Mikkel Emil Lange Friis

Timing of homing migration of anadromous brown trout, Arctic char and Atlantic salmon in two rivers in Northern Norway.

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Acknowledgements

Selv om det siste året kan ha sett mørkt ut for studenter generelt, er det alltid fint vær om man veit hvor det sitter, væ! Det kan noen sitere meg på.

Mikkel Emil Lange Friis

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Abstract

Brown trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*) and Atlantic salmon (*S. salar*) may all undertake marine feeding migrations. However, the time spent at sea, and the subsequent timing of upstream migration varies between the three species, as well as between populations. In the present study, video analysis was used to assess the timing of homing migration of 7 755 anadromous brown trout, 2 381 Arctic char and 497 Atlantic salmon in the rivers Fjæreelva and Botnelva, Nordland county, in 2019 and 2020. The video systems provided an accurate time of registration and allowed for determination of species, swimming direction, estimation of body length and detection of adult salmon lice (*Lepeophtheirus salmonis*) infestation rates. Arctic char was the earliest upstream migrant, followed by brown trout and Atlantic salmon, respectively. In addition, Arctic char displayed a shorter, more concentrated, period of upstream migration than brown trout and Atlantic salmon. Brown trout, Arctic char and Atlantic salmon with greater body length migrated upstream earlier than shorter conspecifics in both rivers in 2019, likewise for brown trout and Arctic char in Botnelva in 2020. In Fjæreelva in 2020, the opposite pattern, with shorter upstream migrants arriving earlier, was observed for brown trout and Arctic char. River temperatures indicated that individuals of all three species might have experienced high, and perhaps physically limiting, temperatures during their upstream migration. Arctic char ascended the river at higher light intensities than brown trout and Atlantic salmon, likely due to its earlier and denser migration timing. Brown trout appeared to favor darker light conditions during river ascent in time periods when dark conditions were present. In a period with high water flow, brown trout migrated during hours of higher light intensity, suggesting an altered behavior in response to increased water level and turbidity. The video quality was sufficient to evaluate salmon lice infestation on 7 657 individuals, whereas 26% had visible salmon lice. Brown trout and Atlantic salmon with visible salmon lice were recorded earlier in both rivers in 2019 than individuals without. This pattern was also observed for Atlantic salmon in both rivers in 2020. Individuals of all three species, both rivers and years combined, with visible salmon lice had a greater body length than individuals without. The recorded infestation levels, were however, considered as low in both rivers both years. The present study demonstrated that even though brown trout, Arctic char and Atlantic salmon display differences in upstream migratory behavior, they shared some common features. Individuals of all three species were recorded at all levels of water temperature, light intensity and water runoff within their migratory period, indicating that these abiotic factors did not appear to pose absolute restrictions upon the timing of upstream migration.

IV

Sammendrag

Brunørret (*Salmo trutta*), Arktisk røye (*Salvelinus alpinus*) og Atlanterhavslaks (*S. salar*) kan begi seg ut på marine næringsmigrasjoner. Men, tiden de bruker i havet og tidspunktet for tilbakevandring til elva varierer mellom artene, så vell som mellom ulike populasjoner. I dette studiet ble videoanalyse brukt til å vurdere oppvandringstidspunkt for 7 755 anadrome brunørret, 2 381 Arktiske røyer og 497 Atlanterhavslaks i 2019 og 2020 i Fjærevassdraget og Botnvassdraget i Nordland fylke. Videosystemet ga nøyaktig registreringstidspunkt og tillot for bestemmelse av art, svømmeretning, estimering av kroppslengde og vurdering av påslag av lakselus (*Lepeophtheirus salmonis*). Arktisk røye var den arten som migrere oppstrøms tidligst, etterfulgt av brunørret og Atlanterhavslaks. Oppvandringsperioden var også kortere og mer konsis for Arktisk røye enn for de to andre artene. Innad i artene ble det observert at større individer vandret tilbake til vassdraget tidligere enn mindre individer, for samtlige arter i begge vassdragene i 2019, og for brunørret og Arktisk røye i Botnvassdraget i 2020. Det motsatte ble observert for brunørret og Arktisk røye i Fjærevassdraget i 2020, hvor mindre migranter ble registrert tidligere. Temperaturmålinger i elva indikerte at individer av alle tre artene kan ha opplevd høye, og muligens fysisk utfordrende, vanntemperaturer i løpet av elveoppvandringen. Arktisk røye vandret opp ved høyere lysintensitet enn brunørret og Atlanterhavslaks, trolig grunnet dens tidligere og mer konsise oppstrømsmigrasjonsperiode. Brunørret så ut til å foretrekke mørkere lysforhold ved elveoppvandringen når mørke forhold var oppnåelige. I perioder med økt vannføring ble brunørret observert å vandre opp ved høyere lysstyrker, muligens som følge av økt vannivå og turbiditet. Videokvaliteten var tilstrekkelig til å vurdere påslag av voksen lakselus for 7 657 individer, hvorav 26% av disse hadde synlige lakselus. Brunørret og Atlanterhavslaks med synlig påslag av lakselus ble oppdaget tidligere ved videoovervåkningen enn deres artsfrender uten synlig lus i begge vassdragene i 2019. Dette ble også observert for Atlanterhavslaks i begge vassdragene i 2020. Flere større individer hadde synlige lakselus påslag enn sine mindre artsfrender, men den synlige lakselusbyrden så ut til å være lav i begge vassdragene begge årene. Dette studiet viste at selv om brunørret, Arktisk røye og Atlanterhavslaks viser ulikheter i deres elveoppvandrings-atferd, hadde de noen fellestrekk. Individer av alle tre artene ble registrert på video ved alle nivåer av vanntemperatur, lysstyrke og vannføring innenfor deres migrasjon periode, noe som indikerer at disse miljøfaktorene ikke så ut til å sette noen absolutt begrensing for oppstrømsmigrasjonsperioden.

Table of content

1 Introduction

Brown trout (*Salmo trutta* L.), Arctic char (*Salvelinus alpinus* L.) and Atlantic salmon (*S. salar* L.) are freshwater species in the salmonid family. All three species display large ecological variation between populations, individuals and various life stages (Klemetsen *et al.*, 2003). Many salmonids, including these three species, can undertake marine feeding migrations in order to take advantage of the higher productivity and prey abundance at sea (Gross *et al.*, 1988). This particular seaward migration strategy is termed anadromy (Shaw, 2016). The migration patterns and degree of anadromy varies between species, populations and individuals (Hvidsten *et al.*, 1998; Thorstad *et al.*, 2016; Jensen *et al.*, 2020).

Amongst anadromous brown trout, Arctic char and Atlantic salmon, the Arctic char typically travels the shortest distances, ~10 – 50 km (Moore, 1975; Finstad & Heggberget, 1993; Davidsen *et al.*, 2019), and spends the shortest time at sea, 30 – 45 days, before returning to their home river (Finstad & Heggberget, 1993; Davidsen *et al.*, 2019; Jensen *et al.*, 2020). Brown trout tend to travel further in the marine habitat than the Arctic char, and are usually found within 30 – 100 km of their natal river (Klemetsen *et al.*, 2003; Jonsson & Jonsson, 2014; Jonsson *et al.*, 2018). While some brown trout return to freshwater within a few days, others may stay out for moths or sometimes one or several years (Bendall *et al.*, 2005; Eldøy *et al.*, 2019; Jensen *et al.*, 2020). In contrast to brown trout and Arctic char, Atlantic salmon commonly migrate hundreds or thousands of kilometers to feeding areas in the North Atlantic ocean, spending 1 – 4 years at sea, before returning upon having reached sexual maturity (Jonsson *et al.*, 1991; Hansen *et al.*, 1993).

Anadromous brown trout and Arctic char may return to freshwater either to overwinter or spawn, which usually occur in late autumn – early winter (Klemetsen *et al.*, 2003; Jonsson & Jonsson, 2011). Some studies have, however, shown that northern brown trout and Arctic char can utilize the marine habitats during winter (Jensen & Rikardsen, 2008; 2012). Atlantic salmon do not return before they have attained sexual maturity and hence commonly overwinter at sea prior to their first spawning migration (Hansen *et al.*, 1993). Overwintering in freshwater reduces energy expenditure as osmoregulation in seawater gets increasingly difficult with decreasing temperatures (Finstad *et al.*, 1988; Thomsen *et al.*, 2007). The tendency of overwintering in freshwater seems to depend on the physical characteristics of the freshwater habitat, and the availability of pools or lakes in the watercourse (Jonsson *et al.*, 2001; Knutsen *et al.*, 2004; Olsen *et al.*, 2006; Jensen & Rikardsen, 2012).

Water flow and water temperature are thought to be the most important factors affecting the upstream migration of salmonids (Jonsson & Jonsson, 2011). Increasing water flow may facilitate migration, but to high flows may also reduce migratory activity as energy expenditure increases and obstacles can become difficult to pass (Berg & Jonsson, 1990; Jonsson & Jonsson, 2002; Jonsson *et al.*, 2018). As larger individuals require more water to move, and smaller streams are more affected by high levels of discharge, the importance of an increase in waterflow seems to vary with the size of the fish (Jonsson *et al.*, 1990; Erkinaro *et al.*, 1999;

Karppinen *et al.*, 2004) and the size of watercourse (Jonsson & Jonsson, 2002), as well as water flow in the river prior to migration (Tetzlaff *et al.*, 2005). Being ectotherms, water temperature highly affects the metabolism and energetic cost (Elliott, 1976; Enders *et al.*, 2005), and swimming performance (Ojanguren & Branta, 2000) of fish. Therefore, water temperature is considered to influence the vulnerability of predation and (Heggenes *et al.*, 1993) and salmonids ability to pass obstacles during upwards migration (Jensen *et al.*, 1986).

The preference for migration during nocturnal conditions, or in periods of increased turbidity, is likely a strategy used to reduce the risk of predation (Banks, 1969; Moore *et al.*, 1995; Svendsen *et al.*, 2004; Bendall *et al.*, 2005; Ibbotson *et al.*, 2011). In general, nocturnal movement appears to be favored during downstream and upstream migration (Moore *et al.*, 1995; Bendall *et al.*, 2005; Thorstad *et al.*, 2008; Ibbotson *et al.*, 2011). However, migration is also known to occur during both day and night in periods of midnight sun (Moore, 1975; Karppinen *et al.*, 2004; Davidsen *et al.*, 2005), in daylight during the upstream passage of some migration barriers (Thorstad *et al.*, 2008), and in daylight during upstream migration in water with increased turbidity (Hellawell *et al.*, 1974).

Stressors may cause salmonids to return to freshwater earlier than expected. Such behavior, often termed premature return, have been documented in response to salmon lice (*Lepeophtheirus salmonis* K.) infestation on anadromous brown trout (Birkeland & Jakobsen, 1997; Halttunen *et al.*, 2018; Serra-Llinares *et al.*, 2020). Premature home migration of individuals suffering salmon lice infestation appears to enhance survival (Birkeland, 1996) as it causes delousing (Finstad *et al.*, 1995; Birkeland & Jakobsen, 1997), and reduces the physiological effects of infection (Bjørn *et al.*, 2001). Premature return can however lead to compromised future fitness due to reduced growth opportunities (Thorstad *et al.*, 2015; Halttunen *et al.*, 2018; Serra-Llinares *et al.*, 2020).

As a changing climate is likely to affect the flow and temperature regimes of freshwater habitats (Jonsson & Jonsson, 2009), the competitive ability of sympatric salmonid species may change (Jonsson & Jonsson, 2009; Winfield *et al.*, 2010). Farming of Atlantic salmon in open caged aquaculture, and associated genetic degradation of wild Atlantic salmon stocks and increased salmon lice infestation pressure on wild fish, poses a major threat to anadromous populations in Norway (Thorstad *et al.*, 2015; ICES, 2016; Anon, 2019). In addition, disease pressure is believed to increase as both marine and freshwater environments gets warmer (Jonsson & Jonsson, 2009) and with the expansion of aquaculture (Vollset *et al.*, 2021). Changes in climate and the influence from farming of Atlantic salmon may alter migration patterns and reduce the benefits of anadromy (Finstad & Hein, 2012; Thorstad *et al.*, 2015; Quinn *et al.*, 2016; Eldøy *et al.*, 2021). While the effect of some factors are well established, the future effect of others are uncertain and poorly understood (Forseth *et al.*, 2017). Because of the large variation between species, populations and individuals, better knowledge is needed on a global as well as a local scale in order to maintain proper management of salmonids in the future.

The objective of the present study was to reveal differences in timing of homing migration between anadromous brown trout, Arctic char and Atlantic salmon within the same watercourse, and between two different watercourses. Secondly, it was evaluated whether the timing of the homing migration in the lower part of the respective watercourses of these three species was influenced by water temperature, water flow, daylight and/or presence of attached adult salmon lice.

The following hypotheses were tested:
a) Anadromous Arctic char returned earlier to the watercourse than brown trout and Atlantic salmon.
b) Anadromous brown trout, Arctic char and Atlantic salmon with longer body length returned earlier to the watercourse than shorter conspecifics.
c) During time periods when dark conditions were present, individuals of all three species favored darker light conditions during upstream migration.
d) Infestation of salmon lice triggered premature home migration in brown trout and Arctic char.

2 Material and methods

2.1 Study area

Data was gathered from video surveillance of anadromous salmonids in the two rivers Fjæreelva and Botnelva (fig. 1), in Nordland county, northern Norway, in 2019 and 2020.
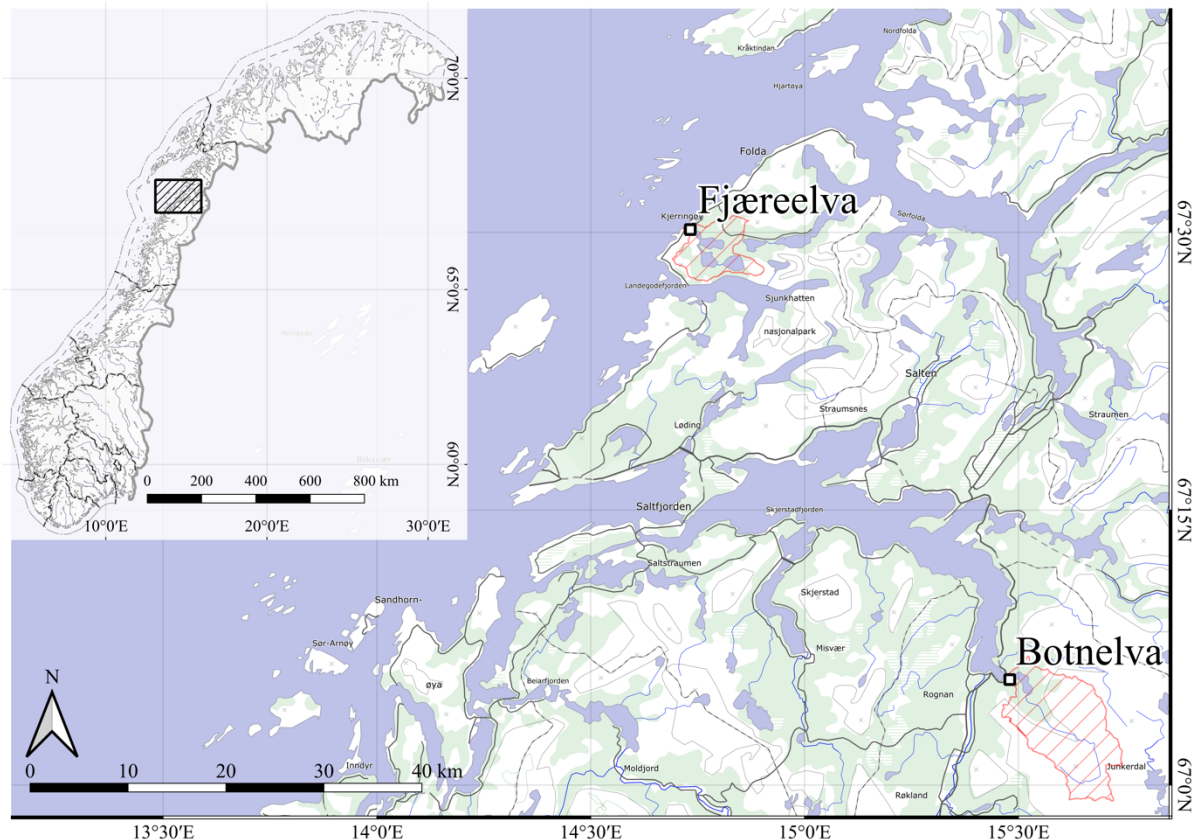
Figure 1: Overview of the study areas. Squares, "Fjæreelva" and "Botnelva", notes the location of the video tunnels in each river. The red shaded area displays the drainage area of each watercourse.

