in terms of total energy loss for female and male fish that had stayed one year in sea before the first spawning, but males had a higher loss of somatic energy (36%) than females (25%) after spawning (Jonsson *et al.*, 1991b). Higher somatic energy loss is not surprising since the reproductive success of males is highly connected to the access of females and must compete and fight with other males. The higher energy loss for males in form of somatic energy (mainly fat) compared to loss of gonadal energy in females, suggests that higher reserves of somatic energy that are left after spawning favours higher survival of females and therefore gives higher proportions of female repeat spawners in the studied rivers (Jonsson & Jonsson, 2003).

The increased proportions of repeat spawners in Beiarelva and Stjørdalselva between 1984-1987 and 2020-2021 may be explained by changes in management approaches in rivers and at sea. Both catches of Atlantic salmon and the number of Atlantic salmon individuals returning to Norwegian rivers for spawning, were lower in 2021 than ever recorded before. Since the 1980s, numbers of returning Atlantic salmon individuals for spawning have been halved. Still, there has been a remarkable improvement in the management goals from 2009. The long-term improvement from 2009 was due to stricter angling regulations both in rivers and at sea, and thus reduced exploitation of the Atlantic salmon. In 2021, 29% of Atlantic salmon that migrated back to the rivers for spawning, were caught in the rivers and sea. In contrast, 60% were caught in the 1980s (VRL, 2022). In 1989, selective harvest of Atlantic salmon with drift nets was prohibited in fisheries in Norway, which gave subsequently a reduction of catches from 852 to 495 tons in the coastal fishery in one year (Lovdata, 1986; Miljødirektoratet, 2017). This has resulted in a reduction of the catches in sea, and only 8% of the Atlantic salmon was caught in the sea in 2021. The exploitation in the rivers has also been reduced from 47% of the returning salmon being caught until 2005, with a reduction to only 20% caught in angling in 2021. In 2021, 38% of the Atlantic salmon caught in the rivers was released back to the rivers, which is the highest registered amount of catch and release (VRL, 2022). The increased practice of catch and release is also seen on a global scale (April *et al.*, 2021).

These regulations and changes in exploitation of Atlantic salmon may have affected the increased proportions of repeat spawners from 1984-1987 to 2020-2021 in Beiarelva and Stjørdalselva. Since less Atlantic salmon are caught both in the sea and rivers, several individuals will get the chance of surviving to a next spawning and become repeat spawners. In Stjørdalselva, a stricter catch and release practice was introduced in 2012, and recent years

show up to 45% catch and release of the Atlantic salmon caught during the angling season (G. D. Fordal, Personal communication, 24 March 2023, Appendix 1). More practise of catch and release on large female Atlantic salmon (body length > 65 cm), compared to males, may contribute to the higher observed proportions of female repeat spawners in this thesis. In Beiarelva, stricter regulations of large Atlantic salmon have been practised since 2012 (Sjursen *et al.*, 2018), and catch reports show up to 79 % catch and release of Atlantic salmon caught during the angling season (Appendix 1). The catch and release approach in Beiarelva does not differ between sexes (Beiarelva SA, 2023), and female fish are not more protected than males, which may explain part of the observed sex frequencies that did not differ. The observed proportions of repeat spawners may be affected by the sampling during the angling season. In Stjørdalselva, it is mandatory to take scale samples of all killed fish, but this rule does not apply to fish that are released alive back to the river (SJFF, 2022). Increased focus on catch and release of certain length classes and sexes, as in Beiarelva and Stjørdalselva, may affect the total scale sample material, and further influence the observed proportions of repeat spawners in the rivers. This means, that potential repeat spawners are not taken scale samples of since this to a great degree only applies to the killed fish.