2.1.1 River Fjæreelva

River Fjæreelva (67.50 N°, 14.73 E°) is located on Kjerringøy peninsula in Bodø municipality (fig. 2). Fjæreelva is approximately 1.4 km long and flows into an open coastal area in Karlsøyfjorden. The video tunnel used for surveillance (fig. 3) was placed about 1.1 km upstream of the river outlet, 4 – 5 meters above sea level. The Fjære watercourse drains an area of 34.21 km², and consist of five lakes, as well as several tributaries and small streams. The lower part of the watercourse drains from areas influenced by agriculture, while the upper part drains through forests, marshlands and mountain areas. The anadromous stretch is approximately 13 km, 6 – 7 of which are small rivers and streams. In addition to anadromous brown trout, Arctic char and Atlantic salmon, the watercourse house resident individuals of the same species. Further, European eel (*Anguilla anguilla*), European flounder (*Platichthys flesus*), and three-spined stickleback (*Gasterosteus aculeatus*) resides in the watercourse. Pink salmon (*Oncorhynchus gorbuscha*), rainbow trout (*O. mykiss*) and farmed Atlantic salmon have also been observed migrating upstream in Fjæreelva.
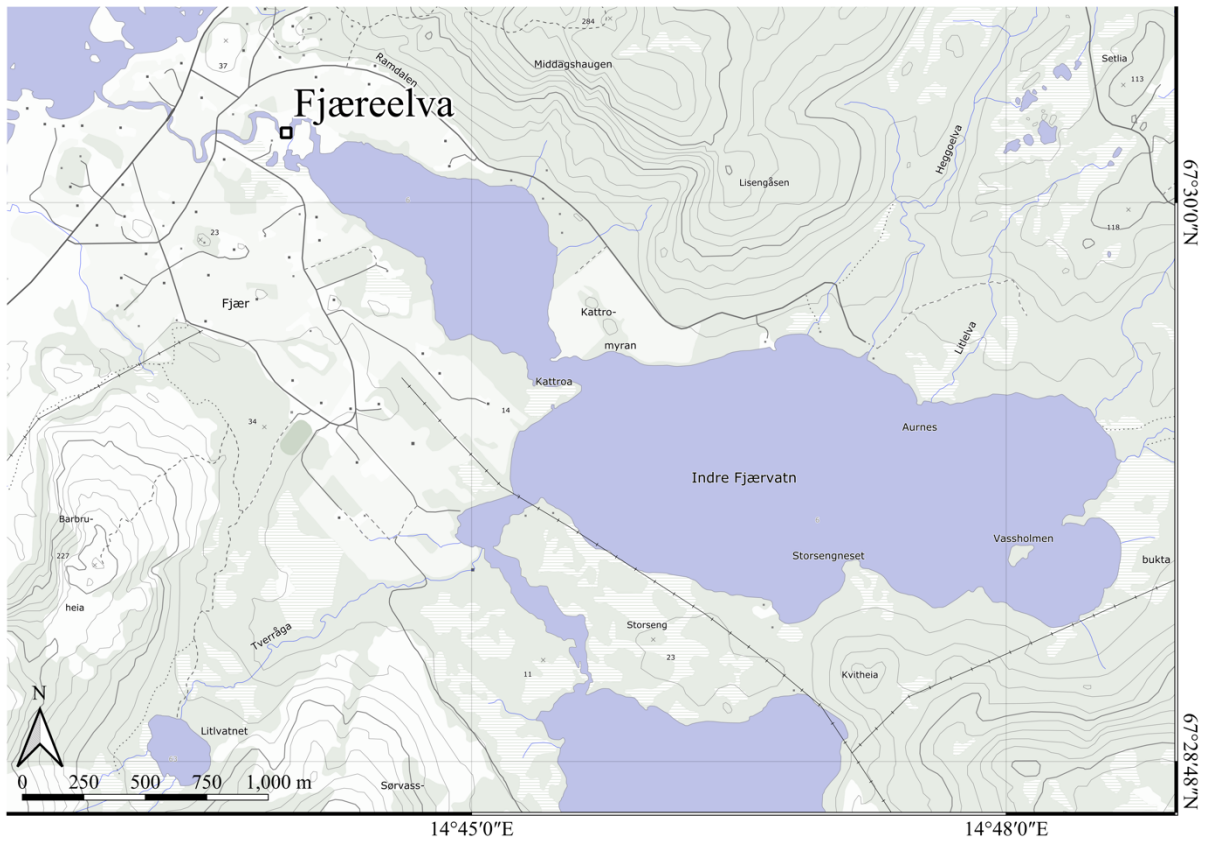
Figure 2.: The lower part of Fjære watercourse. The square is the location of the video tunnel in river Fjæreelva.

Figure 3: The video tunnel in river Fjæreelva with pit-antenna, guiding-fences, shade-cover and fences mounted on the side protect the tunnel from passing cows. The river flows from right to left. Picture was taken 21 August 2020.

2.1.2 River Botnelva

River Botnelva (67.09 N°, 15.50 E°) is situated in the inner part of Saltdalsfjorden, east of the river Saltdalselva, in Saltdal municipality (fig. 4). Botnelva is approximately 0.6 km long. The video tunnel used for surveillance (fig. 5) was placed at the river inlet, which is a smaller extension of the lake it drains, approximately 12 meters above sea level. The Botn watercourse drains an area of 98.64 km^2 and consists of one large and several smaller lakes, as well as several tributaries and small streams, most of which are inaccessible for anadromous fish. The anadromous stretch is approximately 8 km, which includes parts of the main river Knallerdalselva. The watercourse mainly drains from pine forests and mountain areas. In addition to anadromous brown trout, Arctic char and Atlantic salmon, freshwater resident individuals of the three species, as well as European eel and three-spined stickleback resides in the watercourse. Pink salmon and farmed Atlantic salmon have also been observed migrating upstream in Botnelva.
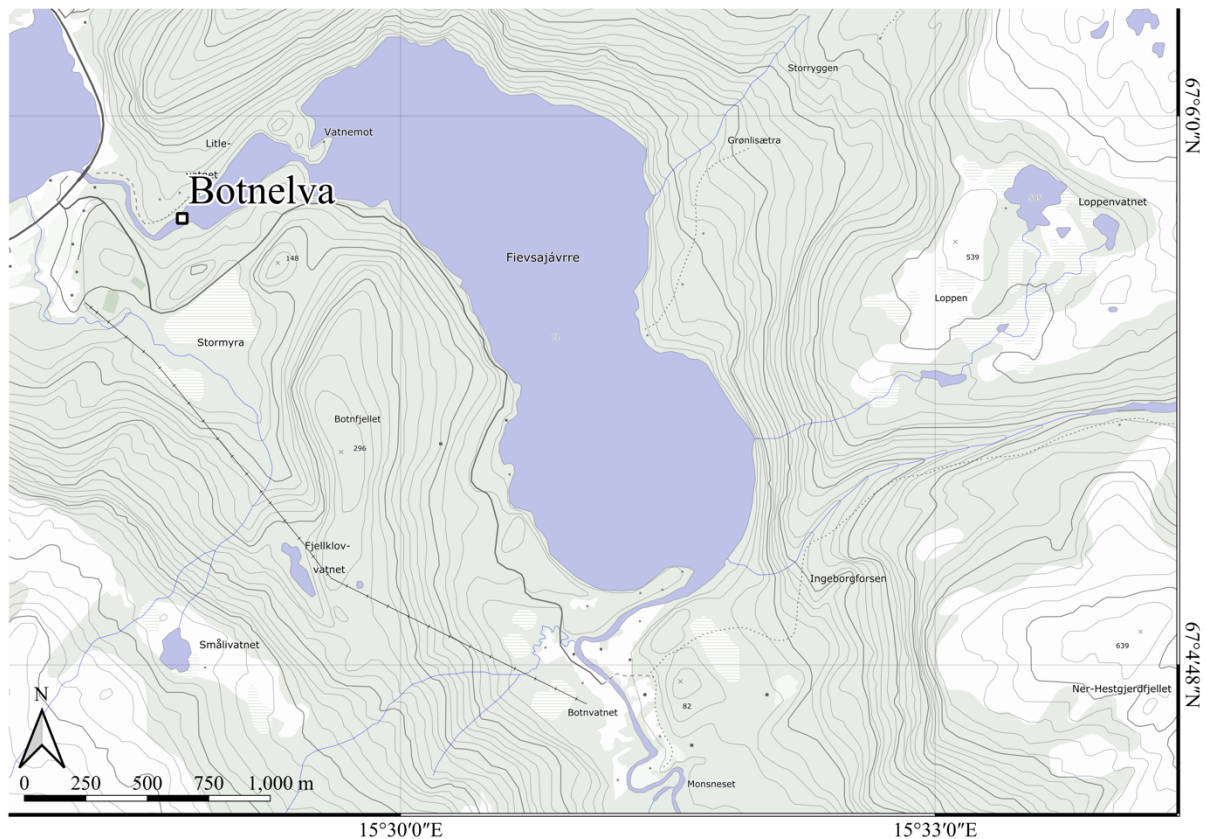
Figure 4: The lower part of Botn watercourse. The square is the location of the video tunnel in river Botnelva.

Figure 5: The video tunnel in river Botnelva with attached pit-antenna and guiding-fences. The river flows from right to left. Picture was taken 29 September 2020.

2.2   Environmental variables

2.2.1 Water temperature

Water temperature was measured every forth hour using DST centi-TD loggers (STAR:ODDI, Reykjavik, Iceland) placed next to the video tunnels on the riverbed. Each fish recorded by the video system (see below) was assigned the measured water temperature corresponding to the four-hour period in which it was registered.

2.2.2 Light intensity

Light intensity (lx) was measured every hour with a pendant temp/light data logger (HOBO ONSET, Bourne, USA) placed approximately 2 m above the river in an open area close to the video tunnel. Each fish recorded by the video system (see below) was assigned the measured light intensity corresponding to the clock-hour in which it was registered.

Hourly light intensity measurements varied from 0 – 209 424 lx. The highest measured light intensity in the hour of a registration was 176 357 lx. Due to the large variation in hourly light intensity values, and the fact that 84% of all registered fish were registered at hourly light intensities below 10 000 lx, two different approaches were used to counteract the large spread in light intensity measurements. In analyses where continuous values of light intensity were appropriate, values above 10 752 lx (1 000 lumen per square feet), which corresponds to the conditions of full daylight when the sun is more than 10° above the horizon (Schlyter, 2017), were assigned a value of 10 752 lx. In analyses where light intensities were used as categorical variables, each clock-hour were assigned one of four light intensity categories (table 1) corresponding to the sun's angle (AMS, 2012c; b; a; Schlyter, 2017).

Table 1: Light intensity categories, corresponding hourly measured light intensity, and corresponding conditions to each category.

Light intensity category	Light intensity (lx)	Conditions
Night conditions	Lux ≤ 1	Nautical twilight (sun 6° to 12° below the horizon). Astronomical twilight (sun 12° to 18° below the horizon). Night (sun ≥18° below the horizon).
Twilight conditions	Lux ≤ 585 & Lux > 1	Very dark overcast day. Civil twilight (sun 0° to 6° below the horizon).
Dimmed light	Lux ≤ 10 752 & Lux > 585	Very dark day. Overcast day. Sun between 0° and 10° above the horizon.
Bright light	Lux > 10 752	Full daylight. Direct sunlight. Sun ≥ 10° above the horizon.

2.2.3 Water runoff

Water depth was measured using DST centi-TD loggers (STAR:ODDI, Reykjavik, Iceland) placed next to the video tunnels on the riverbed in 2019. Because the loggers only registered water depth in 2019, the proxy "water runoff" was used to estimate changes in water level. Four interpolated weather variables from xgeo.no and senorge.no was compared to the depth measurements from 2019 and known events, such as floods. Of the assessed variables "Precipitation", "Rain and snowmelt", "Rain and snowmelt last week" and "Runoff", "Runoff" had the highest correlation with the measured depth in 2019 in river Fjæreelva (linear model, $R^2 = 0.47$) and Botnelva (linear model, $R^2 = 0.40$), and was therefore chosen. The model for runoff considers precipitation, evapotranspiration, and the difference in water storage in soil or snow based on data from the Norwegian Water Recourses and Energy Directorate, the Norwegian Meteorological Institute and the Norwegian Mapping Authority.

2.3 Video analysis

2.3.1 Video tunnel

Video tunnels (Simsonar FC, Oulu, Finland) were installed in rivers Fjæreelva and Botnelva in 2019 and 2020 (fig. 3 and 5). The tunnels used were 140 cm in length and equipped with a stereo camera recording in 10 frames per second (FPS), led-light, and a measuring ruler and/or on-drawn length-intervals. In Fjæreelva in 2020, and Botnelva in 2019 and 2020, PIT-antennas (Oregon RFID, Portland, USA) were installed on the downstream side of the video tunnels. Guiding-fences, stretching from the riverbed to above the surface across the entire river, were installed in the river to direct all fish over ~20 cm in length through the video tunnel and PIT-antenna. Data from the video camera and PIT-antennae was stored on land.

2.3.2 Analysis program

A video processing program (Simsonar FC, Finland) was used to analyze the video recordings in real time. Two stages of pattern-recognition were used in the automatic recognition of registrations. In the first phase, the software decided whether the registered movement was a fish or not by filtering out branches, leaves and/or shadows from the sun. The first phase was done offline, without internet connection. In the second phase, images of pre-recognized fish were sent to a cloud service, via internet connection, which determined the species. Both phases used neural network with an open-source framework used to teach the system. This framework allowed for validation of image recognition by separating some of the training materials as test materials for recognition.

Through daily reports, the software provided accurate time of registration, suggestion on species, body length and swimming direction for all registrations. In general, these daily reports were the basis for further analysis. If a daily report had none, or fewer registrations than what would be expected compared to neighboring days, a sped-up playback was used to investigate if the daily report lacked registrations. The sped-up playback provided time of registration, suggestion on species, body length and swimming direction. All registrations, both daily reports and sped-up playbacks, were analyzed manually afterwards to determine species, and to ensure the quality of the length measurements and the swimming direction.

The quality of species determination was classified as "certain", "uncertain" or "impossible" for each registration. The quality of species determination was affected by the video quality, swimming pattern and morphological appearance as these factors influence the ability to distinguish different species from one another. The presence of attached adult salmon lice was registered if the video quality was sufficient, as were wounds potentially caused by salmon lice infestation. Usually, the registered fish were only seen from one side, meaning only one side of the fish was available to determine if any lice were present. As a result, the number of fish with the presence of salmon lice and wounds must be regarded as a minimum count. The data represents a net movement of fish in an upwards direction. Upwards and downwards registrations of what was assumed to be the same individual, based on species, length and time between registrations, were eliminated. Parr, smaller salmonids (≤ 18 cm), larger resident salmonids and other fish species were excluded from the final analysis.

2.4 Quality assurance

2.4.1 Comparison of data from PIT-registration and video analysis

From 26 – 28 April 2020, three Atlantic salmon and 15 brown trout were PIT-tagged in Fjære watercourse. One brown trout was reported dead. In total nine individuals (one Atlantic salmon and eight anadromous brown trout) were detected on the PIT-antenna by the video tunnel. Seven of the nine PIT-tagged individuals were recorded as they passed through the video tunnel. The remaining two might have been close enough to the video tunnel and PIT-antenna in order

to be registered, without passing through. The physical measurements from the seven PIT-tagged anadromous brown trout registered through video analysis (total body length 48 – 64 cm) were compared to the estimated measurements from the video analysis. All seven were determined to be the correct species. Comparison between the body length obtained from the video analysis and the measured body length during PIT-tagging showed a median overestimation of 2 cm during the video analysis. The only underestimation was -7 cm, and the largest overestimation was +5 cm.

Similar comparisons from river Botnelva from 2018, and 2019 and 2020 combined, gave a 100% species accuracy and a ± 5 cm deviation of estimated length through video analysis compared to the measured length at PIT-tagging (Sjursen *et al.*, 2021).

2.4.2 Video quality and detection rate

Periodic increase in algae growth reduced the image clarity and the contrast of the fish against the background of the tunnel, especially in river Fjæreelva. Image clarity and contrast, in addition to light and light reflection from the sun, seemed to be important factors for the Simsonar FC program's ability to detect all passing fish. While there was almost no algae growth in the video tunnel in river Botnelva, the video tunnel in Fjæreelva was completely covered during shorter periods. The difficulty of maintaining a clear tunnel to avoid the loss of detections varied between watercourses and with seasons. To prevent growth, the tunnel had to be cleaned regularly. Proper cleaning was difficult and labor intensive, and too hazardous during time periods with strong water currents. Therefore, the video quality varied throughout the season, which in turn affected the detection of fish, length measurements and species recognition.

To investigate the detection rate of Simsonar FC in Fjæreelva in 2020, four days were examined manually by looking through every second of video in a speed of 10/1. The days were chosen to represent days of varying video quality. The manual examination indicated that the capabilities of Simsonar FC to register passing fish was 94% in Fjæreelva in 2020 when the video quality was sufficient, but the potential of overlooking registrations increased as the video quality decreased. Smaller and darker fish, often stationary brown trout, appeared to have the highest likelihood of being overlooked. But also larger, silver colored, brown trout and Atlantic salmon passed through without being registered. Ideally, all days with inadequate video quality should have been examined manually for the results to be as accurate as possible, but such a manual examination was not doable due to the time-consuming nature of this task.

2.4.3 Repeated upstream registrations

Individuals were observed migrating upstream several times, without being detected moving downstream, possibly causing repeated upstream registrations on the video in river Fjæreelva in 2020. One anadromous brown trout was registered on the PIT-antennae four times. By comparing the video recordings to the time of which it passed through the PIT-antennae, it was

apparent that the brown trout swam upstream all four times. A couple of larger fish that were believed to be the same individual, due to easy distinguishable and recognizable characters, were also observed swimming upstream several times without being detected moving downstream. In such cases, only one registration was kept for the final analysis.

Repeated upstream registrations likely meant there was a hole in the guiding-fence. Larger holes could appear during floods (table 2), which would make it possible for larger fish to move past the video tunnel and PIT-antenna without being recorded. All the recognized incidents of repeated upstream registrations happened during or after a flood. Other, less likely, possibilities are that the fish jumped over the guiding-fence or was physically transported past the fence. It is also possible that fish swam through without being detected due to temporary reduction in detection range of the PIT-antenna and/or reduced video quality. To avoid such incidents, the guiding-fence was manually examined on a regular basis, the range of the PIT-antennae was tested with different sizes of PIT-tags, and the recording between repeated upstream registrations was investigated manually or through sped-up playback.

2.5   Data analysis

2.5.1 Study period

A total of 10 640 anadromous brown trout, Arctic char and Atlantic salmon were recorded moving upstream using the Simsonar FC program in rivers Fjæreelva and Botnelva in 2019 and 2020. The period of recording included a total of 500 days, both years and rivers combined. Floods and technical problems led to potential loss of registrations several times during the study period (table 2).

Table 2: Period of malfunction believed to affect the number of registered anadromous brown trout, Arctic char and Atlantic salmon during the study period in rivers Fjæreelva and Botnelva in 2019 and 2020.

Incident	Time period	Cause
Fjæreelva 2019		
Hole in guiding-fence	30 June – 3 July	Flood
No recording	23 June – 26 June	Technical problems
No recording	6 July – 7 July	Technical problems
Fjæreelva 2020		
Hole in guiding-fence	16 September – 30 September	Flood
No recording	09 September – 11 September	Technical problems
Botnelva 2019		
Hole in guiding-fence	22 May – 28 May	Flood
Hole in guiding-fence	7 June – 7 July	Flood
Botnelva 2020		
Late start on the study period	03 August	Flood and flood warning
Hole in guiding-fence	21 September – 30 September	Flood
No recording	15 August – 25 August	Technical problems

2.5.2 Quality of species recognition

Of the total 10 640 registrations, 10 394 individuals (98%) were determined to have a "certain" species determination, 239 individuals (2%) an "uncertain" species determination and 7 individuals (< 1%) an "impossible" species determination. The fish recorded with an "impossible" quality were removed from the dataset. 175 individuals (73%) of the fish registered as "uncertain" were recorded in river Fjæreelva in 2020, and the majority of these were considered as anadromous brown trout late in the season. Removing these 175 registrations from a distinct time period could create a bias in the data. To avoid bias, all fish registered as "uncertain" were therefore included in final analysis.

2.5.3 Duration of the upstream migratory period, D_{90}

The time period in which the middle 90% of a given species within each river each year was registered at the video tunnel, D_{90}, was used to evaluate the duration of the upstream migratory periods for each of the three species within each river and year. D_{90} was calculated as the number of days from the 5th to the 95th percentile of registrations for each within river and year species group.

2.5.4 Salmon lice data

From the 10 633 anadromous brown trout, Arctic char and Atlantic salmon, 26 fish (< 1%) were registered with a "certain", 7 631 (72%) with an "uncertain" and 2 976 (28%) with an "impossible" quality of registrations of salmon lice. The 2 976 registrations determined to have an "impossible" quality were excluded from the comparison of fish with detected salmon lice or none detected salmon lice. Of the registrations with a "certain" or "uncertain" quality of registrations of salmon lice, 1 900 (25%) were registered with "1 to 10" lice, 53 (< 1%) with "more than 10" lice and 5 704 (74%) with "none" lice. Reduced video quality due to algae growth was the major cause of "impossible" quality. In addition, swimming speed and position in the tunnel could make it impossible to see the areas where salmon lice usually attach. The proportion of fish registered with an "impossible" quality of registrations of salmon lice varied greatly between years and watercourses.

Registrations with "none" detected salmon lice did not mean that no salmon lice were present, only that none were detected during the video analysis. The more appropriate term "NoneDetected" was therefore used. As "1 to 10" registered salmon lice in reality could be higher than 10, the registration with "1 to 10" and "more than 10" were grouped together to a total of 1 953 (26%) registrations with salmon lice "Detected". Because most fish only were visible from one side, and 2 976 fish were removed due to insufficient quality of registration, the number of fish with "Detected" salmon lice must be regarded as a minimum count.

2.5.5 Statistical analysis

Data management and all statistical analyses were conducted in R studio version 1.4.1106 (RStudio Team, 2021) running R version 4.05 (R Core Team, 2021), with $p < 0.05$ as chosen level for statistical significance. The tested variables: Julian date day-of-year number (DOY), body length, water temperature, light intensity, and water runoff, had a non-Gaussian distribution, based upon performed Shapiro-Wilk normality tests ($p < 0.05$) and the shapes of plotted histograms, for each of the within river and year and river species groups. Therefore, median and percentile ranges were used to describe the differences between groups. As all within river and year species groups were unpaired, and did not meet the general assumption of normality, comparisons between groups were done using Wilcoxon rank sum test with continuity correction (also known as Mann-Whitney U test). To test for possible correlations between upstream migration date and body length, and upstream migration date and attached adult salmon lice, two different linear regression models were performed. Linear regression models assume a normal distribution of data, however this assumption can be avoided if the sample size of the tested variable is large enough, due to the central limit theorem.

3   Results

3.1   Environmental factors

Water temperature: measured on the riverbed next to the video tunnels; water runoff: as an interpolated weather variable; and light intensity: measured 2 m above the river surface, were registered in Fjæreelva and Botnelva throughout the study periods of 2019 and 2020. Since both watercourses are situated north of the Arctic circle, the sun does not set from week 21 – 27, which was reflected by bright light conditions during midsummer. In general, hourly measured light intensity varied greatly throughout each day, and between days and seasons, as it was influenced by the sun's placement and local weather conditions. Both rivers flooded in April/May in 2019 and 2020 in response to the snowmelt. Water temperature, water runoff and light intensity registered in the two rivers during the two years of video registration are described in detail below.

3.1.1   River Fjæreelva

In 2019, water temperature, runoff and light intensity were registered from 13 June – 16 October (fig. 6). The daily average of measured water temperature (fig. 6 A) reached a peak in mid-June, before reaching the highest daily average temperature, 22.2 °C, the 28 July. Temperatures then decreased until the last day of measuring, 16 October, 2.3 °C. The interpolated runoff values (fig. 6 A) were low throughout the study period. The highest runoff was 1.6 mm/d, 03 July. The highest hourly measured light intensity (fig. 6 B) happened 16 June (week 24) at 14h and measured 209 427 lx. Measurements of 0 lx did not occur until week 30.

In 2020, abiotic variables were registered from 27 April – 14 October (fig. 7). The daily average of measured water temperature (fig.7 A) increased until it reached the highest measured value, 20.2 °C, the 22 June, after which it remained higher than 12.9 °C until September. The lowest measured water temperature, 3.4 °C, was measured on first day of the study period, 27 April. Interpolated runoff values (fig. 7 A) indicated elevated water levels in the beginning of the study period, and a sharp increase towards the end. The highest runoff was 7.4 mm/d, the 22 September. The highest hourly measured light intensity (fig. 7 B) happened 09 May (week 24) at 16h and measured 195 646 lx. Measurements of 0 lx did not occur from week 19 until week 30.

Figure 6: **A.**: Daily mean of measured water temperature (red line), interpolated runoff values (dashed line). **B.**: Box-and-whiskers plot displaying the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers) and outliers (dots, >1.5*IQR) for measured light intensity from 13 June – 16 October in river Fjæreelva in 2019.

Figure 7: **A.**: Daily mean of measured water temperature (red line), interpolated runoff values (dashed line). **B.**: Box-and-whiskers plot displaying the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers) and outliers (dots, >1.5*IQR) for measured light intensity from 27 April – 14 October in river Fjæreelva in 2020.

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3.1.2 River Botnelva

In 2019, water temperature, runoff and light intensity were registered from 20 May – 13 October (fig. 8). The daily average of measured water temperature (fig. 8 A) increased until it reached the highest measured value, 16.1 °C the 29 July, after which it remained higher than 14.5 °C until the end of August. The lowest measured water temperature was 4.7 °C the 26 May. The values from the interpolated runoff (fig. 8 A) indicates elevated water levels in June and early July. The highest hourly measured light intensity (fig. 8 A) happened 08 September (week 35) at 13h and measured 161 202 lx. Measurements of 0 lx did not occur until week 30.

In 2020, abiotic variables were registered from 03 August – 13 October (fig. 9). The daily average of measured water temperature (fig. 9 A) ranged from 10.9 – 13.4 °C throughout August. The highest daily average was 13.4 °C the 22 August, and the lowest was 7.4 °C the 22 September. The interpolated runoff values (fig. 9 A) were low through the first half of the study period before it reached a peak of 2.4 mm/d the 23 September. The highest hourly measurement happened 09 September (week 36) at 10h and measured 106 070 lx. Measurements of 0 lx were present throughout the entire study period as the period of midnight sun ended several weeks before the start of the study period.
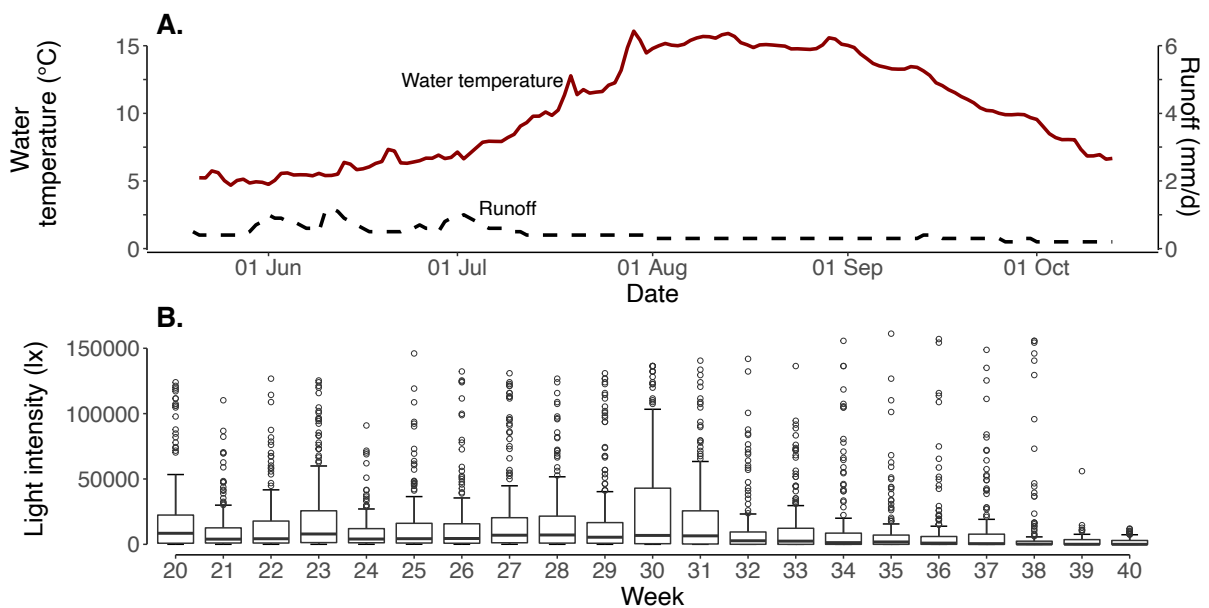
Figure 8: **A.**: Daily mean of measured water temperature (red line), interpolated runoff values (dashed line). **B.**: Box-and-whiskers plot displaying the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers) and outliers (dots, >1.5*IQR) for measured light intensity from 20 May – 13 October in river Botnelva in 2019.
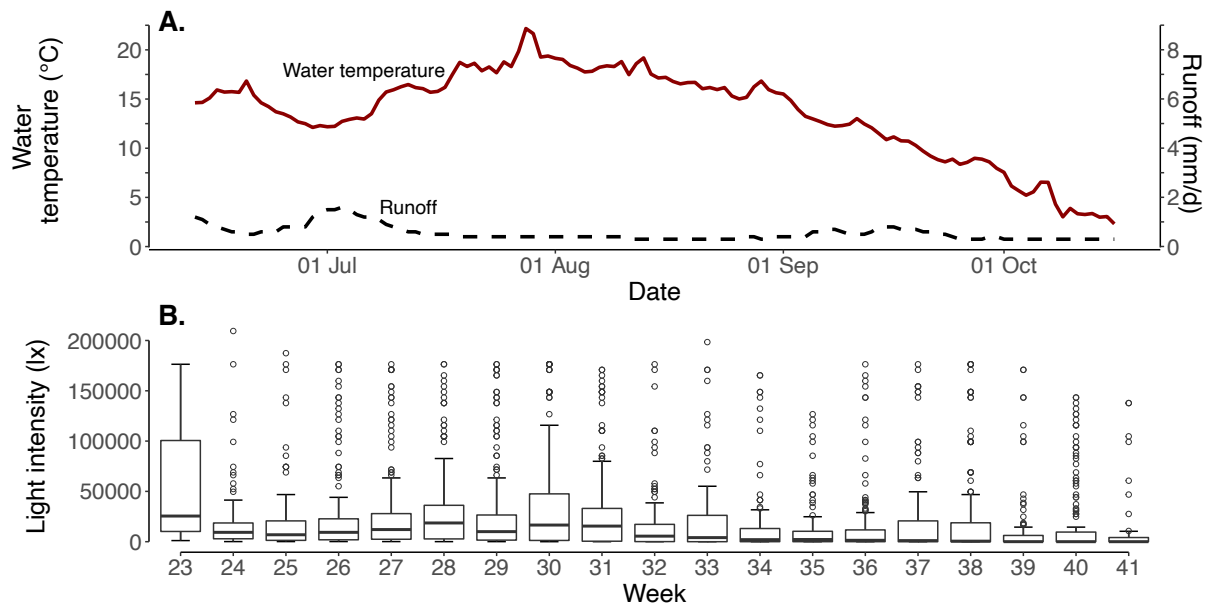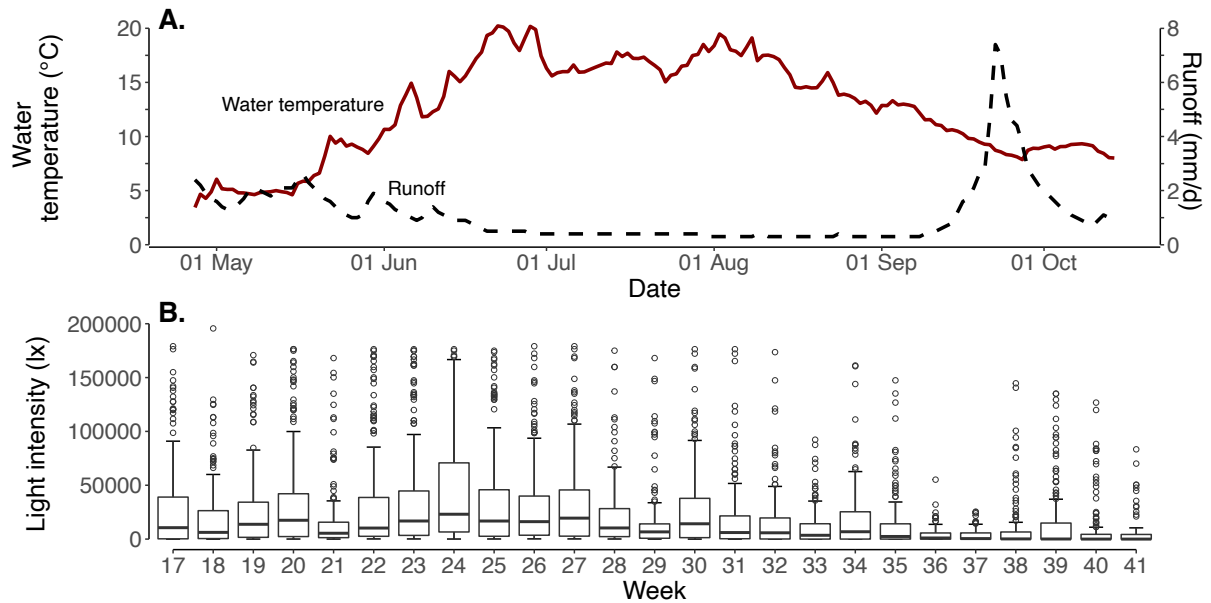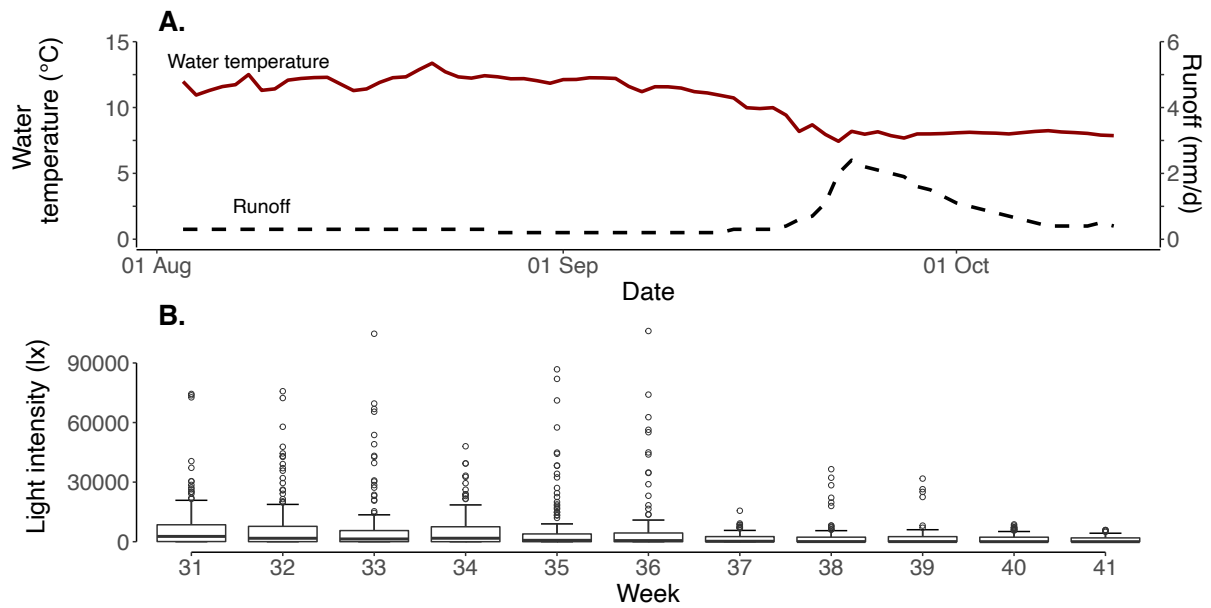
Figure 9: **A.**: Daily mean of measured water temperature (red line), interpolated runoff values (dashed line). **B.**: Box-and-whiskers plot displaying the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers) and outliers (dots, >1.5*IQR) for measured light intensity from 03 August – 13 October in river Botnelva in 2020.