Less harvest and selective harvest in the sea, may contribute to higher proportions of repeat spawners as seen in this thesis. This is supported by Jokikokko & Jutila (2005) who found that the proportion of repeat spawners increased from 0.5% to 2.8% between two periods most likely due to stricter fishing rules in the Finnish coastal fishery. Ban of drift nets in Norway has shown to increase catches of one- and two-sea-winter Atlantic salmon in three and four studied rivers, respectively (Jensen *et al.*, 1999). Changes in selective fisheries can reduce the size selective mortality of Atlantic salmon and contribute to the presence of several year classes of salmon, which is shown to improve the survival of large fish, that potentially can give increases in the proportion of repeat spawners since they are multi-sea winter fish (Moore *et al.*, 1995; Dempson *et al.*, 2004; Jokikokko & Jutila, 2005). Increasing amounts of multi-sea winter salmon has been shown to correlate with increases in number of repeat spawners in mid- and north latitudinal populations in Canada due to closure of commercial fisheries (Bordeleau *et al.*, 2020).

The present study found that, in both Beiarelva and Stjørdalselva, repeat spawners on average were younger at the first spawning event than first-time spawners. This was supported by the modelling of the data from Stjørdalselva, suggesting that increased sea age at first spawning increases the chance of becoming a first-time spawner for fish ≥ 880 mm. Previous studies have shown that sea age and size at maturity is related to a locus in the *vgll3* gene, affecting when

the Atlantic salmon reach sexual maturation (Barson *et al.*, 2015; Aykanat *et al.*, 2019). Aykanat *et al.* (2019) found that the probability of surviving to a next spawning was associated with the genotype that gave low sea age at the first reproductive event compared to the genotype that gave high sea age. This gene can potentially explain part of the lower sea age at the first spawning for repeat spawners in this thesis, but genetics was not investigated in this thesis. The lower age at first spawning for repeat spawners is expected since smaller fish invest less energy than large fish into spawning, and hence have a better chance to survive spawning and spawn again at a later point in time (Aykanat *et al.*, 2019; Bordeleau *et al.*, 2019) This corresponds to previous findings where Atlantic salmon that matured after one sea winter were more likely to become repeat spawners than older fish (Persson *et al.*, 2022). An assumption, that longer stays at sea gives higher probability of marine mortality due to predation before returning for spawning, can also be taken into consideration when it comes to sea age at maturity. The findings in the present study applies to fish ≥ 880 mm. One can therefore not say that the repeat spawners are younger at first spawning event in general in the total population with background in this study since small and medium-sized salmon are left out of the study.

The age at maturity for first-time and repeat spawners may be related to the growth conditions in the marine feeding habitat. Growth during the first year in the sea was not found to differ between first-time and repeat spawners in neither Beiarelva nor Stjørdalselva in the two periods, but modelling of the data from Stjørdalselva predicted a higher tendency of becoming a first-time spawner with increasing growth the first year at sea. High growth the first year in the sea have been shown to give later maturing Atlantic salmon (Jonsson & Jonsson, 2007), which supports the higher age at maturity for first-time spawners compared to individuals that grow slow the first year in the sea and then reach sexual maturity earlier at a younger age. In Stjørdalselva, a reduction in growth during the first year in sea for all Atlantic salmon was found in 2020-2021 compared with 1984-1987, which is supported by other studies for fish from central and southern Norway (Harvey *et al.*, 2022; Vollset *et al.*, 2022). This finding can be explained by environmental factors in the marine feeding habitat where an ecological regime shift took place around 2005, resulting in warmer water masses and subsequent less prey availability and higher competition for prey with an increased mackerel stock (*Scomber scombrus* L.) that expanded northwards (Utne *et al.*, 2022; Vollset *et al.*, 2022; Strøm *et al.*, 2023). Decreased growth rates the first year in sea, may favor longer residence in the sea before returning to the river for spawning because it takes longer time to build up energy reserves and develop gonads (Otero *et al.*, 2012; Rikardsen *et al.*, 2021; Vollset *et al.*, 2022). This supports

the finding of mostly 2-3 sea winter fish at first spawning event in Beiarelva and Stjørdalselva. Still, the findings in this study can be affected by the choice of sample size with fish ≥ 880 mm, which can select out small fish that don't survive to this length class, but potentially can have spawned as one-sea winter fish. In addition, we cannot predict if the categorized first-time spawners would have survived to a second spawning if they weren't caught by an angler. However, increased body size and age at first spawning event have shown to give lower probability of repeat spawning (Aykanat *et al.*, 2019; Persson *et al.*, 2022).