3.2 Video registrations of upstream migrating fish

3.2.1 Date of registration in river Fjæreelva, 2019

From 13 June (DOY 164) until 16 October 2019 (DOY 289), 2 149 upstream migrating brown trout, 614 Arctic char and 167 Atlantic salmon were registered in river Fjæreelva. The median dates of registration and the duration of the time in which 90% of the individuals were registered, D_{90}, indicated an earlier, more dense, period of upstream migration for Arctic char than the two other species (table 3). There were significant differences in registered dates between all three species (table 4). Brown trout and Atlantic salmon had a longer upstream migration period, which varied more in intensity (fig. 10).

Table 3: Median date of registration, D_{90} (number of days from 5th to 95th percentile of registrations), and the range of D_{90} for registered upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in river Fjæreelva in 2019.

	Brown trout	**Arctic char**	**Atlantic salmon**
Median date of registration	18 July DOY 199	18 June DOY 169	26 August DOY 238
D_{90}	93 days 28 June – 28 September DOY 179 – 271	13 days 14 June – 26 June DOY 165 – 177	99 days 27 June – 03 October DOY 178 – 276

Table 4: The total number of compared registrations (*n*), W-value and *p*-value for performed Wilcoxon rank sum tests on compared differences in Julian dates of registration between upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in river Fjæreelva in 2019.

Compared groups	Total *n*	W	*p*
Brown trout – Arctic char	2763	1300826	**< 0.001**
Brown trout – Atlantic salmon	2316	156676	**< 0.01**
Arctic char – Atlantic salmon	781	1023.5	**< 0.001**
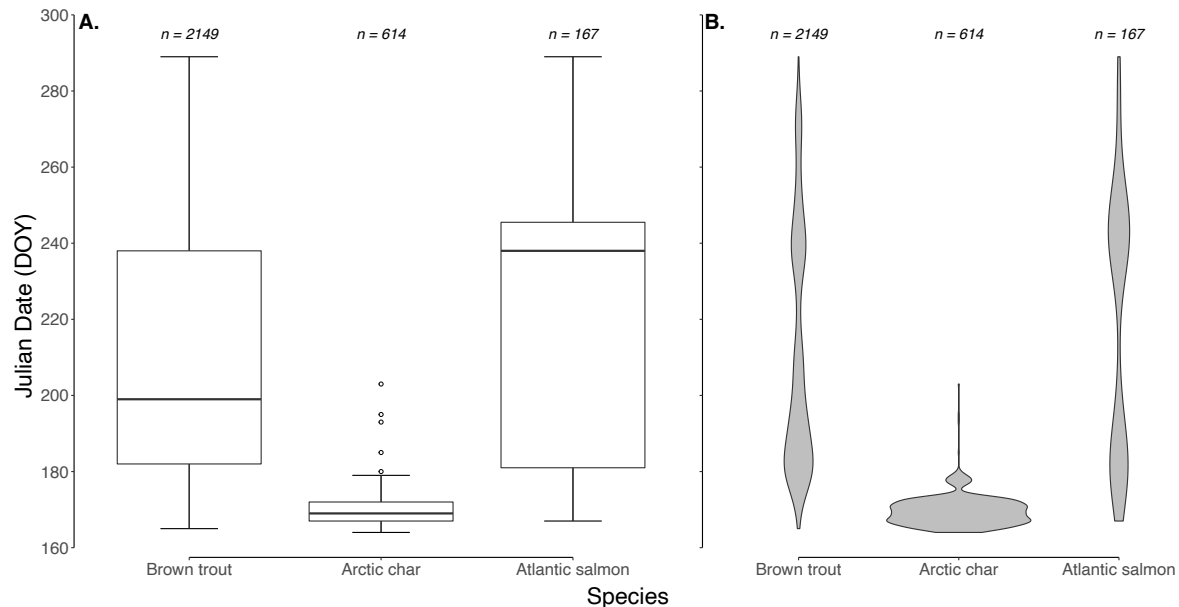
Figure 10: Registered dates of upstream migrating anadromous brown trout, Arctic char and Atlantic salmon from 13 June – 16 October 2019 in river Fjæreelva. The box-and-whiskers plot, **A.**, displays the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers), outliers (dots, >1.5*IQR) and the number of registrations (*n*) for each of the three species. The violin plot, **B.**, displays the density of samples (width of the violin) and number of registrations (*n*) for each of the three species.

3.2.2 Date of registration in river Fjæreelva, 2020

From 27 April (DOY 118) until 14 October 2020 (DOY 288), 2 248 upstream migrating brown trout, 693 Arctic char and 167 Atlantic salmon were registered in river Fjæreelva. The median dates of registration and the duration of the time in which 90% of the individuals were registered, D_{90}, indicated an earlier, more dense, period of upstream migration for Arctic char than for brown trout and Atlantic salmon (table 5). There were significant differences in registered dates between all three species (table 6). Brown trout and Atlantic salmon had a longer upstream migration period which varied more in intensity (fig. 11 B).

Table 5: Median date of registration, D_{90} (number of days from 5th to 95th percentile of registrations), and the range of D_{90} for registered upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in river Fjæreelva in 2020.

	Brown trout	Arctic char	Atlantic salmon
Median date of registration	22 July DOY 204	18 June DOY 170	14 September DOY 258
D_{90}	93 days 21 June – 21 September DOY 173 – 265	21 days 04 June – 24 June DOY 156 – 176	117 days 18 June – 12 October DOY 170 – 286

Table 6: The total number of compared registrations (*n*), W-value and *p*-value for performed Wilcoxon rank sum tests on compared differences in Julian dates of registration between upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in river Fjæreelva in 2020.

| Compared groups	Total *n*	W	*p*
Brown trout – Arctic char	2941	1491890	**< 0.001**
Brown trout – Atlantic salmon	2474	147584	**< 0.001**
Arctic char – Atlantic salmon	919	9762.5	**< 0.001**
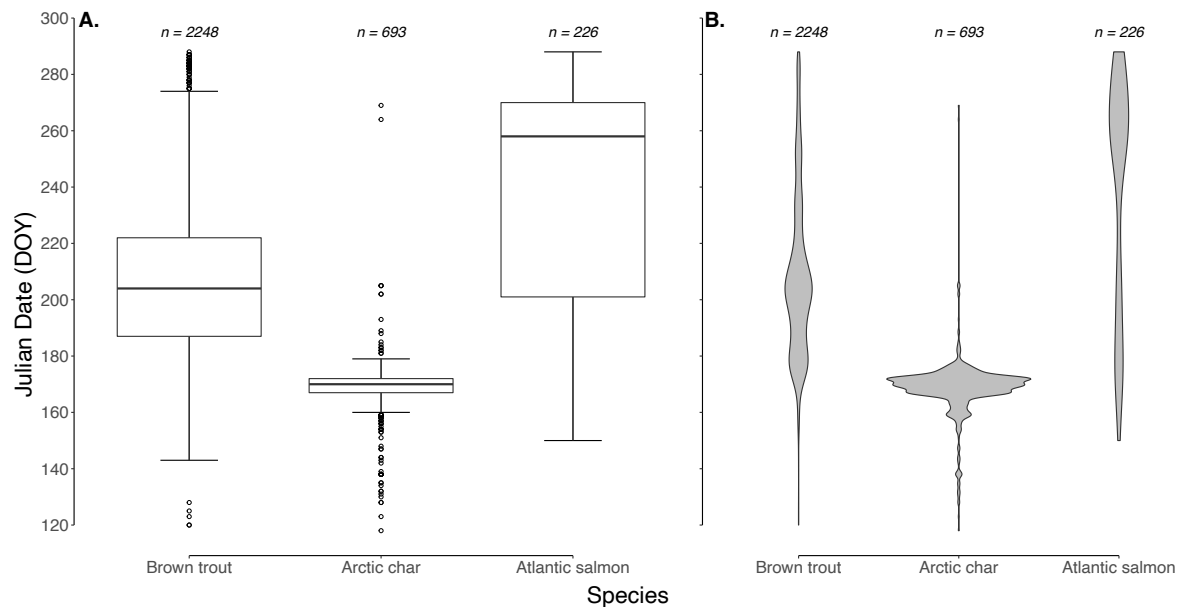
Figure 11: Registered dates of upstream migrating anadromous brown trout, Arctic char and Atlantic salmon from 27 April – 14 October 2020 in river Fjæreelva. The box-and-whiskers plot, **A.**, displays the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers), outliers (dots, >1.5*IQR) and the number of registrations (*n*) for each of the three species. The violin plot, **B.**, displays the density of samples (width of the violin) and number of registrations (*n*) for each of the three species.

3.2.3 Date of registration in Botnelva, 2019

From 20 May (DOY 140) to 13 October 2019 (DOY 286), 2 243 upstream migrating brown trout, 983 Arctic char and 80 Atlantic salmon were registered river Botnelva. The median dates of registration and the duration of the time in which 90% of the individuals were registered, D_{90}, indicated an earlier, more dense, period of upstream migration for Arctic char than for brown trout and Atlantic salmon (table 7). There were significant differences in registered dates between all three species (table 8). The timing of upstream migration was early and intense for Arctic char, late and intense for Atlantic salmon, and longer with more varying intensity for brown trout (fig. 12).

Table 7 Median date of registration, D_{90} (number of days from 5th to 95th percentile of registrations), and the range of D_{90} for registered upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in river Botnelva in 2019.

	Brown trout	Arctic char	Atlantic salmon
Median date of registration	26 August DOY 238	02 August DOY 214	02 October DOY 275
D_{90}	78 days 20 July – 05 October DOY 201 – 278	21 days 20 July – 09 August DOY 201 – 221	82 days 21 July – 10 October DOY 202 – 283

Table 8: The total number of compared registrations (*n*), W-value and *p*-value for performed Wilcoxon rank sum tests on compared differences in Julian dates of registration between upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in river Botnelva in 2019.

| Compared groups	Total *n*	W	*p*
Brown trout – Arctic char	3226	1860986	**< 0.001**
Brown trout – Atlantic salmon	2323	36754	**< 0.001**
Arctic char – Atlantic salmon	1063	7672	**< 0.001**
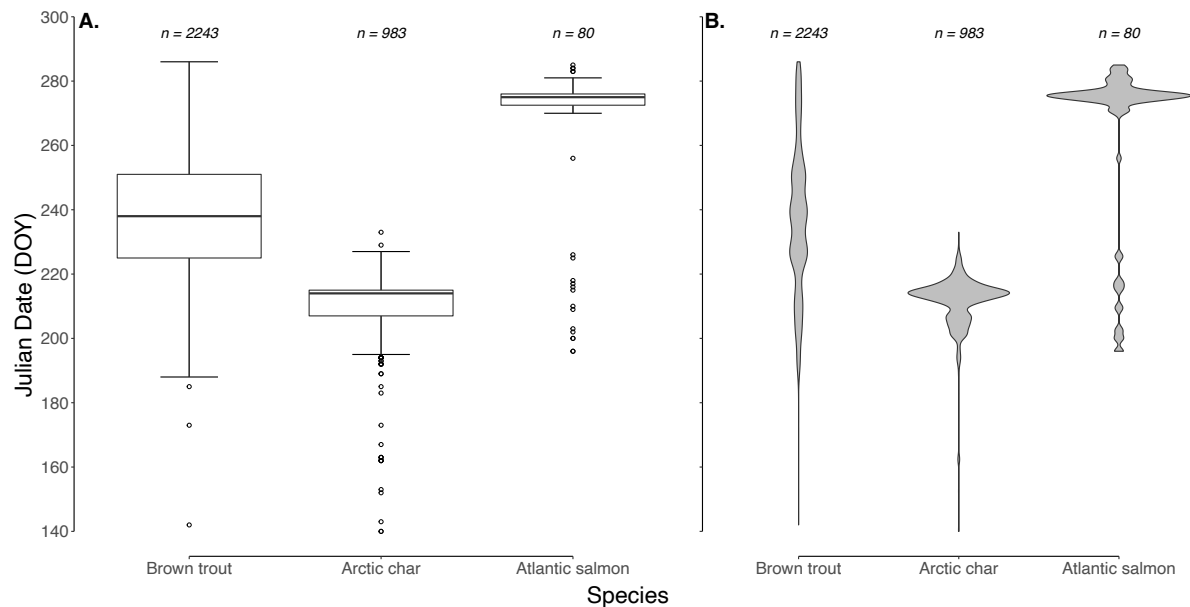
Figure 12: Registered dates of upstream migrating anadromous brown trout, Arctic char and Atlantic salmon from 20 May – 13 October 2019 in river Botnelva. The box-and-whiskers plot, **A.**, displays the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers), outliers (dots, >1.5*IQR) and the number of registrations (*n*) for each of the three species. The violin plot, **B.**, displays the density of samples (width of the violin) and number of registrations (*n*) for each of the three species.

3.2.4 Date of registration in Botnelva, 2020

From 03 August (DOY 216) until 13 October 2020 (DOY 287), 1 115 upstream migrating brown trout, 91 Arctic char and 24 Atlantic salmon were registered in river Botnelva. The median dates of registration and the duration of the time in which 90% of the individuals were registered, D_{90}, indicated an earlier, more dense, period of upstream migration for Arctic char than for brown trout and Atlantic salmon (table 9). There were significant differences in registered migration dates between all three species (table 10). Brown trout and Atlantic salmon had a longer upstream migration period which varied more in intensity (fig. 13).

Table 9: Median date of registration, D_{90} (number of days from 5th to 95th percentile of registrations), and the range of D_{90} for registered upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in river Botnelva in 2020.

	Brown trout	Arctic char	Atlantic salmon
Median date of registration	07 September DOY 251	09 August DOY 222	30 September DOY 274
D_{90}	59 days 09 August – 06 October DOY 222 – 280	9 days 06 August – 14 August DOY 219 – 227	61 days 10 August – 09 October DOY 223 – 283

Table 10: The total number of compared registrations (*n*), W-value and *p*-value for performed Wilcoxon rank sum tests on compared differences in Julian dates of registration between upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in river Botnelva in 2020.

Compared groups	Total *n*	W	*p*
Brown trout – Arctic char	1206	93598	**< 0.001**
Brown trout – Atlantic salmon	1139	8195	**< 0.01**
Arctic char – Atlantic salmon	115	106	**< 0.001**
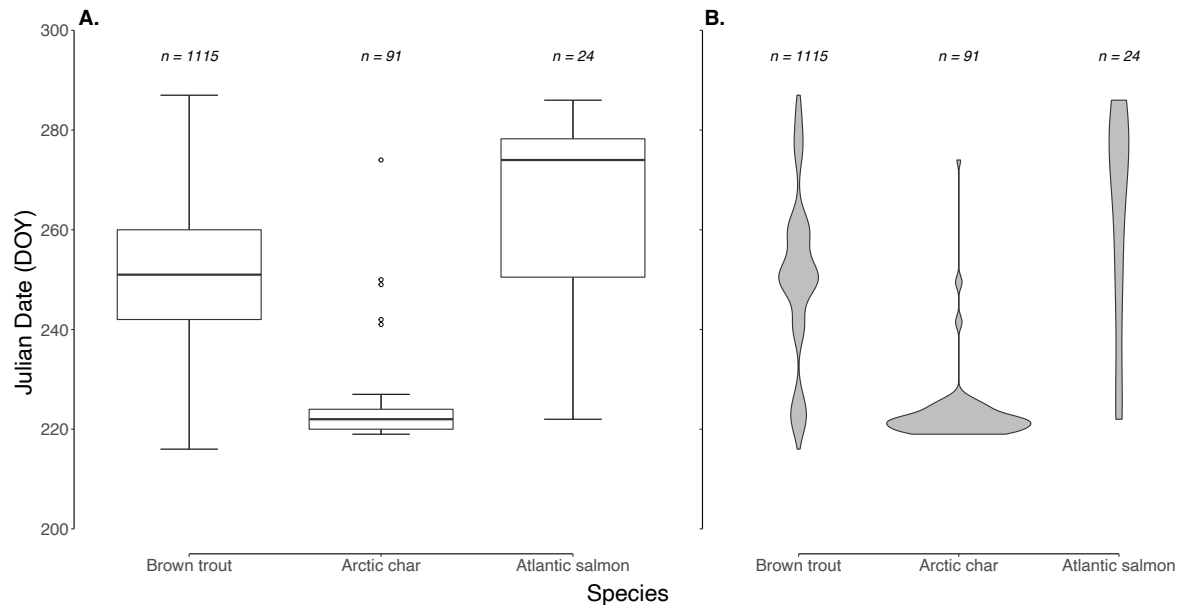
Figure 13: Registered dates of upstream migrating anadromous brown trout, Arctic char and Atlantic salmon from 03 August – 13 October 2020 in river Botnelva. The box-and-whiskers plot, **A.**, displays the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers), outliers (dots, >1.5*IQR) and the number of registrations (*n*) for each of the three species. The violin plot, **B.**, displays the density of samples (width of the violin) and number of registrations (*n*) for each of the three species.

3.2.5 Differences in timing of upstream migration between years and rivers

There were no significant differences in the dates of upstream migration between 2019 and 2020 for brown trout and Arctic char in Fjæreelva, however there was a significant difference between the registered dates of Atlantic salmon between the two years (table 11). In Botnelva, there was no significant difference between the registered dates of Atlantic salmon between the two years, but there was for brown trout and Arctic char (table 11). There was a significant difference in registered dates for all three species between river Fjæreelva and Botnelva, both years combined (table 11).

Table 11: The total number of compared registrations (*n*), W-value and *p*-value for performed Wilcoxon rank sum tests on compared differences in Julian dates of registration between upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in river Fjæreelva in 2019 and 2020, in river Botnelva in 2019 and 2020, and between rivers Fjæreelva and Botnelva both years combined.

Compared groups	Total *n*	W	*p*
Fjæreelva: 2019 – 2020			
Brown trout – Brown trout	4937	2450678	> 0.05
Arctic char – Arctic char	1307	207842	> 0.05
Atlantic salmon – Atlantic salmon	393	12415	**< 0.001**
Botnelva: 2019 – 2020			
Brown trout – Brown trout	3358	785669	**< 0.001**
Arctic char – Arctic char	1074	3373	**< 0.001**
Atlantic salmon – Atlantic salmon	104	957	> 0.05
Fjæreelva – Botnelva			
Brown trout – Brown trout	7755	11840064	**< 0.001**
Arctic char – Arctic char	2381	1384765	**< 0.001**
Atlantic salmon – Atlantic salmon	497	31311	**< 0.001**

In general, Arctic char migrated upstream first, followed by brown trout and Atlantic salmon (fig. 14). When comparing the two rivers, Arctic char, brown trout and Atlantic salmon were registered earlier during the upstream migration in river Fjæreelva than in river Botnelva (fig. 14).
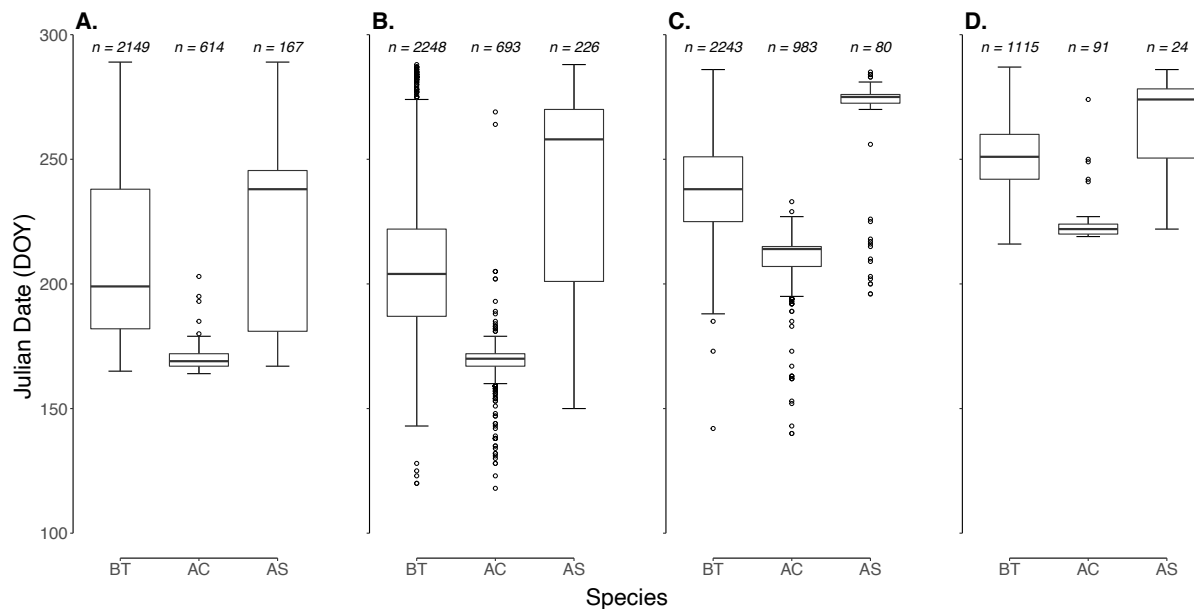
Figure 14: Registered dates of upstream migrating anadromous brown trout (BT), Arctic char (AC) and Atlantic salmon (AS) river: **A.** Fjæreelva in 2019, **B.** Fjæreelva in 2020, **C.** Botnelva in 2019, and **D.** Botnelva in 2020. The box-and-whiskers plots displays the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers), outliers (dots, >1.5*IQR) and the number of registrations (*n*) for each of the three species.

3.2.6 Correlation between dates of upstream migration and body length

Linear regression models were used to investigate potential relationships between the date of upstream migration and estimated body length (Appendix 1). Larger upstream migrating brown trout, Arctic char and Atlantic salmon were registered at the video tunnel earlier than shorter conspecifics in river Fjæreelva in 2019 (fig. 15 A), and in Botnelva in 2019 (fig. 15 C). This pattern was also observed for brown trout and Arctic char in Botnelva in 2020 (fig. 15 D). However, the opposite pattern, with shorter upstream migrants arriving earlier, was observed in Fjæreelva in 2020 for brown trout and Arctic char (fig. 15 B). The low goodness-of-fit (R^2) observed for most of the estimated models (fig. 15 A; B; C; D) suggest that other, not included, factors were more important in determining the date of upstream migration than the tested variable body length.
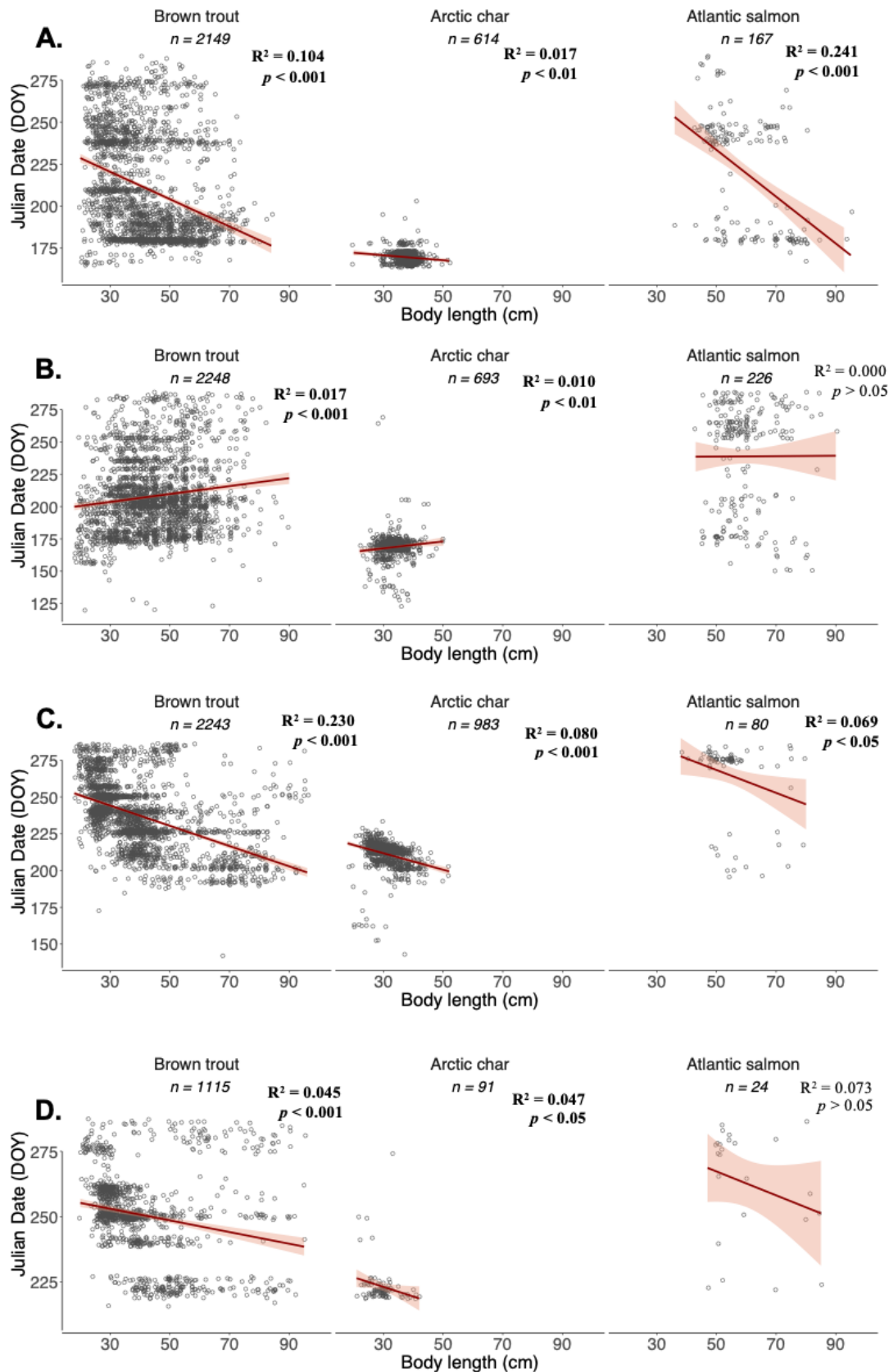
Figure 15: Registered dates of upstream migration as a function of body length (cm) for anadromous brown trout, Arctic char and Atlantic salmon in: **A.**: Fjæreelva 2019, **B.**: Fjæreelva 2020, **C.**: Botnelva 2019, and **D.**: Botnelva 2020. Dots display individual registrations (jittered to reduce overplotting), lines display linear regression models (function y ~ x) with 95% confidence intervals, *n* is the total number of registrations, R^2 is the calculated linear relationship between observed and estimated values, and *p* is the level of significance. Statistically significant *p*-values and affiliated R^2 are in bold.

3.3 Timing of upstream migration and abiotic factors

3.3.1 Upstream migration and water temperature

A significant difference in water temperature at the time of upstream migration through the video tunnel was detected between brown trout, Arctic char and Atlantic salmon in both rivers both years (table 12). In both rivers in both years, Arctic char had the highest median water temperature at registration, brown trout the second highest and Atlantic salmon the lowest (table 13). However, the differences in registered median water temperatures between brown trout and Arctic char were small, and the 25th to 75th percentile ranges overlapped. Median values for the daily average in each river each year throughout the study periods indicated that Fjæreelva was warmer than Botnelva in both 2019 and 2020.

Table 12: The total number of compared registrations (*n*), W-value and *p*-value for performed Wilcoxon rank sum tests on compared differences in water temperature (measured every 4 h, °C) at registration between upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in rivers Fjæreelva and Botnelva in 2019 and 2020.

Compared groups	Total *n*	W	*p*
Fjæreelva 2019			
Brown trout – Arctic char	2763	496578	**< 0.001**
Brown trout – Atlantic salmon	2316	204696	**< 0.01**
Arctic char – Atlantic salmon	781	75962	**< 0.001**
Fjæreelva 2020			
Brown trout – Arctic char	2941	695748	**< 0.001**
Brown trout – Atlantic salmon	2474	386508	**< 0.001**
Arctic char – Atlantic salmon	919	123082	**< 0.001**
Botnelva 2019			
Brown trout – Arctic char	3226	951655	**< 0.001**
Brown trout – Atlantic salmon	2323	150282	**< 0.001**
Arctic char – Atlantic salmon	1063	70204	**< 0.001**
Botnelva 2020			
Brown trout – Arctic char	1206	35066	**< 0.001**
Brown trout – Atlantic salmon	1139	19383	**< 0.001**
Arctic char – Atlantic salmon	115	1832	**< 0.001**

Table 13: Median and 25th to 75th percentile of water temperature (measured every 4 h, °C) at registration for upstream migrating anadromous brown trout, Arctic char and Atlantic salmon, as well as the median and 25th to 75th percentile of the daily average water temperature throughout the study period in rivers Fjæreelva and Botnelva in 2019 and 2020.