The present study found no differences in smolt age and smolt length between first-time and repeat spawners, but there was a decrease in smolt length in Beiarelva and smolt age in Stjørdalselva between the periods for first-time spawners. The mean smolt age was lower in Stjørdalselva than Beiarelva, most likely explained by decreased freshwater growth rates with increasing latitude, giving older smolts in Beiarelva (L'Abée-Lund *et al.*, 1989). Smolt length and smolt age can be seen as two measurements of the growth in freshwater (Økland *et al.*, 1993; Jonsson & Jonsson, 2007). Explanations for the change in smolt age and length for first-time spawners may be impacted by environmental changes in freshwater, such as increase in temperature, giving shorter and younger individuals that migrates earlier to the sea (Russell *et al.*, 2012; Hedger *et al.*, 2013). Still, first-time spawners in Beiarelva were shorter in 2020-2021 than 1984-1987 even though the smolt age was identical in the two periods, indicating less freshwater growth per year. Higher annual water temperature in Beiarelva after the hydropower regulation in 1993 seems not to have affected the smolt age (Sjursen *et al.*, 2018), but other factors may have affected the growth.

The condition factor did not differ between first-time and repeat spawners. The condition factor measured after capture in the river is perhaps not a good measurement when it comes to iteroparity since the salmon decides whether it will return to the river for spawning or stay in the sea long before they are caught in the river (Jonsson & Jonsson, 2004; Barson *et al.*, 2015; Aykanat *et al.*, 2019). Therefore, the condition factor at sea would have been more relevant than in the river when it comes to comparing first-time and repeat spawners. In addition, the fish were weighed and measured by the anglers, and can be somewhat misleading since many anglers only measure the length of the fish with approximately marks for length on the rod, and estimate the weight based on the length. The condition factor in this study may still give an indication of the condition of the fish since the total sample size was relatively large.

The present study showed that repeat spawners were captured earlier during the angling season than first-time spawners in Stjørdalselva, but the capture date did not differ in Beiarelva. In

Stjørdalselva, modelling of the data supported that increased total body length gave higher probability of becoming a repeat spawner than first-time spawner. Previous studies have shown that large Atlantic salmon (> 880 mm) migrates and ascends the rivers earlier during the angling season than small Atlantic salmon (Niemelä *et al.*, 2006b; Harvey *et al.*, 2017; Berntsen *et al.*, 2018). Niemelä *et al.* (2006b) also found that repeat spawners ascended the rivers earlier than first-time spawners of the same age, but this was not investigated in the present study. The observed difference in capture date may be affected by the fishing rules in Stjørdalselva. Catch limits on large salmon in the rivers may affect when the large salmon are caught during the angling season. Anglers will to a great extent kill the large salmon that they catch early during the season, and release large fish later in the season, based on the uncertainty of whether they will catch another large salmon later in the season. Early ascending of the rivers and early catch of large salmon can potentially give different selective exploitation during the angling season where the large Atlantic salmon will have highest angling pressure early in the season (Harvey *et al.*, 2017).

In conclusion, this thesis found a significant and close to significant increase in proportions of repeat spawners in Stjørdalselva and Beiarelva, respectively, from 1984-1987 to 2020-2021. Changes in management approaches and ecological factors both in the rivers and at sea have most likely affected the observed increase in proportions of repeat spawners between the two periods. Further, repeat spawners contributed with high amounts to life history variation, despite repeat spawners constituted a low percentage of the total individuals in the rivers. This illustrates that repeat spawners can influence the population dynamics significantly in terms of genetic and life history diversity. Statistical modelling of the data collected in this study predicted a higher tendency for females to become repeat spawners than males in Stjørdalselva, but this was not found in Beiarelva. In addition, repeat spawners were captured earlier in the angling season and had a larger body length compared to first-time spawners in Stjørdalselva in 2020-2021. To protect potential large repeat spawners in the future, management approaches can be to have stricter catch regulations of large salmon earlier in the angling season, especially for large females. However, regulations must be adjusted to different rivers, as capture date differed between Beiarelva and Stjørdalselva. As the findings applied to fish longer or equal to 880 mm, conclusions for smaller fish based on these findings should be taken with caution without further investigations. This since the findings in this thesis may apply differently to different length classes of Atlantic salmon.