	Brown trout	Arctic char	Atlantic salmon	Study period
Fjæreelva 2019				
Median	14.1 °C	15.1 °C	13.1 °C	14.9 °C
25th to 75th percentile	12.2 – 15.8 °C	14.5 – 15.7 °C	12.2 – 14.9 °C	11.2 – 16.8 °C
Fjæreelva 2020				
Median	16.1 °C	16.7 °C	10.6 °C	12.9 °C
25th to 75th percentile	15.0 – 17.3 °C	14.8 – 18.1 °C	9.18 – 15.2 °C	9.05 – 16.5 °C
Botnelva 2019				
Median	14.7 °C	14.8 °C	9.0 °C	9.9 °C
25th to 75th percentile	12.2 – 15.1 °C	12.6 – 15.2 °C	8.5 – 9.6 °C	6.7 – 14.4 °C
Botnelva 2020				
Median	11.4 °C	11.7 °C	8.2 °C	11.3 °C
25th to 75th percentile	10.0 – 12.0 °C	11.4 – 12.2 °C	8.1 – 11.2 °C	8.1 – 12.1 °C

Differences between the 25th to 75th percentile range of measured water temperature at registration ranged from 0.8 to 6.1°C, indicating that most individuals were registered within a relatively narrow temperature span. However, individuals were registered at temperatures far greater and lesser than the 25th to 75th percentile range, especially in river Fjæreelva (fig. 16).
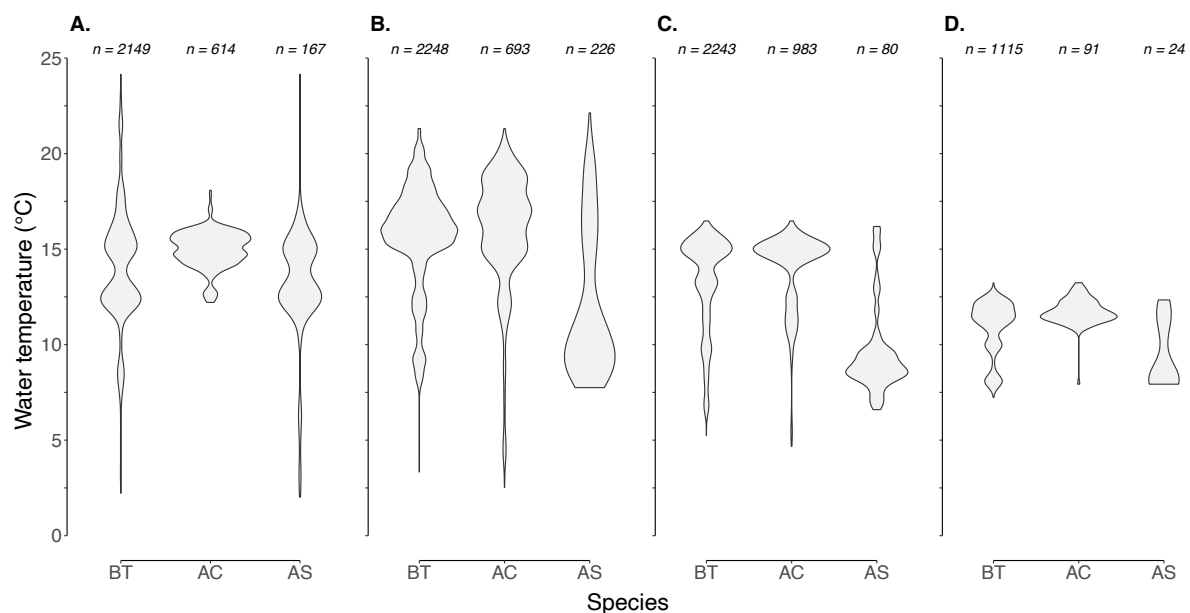
Figure 16: Water temperature (measured every 4 h, °C) at registration for upstream migrating anadromous brown trout (BT), Arctic char (AC) and Atlantic salmon (AS) in river: **A.** Fjæreelva in 2019, **B.** Fjæreelva in 2020, **C.** Botnelva in 2019, and **D.** Botnelva in 2020. The violin plots display the density of samples (width of the violin) and number of registrations (*n*) for each of the three species.

3.3.2 Upstream migration and light intensity

A significant difference in measured light intensity at the time the fish passed through the video tunnel was detected between brown trout, Arctic char and Atlantic salmon in Fjæreelva in both years, and in Botnelva in 2019 (table 14). In Fjæreelva, both years, Arctic char migrated at the

highest light intensity, followed by brown trout and Atlantic salmon (fig. 17). In Botnelva in 2019, Arctic char migrated at the highest light intensity, followed by Atlantic salmon and brown trout (fig. 17). No difference was detected between the three species in Botnelva in 2020 (fig. 17).

Table 14: The total number of compared registrations (*n*), W-value and *p*-value for performed Wilcoxon rank sum tests on compared differences in light intensity (hourly measured lx, values $\geq 10\ 752$ lx were registered as 10 752) at registration between upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in rivers Fjæreelva and Botnelva in 2019 and 2020.

Compared groups	Total *n*	W	*p*
Fjæreelva 2019			
Brown trout – Arctic char	2763	356295	**< 0.001**
Brown trout – Atlantic salmon	2316	211900	**< 0.001**
Arctic char – Atlantic salmon	781	86266	**< 0.001**
Fjæreelva 2020			
Brown trout – Arctic char	2941	356295	**< 0.001**
Brown trout – Atlantic salmon	2474	283825	**< 0.01**
Arctic char – Atlantic salmon	919	122719	**< 0.001**
Botnelva 2019			
Brown trout – Arctic char	3226	706059	**< 0.001**
Brown trout – Atlantic salmon	2323	73723	**< 0.01**
Arctic char – Atlantic salmon	1063	47907	**< 0.001**
Botnelva 2020			
Brown trout – Arctic char	1206	47392	> 0.05
Brown trout – Atlantic salmon	1139	11668	> 0.05
Arctic char – Atlantic salmon	115	1029.5	> 0.05

Figure 17: Light intensity (hourly measured lx, values $\geq 10\ 752$ lx were registered as 10 752) at registration for upstream migrating anadromous brown trout (BT), Arctic char (AC) and Atlantic salmon (AS) in: **A.** Fjæreelva in 2019, **B.** Fjæreelva in 2020, **C.** Botnelva in 2019, and **D.** Botnelva in 2020. The box-and-whiskers plots displays the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers), outliers (dots, >1.5*IQR) and the number of registrations (*n*) for each of the three species.

Within each river and year, the period in which the middle 90% (D_{90}) of Arctic char were registered through the video tunnel, was used to examine possible correlations between the time of passage and light intensity. D_{90} for Arctic char took place early in the study period, in Fjæreelva both years and in Botnelva in 2019, when light intensities were high both day and night. Since the upstream migration of Arctic char took place earlier and within a shorter time window, than what was the case for the other two species, it was only possible to compare correlations between light intensity and upstream migration between the three species for a subsample of brown trout and Atlantic salmon. A significant difference in light intensity was only detected between brown trout and Arctic char in both rivers in 2019 (table 15).

Table 15: The total number of compared registrations (*n*), W-value and *p*-value for performed Wilcoxon rank sum tests on compared differences in light intensity (hourly measured lx, values $\geq$ 10 752 lx were registered as 10 752) at registration between upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in rivers Fjæreelva and Botnelva in 2019 and 2020 in the time period of D_{90} (number of days from 5th to 95th percentile of registrations) for Arctic char.

Compared groups	Total *n*	W	*p*
Fjæreelva 2019			
Brown trout – Arctic char	636	15350	**< 0.05**
Brown trout – Atlantic salmon	68	113.5	> 0.05
Arctic char – Atlantic salmon	576	1289	> 0.05
Fjæreelva 2020			
Brown trout – Arctic char	926	86194	> 0.05
Brown trout – Atlantic salmon	322	5209	> 0.05
Arctic char – Atlantic salmon	670	12454	> 0.05
Botnelva 2019			
Brown trout – Arctic char	1296	146032	**< 0.001**
Brown trout – Atlantic salmon	399	1813.5	> 0.05
Arctic char – Atlantic salmon	913	4626	> 0.05
Botnelva 2020			
Brown trout – Arctic char	271	8528	> 0.05
Brown trout – Atlantic salmon	189	401.5	> 0.05
Arctic char – Atlantic salmon	90	174.5	> 0.05

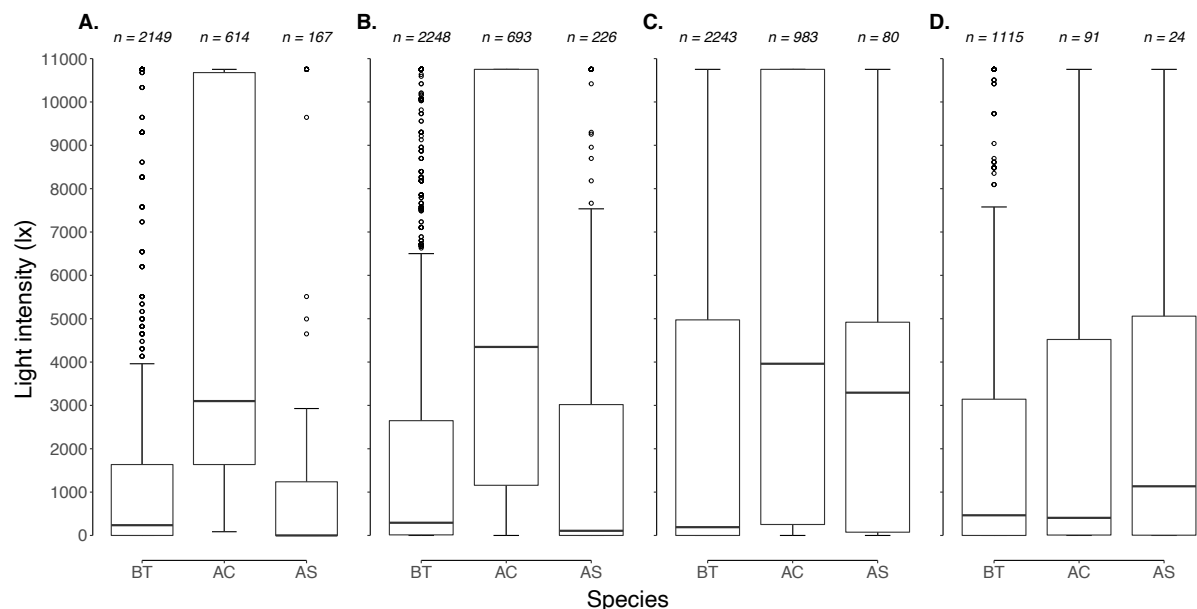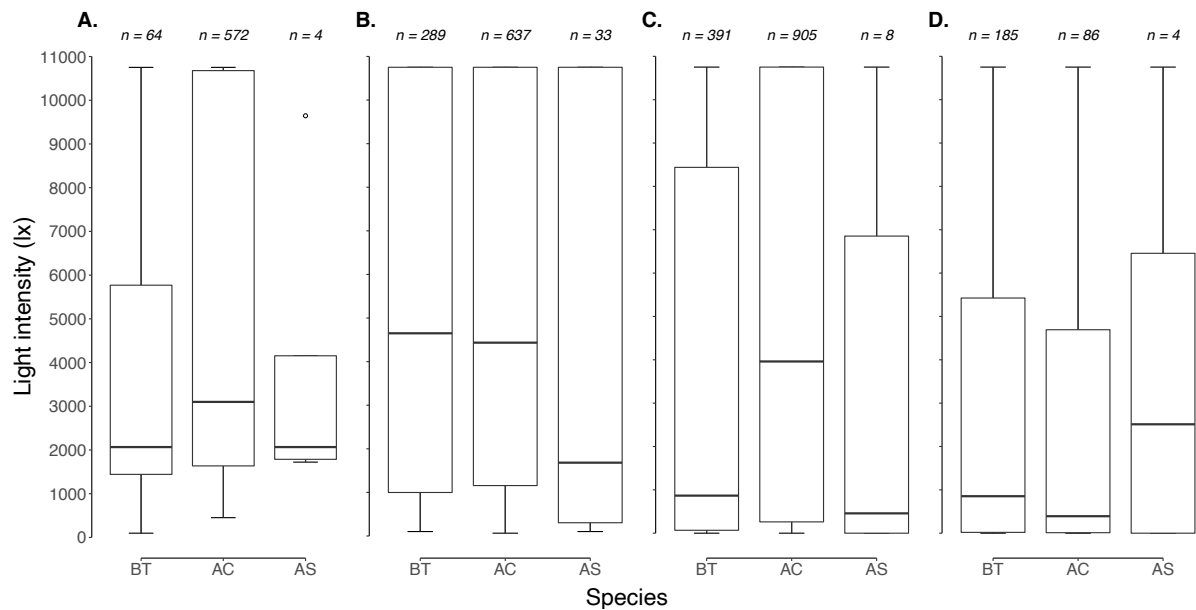**Figure 18**: Light intensity (hourly measured lx, values ≥ 10 752 lx were registered as 10 752) at registration for upstream migrating anadromous brown trout (BT), Arctic char (AC) and Atlantic salmon (AS) in the period of D_{90} (number of days from 5th to 95th percentile of registrations) for Arctic char in: **A.** Fjæreelva in 2019, **B.** Fjæreelva in 2020, **C.** Botnelva in 2019, and **D.** Botnelva in 2020. The box-and-whiskers plots displays the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers), outliers (dots, >1.5*IQR) and the number of registrations (*n*) for each of the three species.

All registered upstream migrating brown trout, Arctic char and Atlantic salmon in river Fjæreelva were assigned a light intensity category based on the hourly average of measured light intensity in the clock-hour of registration (table 1). There were clear interspecific differences in the proportion of individuals assigned different light intensity categories, and clear intraspecific similarities between the two years (table 16).

In both 2019 and 2020, most brown trout and Atlantic salmon were registered at the video tunnel during Twilight conditions and Night conditions (table 16). In contrast, most Arctic char were registered during Dimmed light and Bright light (table 16).

Table 16: Number of registered, and percentage of total, anadromous brown trout, Arctic char and Atlantic salmon in each light intensity categories: Night conditions; ≤ 1 lx, Twilight conditions; > 1 lx & ≤ 585 lx, Dimmed light; > 585 lx & ≤ 10 752 lx, Bright light; > 10 752 lx, in 2019 and 2020 in river Fjæreelva.

	2019			2020		
	Brown trout	Arctic char	Atlantic salmon	Brown trout	Arctic char	Atlantic salmon
Night conditions, *n*	650	0	88	435	2	84
% of total	30.2 %	0 %	52.7 %	19.4 %	0.3 %	37.2 %
Twilight conditions, *n*	716	40	27	841	37	50
% of total	33.3 %	6.5 %	16.2 %	37.4 %	5.3 %	22.1 %
Dimmed light, *n*	549	430	33	709	424	68
% of total	25.5 %	70 %	19.8 %	31.5 %	61.2 %	30.1 %
Bright light, *n*	234	144	19	263	230	24
% of total	10.9 %	23.5 %	11.4 %	11.7 %	33.2 %	10.6 %

3.3.3 Correlation between light intensity, runoff and water temperature

Brown trout in river Fjæreelva was selected for further analysis of potential correlations between the time of registration through the video tunnel and light intensity, runoff and water temperature as the difference in length of the study periods and number of registrations was small between 2019 and 2020. In both 2019 and 2020, Twilight conditions had the highest number of registered brown trout, and the lowest number of hours available, while Bright light had lowest number of registrations, and the highest number of hours available (table 17). Despite the differences in the number of registrations and the available hours within each light intensity category, the proportion of registrations per hour was almost identical when comparing 2019 and 2020 (table 17). Twilight conditions had the highest number of registrations per hour, followed by Night conditions, Dimmed light and Bright light, in that order, for both years.

Table 17: The number of registered anadromous brown trout, the total number of hours throughout the study period, the number of registered anadromous brown trout per hour, and the proportion percent (registrations per hour / total number of registrations per hour) in each light intensity category: Night conditions; ≤ 1 lx, Twilight conditions; > 1 lx & ≤ 585 lx, Dimmed light; > 585 lx & $\leq 10\ 752$ lx, Bright light; $> 10\ 752$ lx, in river Fjæreelva from 13 June 2019 – 16 October 2019 and 27 April 2020 – 14 October 2020.

Year	Light intensity category	Registrations (*n*)	Hours in study period (h)	Registrations per hour	Proportion of registrations per hour
2019	Night conditions	650	662	0.98	0.22
2019	Twilight conditions	716	267	2.68	0.60
2019	Dimmed light	549	903	0.61	0.14
2019	Bright light	234	1172	0.20	0.04
2020	Night conditions	435	624	0.70	0.22
2020	Twilight conditions	841	478	1.76	0.56
2020	Dimmed light	709	1335	0.53	0.17
2020	Bright light	263	1667	0.16	0.05

After the period of midnight sun ended in week 27 measured light intensity at the time of registration of brown trout in river Fjæreelva in 2019 had a median close to zero (fig. 19 A). There was a small dip in measured temperature in week 26 and 27, followed by a weekly increase until a peak in week 31, before steadily declining towards the end of the study period (fig. 19 B). The values for the interpolated runoff data indicated an increase in water level in week 26 – 28, coinciding with the decrease in water temperature. In addition, a small increase in runoff occurred in week 36 – 38, followed by an increase in measured light intensity at registration in week 39 – 40.

Figure 19: **A.**: Light intensity (hourly measured lx, values ≥ 10 752 lx were registered as 10 752), and **B.**: Interpolated runoff values and measured water temperature (average temperature per hour) at registration for upstream migrating anadromous brown trout for week 24 – 42 in 2019 in river Fjæreelva. Weekly values for runoff are illustrated by the gray, filled boxes and circle shaped outliers. Weekly values for registered water temperature are illustrated by the white, empty boxes and triangle shaped outliers. The box-and-whiskers plots displays the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers), outliers (dots, >1.5*IQR) and the number of registrations (*n*) for each week.

Measured light intensity at the time of upstream migration for brown trout in river Fjæreelva in 2020 had a median close to zero after the period of midnight sun ended in week 28, and remained low until week 37 (fig 20 A). From week 37 to week 40 – 41, the measured light intensities during registrations were considerably higher than in the previous weeks. The measured temperature at registration increased the first weeks, remained relatively stable from week 25 to 32, before it decreased towards the end of the study period (fig. 20 B). The values for the interpolated runoff data remained low from week 25 until a rapid increase late in the season, resulting in considerably higher light intensity at registration in week 38 – 40 (fig. 20). The increase in runoff in week 38 corresponds well to an observed flood which led to a hole in the guiding-fence in the middle of week 38. Upon visual comparison, it looks as if the individuals registered during the period with increased runoff in week 37 – 41 migrated during higher light intensities.
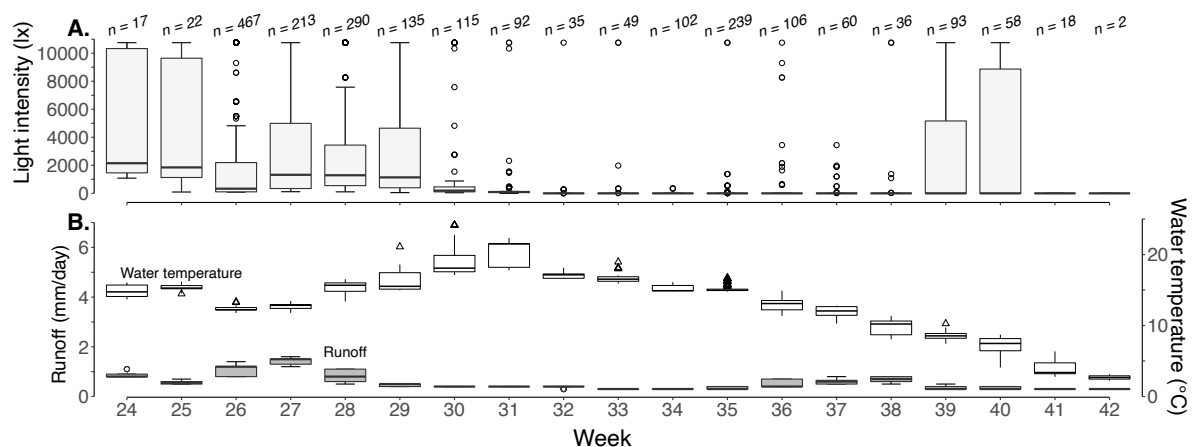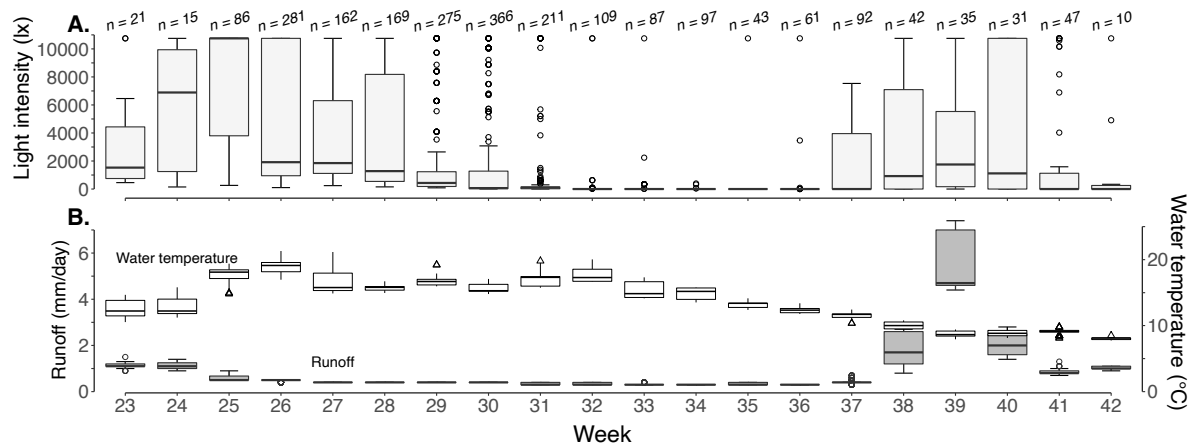
Figure 20: **A.**: Light intensity (hourly measured lx, values ≥ 10 752 lx were registered as 10 752), and **B.**: interpolated runoff values and measured water temperature (average temperature per hour) at registration for upstream migrating anadromous brown trout for week 23 – 42 in 2020 in river Fjæreelva. Weekly values for runoff are illustrated by the gray, filled boxes and circle shaped outliers. Weekly values for registered water temperature are illustrated by the white, empty boxes and triangle shaped outliers. The box-and-whiskers plots displays the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers), outliers (dots, >1.5*IQR) and the number of registrations (*n*) for each week.

To test for congruency between light intensity and water runoff, three time periods of three weeks, with three weeks in-between, were chosen to represent different light regimes throughout the study period. The early part of the migratory period for brown trout, week 26 – 28, was characterized by high light intensity and the sun being above the horizon at all hours. The middle part, week 32 – 34, had lower light intensities at most hours, complete darkness during the night and longer periods of twilight. The later part, week 38 – 40, consisted of even shorter days and longer nights.

In week 26 – 28, in 2019 (table 18) and 2020 (table 19), no upstream migrating brown trout were registered at the video tunnel during Night conditions, and no hours of Night conditions were available. Twilight conditions had the highest number of registrations in 2019, while Dimmed light had the highest number of registrations in 2020. In both years, Twilight conditions had the highest number of registrations per hour. In week 32 – 34, in 2019 (table 18) and 2020 (table 19), Night conditions had the highest number of registrations and the highest number registrations per hour, followed by Twilight conditions in both years. In addition, very few registrations were made during Dimmed light and Bright light for both years. In week 38 – 40, in 2019 (table 18) and 2020 (table 19), registrations were more evenly distributed between the different categories than in the two previous groups of weeks. 67% were registered during Night conditions and Twilight conditions combined in 2019, while 42% were registered during the same conditions in the same time period in 2020.

In general, the proportion of registered brown trout per hour in each light intensity category in 2019 and 2020 showed great similarities in week 26 – 28 and 32 – 34, but differences in week 38 – 40 (fig. 21).

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Table 18: The number of registered anadromous brown trout (*n*), the total number of hours throughout the study period and the number of registered anadromous brown trout per hour in each light intensity category: Night conditions; ≤ 1 lx, Twilight conditions; > 1 lx & ≤ 585 lx, Dimmed light; > 585 lx & ≤ 10 752 lx, Bright light; > 10 752 lx, in river Fjæreelva in: week 26 – 28; 24 June – 14 July, week 32 – 34; 05 August – 25 August, and week 38 – 40; 16 September – 06 October, in 2019.

Week	Light intensity category	Registrations (*n*)	Hours in study period (h)	Registrations per hour
26 – 28	Night conditions	0	0	0
	Twilight conditions	431	61	7.07
	Dimmed light	373	198	1.88
	Bright light	166	245	0.68
32 – 34	Night conditions	168	111	1.51
	Twilight conditions	14	44	0.32
	Dimmed light	1	142	0.01
	Bright light	3	207	0.01
38 – 40	Night conditions	113	233	0.48
	Twilight conditions	13	26	0.50
	Dimmed light	32	103	0.31
	Bright light	29	142	0.20

Table 19: The number of registered anadromous brown trout (*n*), the total number of hours throughout the study period and the number of registered anadromous brown trout per hour in each light intensity category: Night conditions; ≤ 1 lx, Twilight conditions; > 1 lx & ≤ 585 lx, Dimmed light; > 585 lx & ≤ 10 752 lx, Bright light; > 10 752 lx, in river Fjæreelva in: week 26 – 28; 22 June – 12 July, week 32 – 34; 03 August – 23 August, and week 38 – 40; 14 September – 04 October, in 2020.

Week	Light intensity category	Registrations (*n*)	Hours in study period (h)	Registrations per hour
26 – 28	Night conditions	0	0	0
	Twilight conditions	128	30	4.27
	Dimmed light	353	185	1.91
	Bright light	131	289	0.45
32 – 34	Night conditions	214	91	2.35
	Twilight conditions	72	74	0.97
	Dimmed light	4	156	0.03
	Bright light	3	183	0.02
38 – 40	Night conditions	37	214	0.17
	Twilight conditions	8	51	0.16
	Dimmed light	40	145	0.28
	Bright light	23	94	0.24
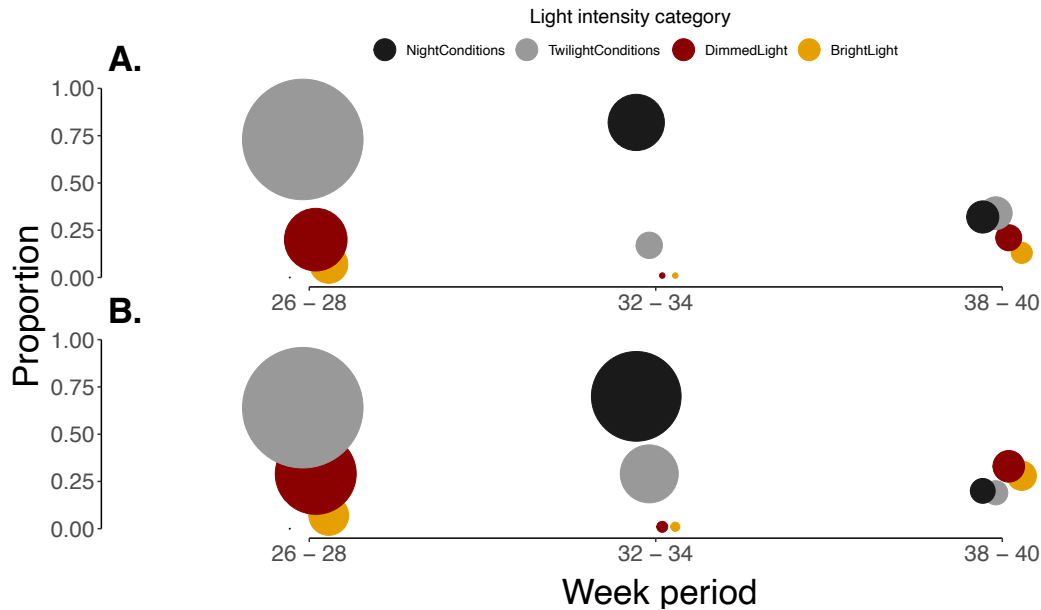
Figure 21: Proportion of registered anadromous brown trout per hour (registrations per hour / total number of registrations per hour) in each light intensity category in week 26 – 28, 32 – 34, and 38 – 40 in river Fjæreelva in **A.**: 2019, and **B.**: 2020. Color of the circles indicate the different light intensity categories (Black: Night conditions; ≤ 1 lx, Gray: Twilight conditions; > 1 lx & ≤ 585 lx, Red: Dimmed light; > 585 lx & ≤ 10 752 lx, Yellow: Bright light; > 10 752 lx). Circle size increases with number of registrations per hour. Circles are jittered to reduce overplotting.

3.4 Correlation of timing of upstream migration and infestation of salmon lice

In Fjæreelva 2019/2020 and Botnelva 2019/2020, a lower proportion of Arctic char: 18%/4%; 3%/4%, than brown trout: 21%/48%; 33%/25%, and Atlantic salmon: 34%/28%; 17%/22%, were registered at the video tunnel with adult salmon lice. Only fish observed with adequate video quality were included in the lice data analysis (section 2.5.4).

Linear regression models were used to investigate whether upstream migrating individuals with detected salmon lice had a different date of registration at the video tunnel than individuals of the same species without detected lice (table 21). Atlantic salmon with detected salmon lice had significantly earlier dates of registration in rivers Fjæreelva and Botnelva in 2019 and 2020. Likewise, brown trout with detected lice had significantly earlier dates of registration in both rivers in 2019, but a later date of registration in Fjæreelva in 2020. Arctic char with detected salmon lice had significantly later dates of registration in Fjæreelva in 2020. Wilcoxon ranked sum tests (Appendix 1) showed significant differences in registration dates between the same within river and year species groups as identified through the linear regression models (table 21).

Table 21: Linear regression models for estimating date of registration during upstream migration for anadromous brown trout, Arctic char and Atlantic salmon in rivers Fjæreelva and Botnelva in 2019 and 2020. Intercept is the Julian date of registration (DOY) with LiceS: NoneDetected as reference value. LiceS: NoneDetected and LiceS: Detected are categorical variables defining whether salmon lice were not detected or detected upon video analysis. Values for variables LiceS: Detected of statistical significance are in bold.

Coefficients	Estimate	SE	t-value	Pr(>|t|)
Fjæreelva 2019 Brown trout				
Intercept	213.17	0.93	228.15	< 0.001
LiceS: Detected	**-19.54**	2.03	-9.63	**< 0.001**
Fjæreelva 2019 Arctic char				
Intercept	169.62	0.22	786.94	< 0.001
LiceS: Detected	-0.67	0.50	-1.33	> 0.05
Fjæreelva 2019 Atlantic salmon				
Intercept	228.56	3.41	67.05	< 0.001
LiceS: Detected	**-28.24**	5.84	-4.84	**< 0.001**
Fjæreelva 2020 Brown trout				
Intercept	194.95	1.12	174.23	< 0.001
LiceS: Detected	**6.07**	1.61	3.76	**< 0.001**
Fjæreelva 2020 Arctic char				
Intercept	166.01	0.44	374.14	< 0.001
LiceS: Detected	**5.87**	2.27	2.59	**< 0.01**
Fjæreelva 2020 Atlantic salmon				
Intercept	212.28	5.15	41.22	< 0.001
LiceS: Detected	**-27.36**	9.67	-2.83	**< 0.01**
Botnelva 2019 Brown trout				
Intercept	240.82	0.59	405.49	< 0.001
LiceS: Detected	**-9.04**	1.04	-8.73	**< 0.001**
Botnelva 2019 Arctic char				
Intercept	211.27	0.30	693.04	< 0.001
LiceS: Detected	-0.20	1.70	-0.12	> 0.05
Botnelva 2019 Atlantic salmon				
Intercept	273.48	2.09	130.94	< 0.001
LiceS: Detected	**-51.40**	5.05	-10.18	**< 0.001**
Botnelva 2020 Brown trout				
Intercept	250.52	0.59	424.24	< 0.001
LiceS: Detected	0.69	1.11	0.62	> 0.05
Botnelva 2020 Arctic char				
Intercept	223.44	0.82	270.91	< 0.001
LiceS: Detected	-2.94	3.91	-0.75	> 0.05
Botnelva 2020 Atlantic salmon				
Intercept	270.89	3.86	70.18	< 0.001
LiceS: Detected	**-29.89**	8.28	-3.61	**< 0.05**

A significant difference in body length between conspecifics with and without detected salmon lice was observed for both rivers Fjæreelva and Botnelva, 2019 and 2020, combined (table 22). Brown trout, Arctic char and Atlantic salmon with detected salmon lice had a longer body length than its respective conspecifics without any detected lice (fig. 22).

Table 22: The total number of compared registrations (*n*), W-value and *p*-value for performed Wilcoxon rank sum tests on compared differences in body length between individuals of the same species with and without detected salmon lice for upstream migrating anadromous brown trout, Arctic char and Atlantic salmon in rivers Fjæreelva and Botnelva, 2019 and 2020 combined.