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Appendix 1

Catch and release development in Beiarelva and Stjørdalselva during the recent years (Table I).

Table I: River and year with number of individuals caught (n) and percentage (%) of caught and released individuals (C&R) of the total catch. Data from catch statistics in each river¹².

River	Year	Total catch (n)	C&R of total catch (%)
Beiarelva	2016	1989	77
	2017	1743	70
	2018	1473	68
	2019	1717	75
	2020	1422	63
	2021	1183	79
Stjørdalselva	2019	1790	39
	2020	1935	41
	2021	2186	45
	2022	2309	39

¹ <https://elveguiden.no/no/laksebors/13>

² <https://laksebors.inatur.no/bors/616>

Appendix 2

Conditional average model statistics for Beiarelva and Stjørdalselva.

1) Beiarelva with sea age at first spawning (Figure 14)

Table II: The conditional average model statistics for the mixed effects models ($\Delta AIC < 4$) for the parameters sea age at first spawning, sex, growth first year in the sea, smolt length, total body length, and capture date on Atlantic salmon individuals being first-time spawner versus repeat spawner in Beiarelva. Significant values ($P < 0.05$) are denoted with asterisk mark (*).

Variable (effect)	Estimate	Std. error	Z value	P-value
(Intercept)	-18.4281	3034.7461	0.006	0.9952
Sea age at first spawning	-14.5628	2361.2697	0.006	0.9951
Sex (Female)	1.1786	0.9329	1.249	0.2118
Total body length	1.7515	0.8120	2.135	0.0328 *
Smolt length	-0.7274	0.5382	1.336	0.1816
Growth first year in sea	-1.1528	0.6239	1.826	0.0679
Capture date	-0.4421	0.4023	1.086	0.2774

2) Beiarelva without sea age at first spawning (Figure 15)

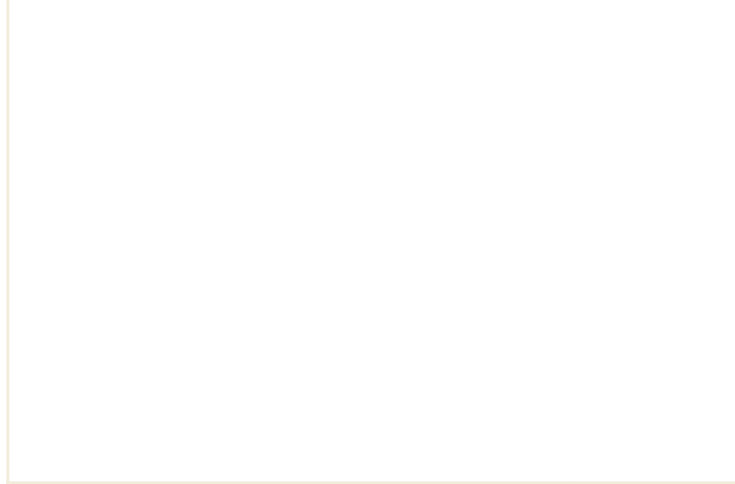
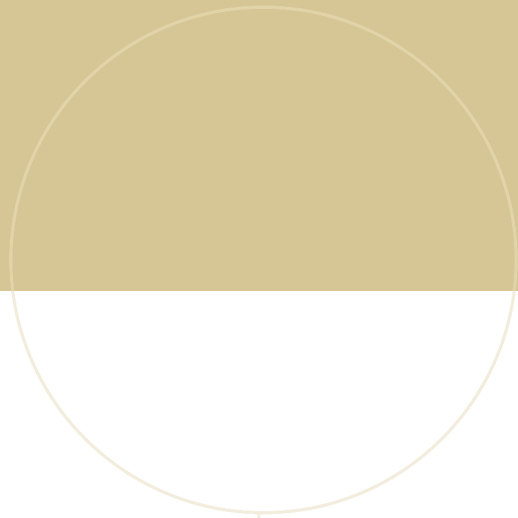
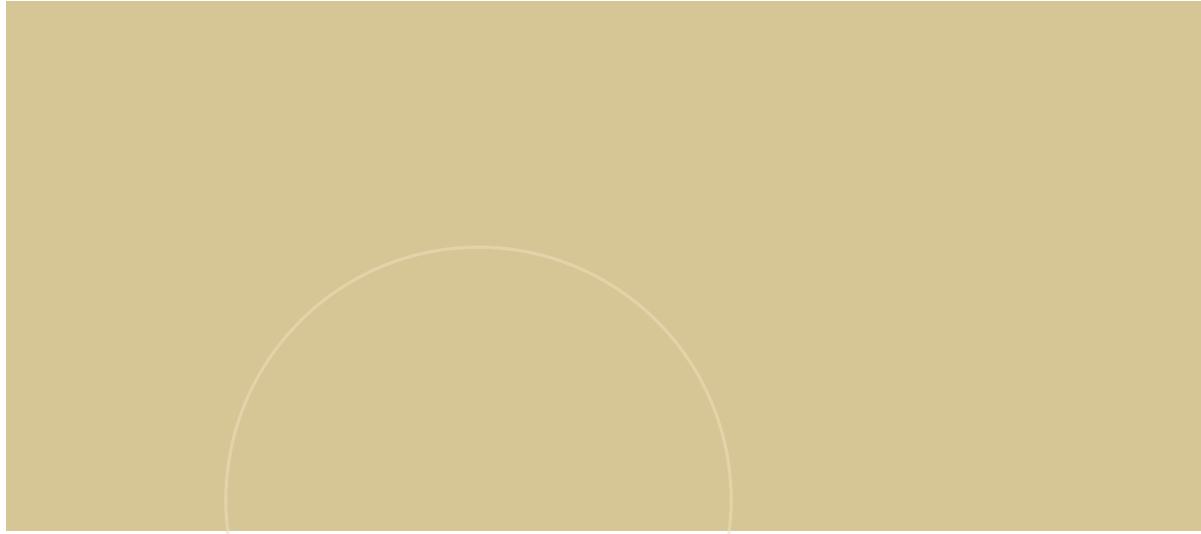
Table III: The conditional average model statistics for the mixed effects models ($\Delta AIC < 4$) for the parameters sex, growth first year in the sea, smolt length, total body length, and capture date on Atlantic salmon individuals being first-time spawner versus repeat spawner in Beiarelva. Significant values ($P < 0.05$) are denoted with asterisk mark (*).

Variable (effect)	Estimate	Std. error	Z value	P-value
(Intercept)	-1.8573	0.4300	4.271	1.94e-05 *
Sex (Female)	0.1673	0.3057	0.541	0.589
Total body length	0.1698	0.2966	0.566	0.572
Smolt length	-0.3095	0.6154	0.497	0.619
Growth first year in sea	-0.1604	0.3032	0.523	0.601
Capture date	0.1010	0.2721	0.367	0.714

3) Stjørdalselva (Figure 16)

Table IV: The conditional average model statistics for the mixed effects models ($\Delta AIC < 4$) for the parameters sea age at first spawning, sex, growth first year in the sea, smolt length, total body length, and capture date on Atlantic salmon individuals being first-time spawner versus repeat spawner in Stjørdalselva. Significant values ($P < 0.05$) are denoted with asterisk mark (*).

Variable (effect)	Estimate	Std. error	Z value	P-value
(Intercept)	-5.5947	1.9209	2.899	0.0375 *
Sea age at first spawning	-3.5160	0.5625	6.222	< 2e-16*
Sex (Female)	2.8546	0.7233	3.928	8.55e-05*
Total body length	2.4880	0.4712	5.256	1.00e-07*
Smolt length	-0.4887	0.3371	1.443	0.14901
Growth first year in sea	-0.9397	0.3088	3.029	0.00245*
Capture date	-0.2911	0.3392	0.854	0.39301



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