Compared groups	Total *n*	W	*p*
Brown trout	5470	2117442	**< 0.001**
Arctic char	1872	64306	**< 0.001**
Atlantic salmon	315	5462	**< 0.001**
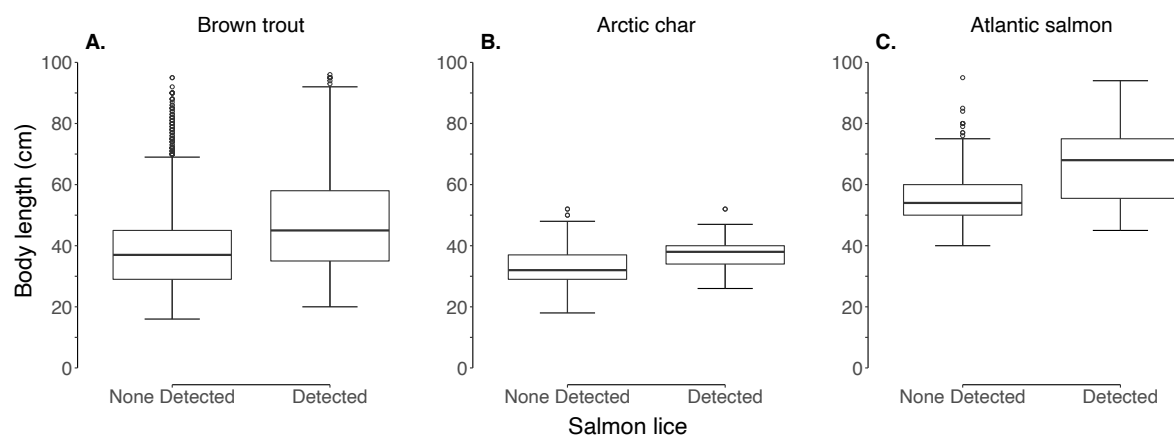
Figure 22: Body length (estimated through video analysis, cm) for anadromous **A.**: Brown trout, **B.**: Arctic char, and **C.**: Atlantic salmon with "None Detected" and "Detected" salmon lice in rivers Fjæreelva and Botnelva, 2020 and 2019, combined. The box-and-whiskers plots displays the median values (middle black line), interquartile range (box, IQR = 25th to 75th percentile), values within 1.5*IQR (whiskers) and outliers (dots, >1.5*IQR).

4   Discussion

Comparisons of timing of river ascent of anadromous individuals of brown trout, Arctic char and Atlantic salmon in river Fjæreelva and Botnelva in 2019 and 2020, revealed that Arctic char was the earliest upstream migrant, followed by brown trout and Atlantic salmon, respectively, within each river and year. Arctic char also displayed a considerably shorter, more concentrated, period of upstream migration than the brown trout and Atlantic salmon. Brown trout and Arctic char in Botnelva each had later dates of registration in 2020 compared to 2019, however no such difference was observed between the two years of studying for brown trout and Arctic char in Fjæreelva. The difference in observed upstream migration dates in Botnelva across the two years likely arose from a reduced study period, which commenced two days after and 22 days prior to the median dates of registration in 2019 for Arctic char and brown trout, respectively. Fewer Atlantic salmon were registered in Botnelva in 2020 compared to 2019, yet no difference in migration dates for Atlantic salmon between the two years were detected. The reduced study period likely caused later median dates of registration for brown trout and Arctic char, but it seems unlikely to be solely responsible for the lower number of recorded Atlantic salmon in 2020 compared to 2019. Within the same time period, 01 September – 13 October, 66 Atlantic salmon were registered in 2019 while only 19 were registered in 2020. Fish might have passed through holes in the guiding-fence during the flood in 2020, which could explain the lower number of recorded Atlantic salmon in 2020. Alternatively, the lower number of registered Atlantic salmon in Botnelva in 2020 could be the result of an interannual variation in returning individuals. In 2018, only 15 Atlantic salmon were registered (from 15 July – 11 September) using the same method as in the present study (Sjursen *et al.*, 2021). Rate of straying can vary considerably between years (Jonsson *et al.*, 2003), which could affect the number of registered individuals. Strays primarily enter nearby rivers supporting large conspecific stocks (Jonsson *et al.*, 2003; Ulvan *et al.*, 2018). Since the Atlantic salmon population in Botn watercourse appears rather small (present study; Sjursen *et al.*, 2021), a fourfold increase in observations due to strays alone seems doubtful. However, due to the small population size, even a moderate number of strays will make a large impact on the yearly counts. Post-spawners are known to exhibit a biennial spawning pattern (Jonsson *et al.*, 1991), which could be the root of a skewed return between year-classes. As most of the registered Atlantic salmon in Botnelva likely were one sea-winter salmon (87%, < 66cm) the return of a successful year class could be a likely explanation. Monitoring across several additional years would be necessary to determine whether the return of Atlantic salmon in Botnelva follows a biennial pattern, or if the reduced number of counts was caused by a shorter period of video surveillance or holes in the guiding-fence.

In 2019, brown trout, Arctic char and Atlantic salmon with greater body length migrated upstream earlier than shorter conspecifics in both rivers. The same pattern was observed for brown trout and Arctic char in Botnelva in 2020. However, the opposite pattern, with shorter upstream migrants arriving earlier, was observed in Fjæreelva in 2020 for brown trout and Arctic char. The "asset-protection-principle" states that the larger the reproductive asset, the more important it becomes to protect it (Clark, 1994). Given the conditions in the river are

adequate for migration, larger individuals may return earlier to freshwater as it provides a more secure habitat (Jonsson & Jonsson, 2011). Fleming *et al.* (1996) reported a close to linear relationship between reproductive success and body weight. However, weight normally varies within seasons and the relationship between body weight and body length appears to be non-linear (Ebel *et al.*, 2015). Thus, the relationship between body length and the instinct to protect a more valuable asset may not be linear in itself. The upstream migration period of brown trout and Atlantic salmon stretched further in time, and tended to follow a multimodal distribution, which suggest a difference in upstream migration dates between groups of individuals within the same population. Fish may return at different times and from different directions due to the use of different marine feeding areas (Ulvan *et al.*, 2018). Although larger individuals would benefit from an earlier return, in order to protect its more valuable assets, the conditions in the river may not be adequate for larger individuals early in the season. For instance, in river Imsa, western Norway, larger multi sea-winter Atlantic salmon returned to coastal home waters earlier than smaller one sea-winter salmon, yet the smaller Atlantic salmon ascended earlier than larger ones, likely due to low water levels in the river during summer (Jonsson *et al.*, 1990). In the same river, no significant difference in dates of upstream migration was identified between small and large anadromous brown trout (Jonsson & Jonsson, 2002). Additionally, migration barriers in the river may affect different size/age groups differently, leading to a within-river distribution of groups (Thorstad *et al.*, 2008), indicating that differences may be species-wise, as well as size dependent, within the same river. In the present study, generally low linear relationships for the fitted models suggest that factors not included in the models were more important in determining the timing of homing migration date than body length alone. Altered within-season migrations may arise from water levels restricting migration and unfavorable river temperatures (Erkinaro *et al.*, 1999; Jonsson & Jonsson, 2009; Gilbert *et al.*, 2016). A variation in mobility with temperature change is expected as salmonids aerobic performance usually increases up to a thermal optimum, above which it rapidly declines (Farrell *et al.*, 2009; Eliason *et al.*, 2011; Gilbert & Tierney, 2018), and low water temperatures have been observed to affect Atlantic salmon ability to pass obstacles (Jackson & Howie, 1967; Jensen *et al.*, 1986). The difficulty of passing obstacles in Fjæreelva and Botnelva was not assessed in detail. As registrations were made during all levels of water runoff and within the whole riverine temperature range during the studied periods, considerable restrictions in movements due low river temperatures and water levels seems unlikely to have happened in the present study.

If not able to seek refuge in colder water, temperatures exceeding 22 – 25 °C, 22 – 23 °C and 22 – 28 °C, depending on the rate of acclimation, are expected to be lethal for brown trout, Arctic char and Atlantic salmon, respectively (Elliott & Elliott, 2010). Registrations within the lethal range described above were observed for both brown trout and Atlantic salmon. As both rivers drain from relatively large lake systems, and the video tunnels were placed close to the river inlets, reaching refuge in colder depths within a relatively short period of time would be possible. In addition, the daily variation in measured water temperature was low in both rivers. In the present study, water temperatures during upstream migration were higher for Arctic char than for brown trout and Atlantic salmon, respectively, within each river and year. Arctic char could benefit the most from utilizing higher temperatures during upstream migration, as

increased predation risk by endothermic predators is associated with lower temperatures (Heggenes *et al.*, 1993), and individuals of Arctic char generally were shorter than individuals of the other two species. The middle 50% of all registrations, were made within a 0.8 – 6.1 °C temperature span. However, individuals were registered at temperatures far lower and higher. In river Fjæreelva, Arctic char migrated upstream at temperatures ranging from 2.5 – 21.3 °C. A study conducted on Arctic char in the Canadian Arctic, found that the species was able to maintain its absolute aerobic scope and a high regular heart rate from ~4 – 16 °C, but the ability to recover from exhaustive exercise became limited at temperatures > 16 °C (Gilbert *et al.*, 2020). Moreover, Arctic char from the same river were able to maintain critical swimming performance, though having impaired recovery from exercise, when brought from 11 – 21 °C over 12 hours, indicating a changing tolerance with acclimation (Gilbert & Tierney, 2018). In another Greenlandic population, Arctic char experienced arrythmia at 11 – 18 °C (Hansen *et al.*, 2017). Due even higher temperatures, 23 – 25 °C, a loss of equilibrium is likely to occur within a couple of hours (Quinn *et al.*, 2011; Penney *et al.*, 2014).

Thermal limits for anadromous and freshwater resident brown trout and Arctic char were assessed in the Botn watercourse in August of 2017 by Mottola *et al.* (2020). The study revealed that most of the anadromous fish, of both species, experienced cardiac arrhythmia at 14 – 16 °C, while freshwater residents reached arrhythmia at 21 – 22 °C, indicating a significantly higher upper critical temperature for freshwater residents. Mottola *et al.* (2020) emphasized that an increase in river temperature of 2 – 4 °C, from ~12 °C at the time of the study, might be sufficient to initiate a mechanism of cardiac impairment. Such an increase was observed in the present study as the water temperature when brown trout and Arctic char passed the video tunnel in Botnelva in August 2019 was measured to 15.1 ± 0.01 °C (mean ± SE). Comparing the body length of the examined fish from August in 2017 to the ones registered in August in 2019: anadromous Arctic char had approximately the same length (29.8 ± 1.4 *vs*. 30 ± 3 cm, mean ± SD), whilst anadromous brown trout in the present study were considerably larger (27 ± 2.8 *vs*. 39 ± 12 cm). A higher upper thermal tolerance for smaller individuals compared to larger conspecifics, and a marked effect of thermal acclimation on critical thermal maximum temperatures, have been demonstrated for cutthroat trout (*O. clarkii)* (Underwood *et al.*, 2012). If applicable to other salmonid species, the larger size of the anadromous brown trout registered in Botnelva in August 2019 would in general have made them more vulnerable to higher temperatures than the individuals examined by Mottola *et al.* (2020). Thus, the possible implications of water temperature for ascending brown trout, Arctic char and Atlantic salmon in rivers Fjæreelva and Botnelva remains unclear after only two years of studies. Measured temperatures at registration reached above previously reported lethal limits for brown trout and Atlantic salmon (Elliott & Elliott, 2010), and close to lethal limits for Arctic char (Gilbert *et al.*, 2020; Mottola *et al.*, 2020). However, water temperatures were only measured at one location in the river, and the availability of thermal refuges was uncharted. Therefore, the duration of exposure to the observed temperatures remains unknown. As the climate changes, temperatures in aquatic environments are expected increase (Jonsson & Jonsson, 2009). If possible, a shift in river ascent to a period with lower temperatures could be necessary to avoid exhausting and potential lethal temperatures. Jensen *et al.* (2019) suggested that anadromous Arctic char are less robust to environmental changes than brown trout based on smolt fitness.

In addition, reduced prevalence of anadromy in Arctic char populations are expected as primary production in freshwater systems increases (Finstad & Hein, 2012). From the observations made in the present study, due to its lower temperature tolerance and more confined time period of migration, anadromous Arctic char seems to be the most vulnerable in regards of heating in the studied rivers in the future.

When examining the study period in full, Arctic char migrated upstream at significantly higher light intensities than brown trout and Atlantic salmon in Fjæreelva in 2019 and 2020, and in Botnelva in 2019. Because Arctic char migrated upstream during a shorter time period earlier in the season, overlapping with the period of midnight sun, more hours of light was available through each day. Riverine migrations during all hours in periods of midnight sun have also been noted in previous studies (Moore, 1975; Davidsen et $al.$, 2005). When examining the period in which the middle 90% of the Arctic char were registered, D_{90}, for all three species, the differences between the species were smaller, and only significant between brown trout and Arctic char in 2019. Thus, differences in light intensity at migration appears to be a result of the difference in timing of homing migration, rather than a difference in preference. In general, upstream migration is believed to mainly occur during twilight and dark periods (Jonsson, 1991), which holds true for the findings in Fjæreelva in the present study, given dark conditions were available. While most brown trout and Atlantic salmon migrated upstream during light intensities corresponding to night and twilight, almost all Arctic char migrated at light intensities ranging from that of an overcast day to a very bright day. Elliott (2011) found that the feeding ability of brown trout was superior to that of Arctic char in daylight and twilight, while Arctic char were superior at lower light intensities. Although feeding appears to be of lower priority during upstream migration (Jonsson & Gravem, 1985), the superior visual feeding ability at lower light intensities for Arctic char suggests that its eyesight alone should not have been a inhibiting its migration during lower light than brown trout. Arctic char may have been more susceptible to predation due to the brighter conditions during their upstream migration and a generally shorter body length. However, schooling behavior, as commonly observed by Arctic char during the passing of the video tunnel, might have mitigated the potentially increased predation risk (Connell, 2000; Jonsson & Jonsson, 2011).

The preference for different light conditions during upstream migration varied between 2019 and 2020, as well as within each season, for anadromous brown trout in river Fjæreelva. In the early (week 26 – 28) and middle (week 32 – 34) part of the migratory period, the preference for different light conditions was close to identical for 2019 and 2020. In both periods, a higher proportion of brown trout migrated upstream during fewer available hours of light intensities corresponding to night and twilight, indicating a preference for darker conditions. The observed preference for darker hours could be an antipredator response as nocturnal migration may reduce the risk of predation from visual predators (Moore et $al.$, 1995; Bendall et $al.$, 2005; Ibbotson et $al.$, 2011). In the later time period (week 38 – 40), brown trout migrated at higher light intensities in 2020 compared to 2019, corresponding to a sharp increase in runoff in 2020 which would increase turbidity in Fjæreelva, due to the morphology of its drainage area. Svendsen et $al.$ (2004) noted that high discharge probably confers protection from predators. In addition, larger water masses may shelter migrating fish from predation (Jonsson & Jonsson,

2002). European otter (*Lutra lutra*), gray heron (*Ardea cinerea*), white-tailed eagle (*Haliaeetus albicilla*) and piscivorous ducks (*Mergus serrator* and *M. merganser*) were observed during fieldwork or through the video analysis, and probably posed the largest natural predation risk to brown trout, Arctic char and Atlantic salmon during upstream migration in Fjæreelva and Botnelva. Generally, smaller fish are more vulnerable to predation than larger individuals (Svenning & Grotnes, 1991; Feunteun & Marion, 1994; Ibbotson *et al.*, 2011), yet a preference for darker conditions may occur in larger fish as well (Bendall *et al.*, 2005). Successful predation on ~50 cm fish by an otter was observed through video analysis in Fjæreelva, suggesting even fish of moderate size were susceptible to predation. Thorstad *et al.* (2008) reasoned that observed antipredator behavior in upstream migrating Atlantic salmon, such as a preference for darkness or turbid water, may be a basic instinct that remains active throughout all life stages. A preference for brighter conditions, as observed along with a sharp increase in runoff in 2020, might own to the loss of antipredator behavior. Loss of antipredator behavior with increased turbidity was also observed by Abrahams and Kattenfeld (1997).

Brown trout with salmon lice visible through video analysis were registered migrating upstream earlier in 2019 in both rivers, as were Atlantic salmon in both rivers both years. However, the opposite pattern, with upstream migrant with visible lice arriving earlier, was observed for brown trout and Arctic char in Fjæreelva in 2020. Salmon lice infestations are known to affect osmoregulation, growth, survival and reproductive development in anadromous brown trout, Arctic char and Atlantic salmon (Tveiten *et al.*, 2010; Skilbrei *et al.*, 2013; Fjelldal *et al.*, 2019; Serra-Llinares *et al.*, 2020), and is considered to be one of the largest threats to wild populations of anadromous brown trout and Atlantic salmon in Norway (ICES, 2016; Forseth *et al.*, 2017; Anon, 2019). The increased physiological stress associated with salmon lice infestation may lead to a premature return to freshwater (Birkeland & Jakobsen, 1997; Bjørn *et al.*, 2001). The salmon lice infestation pressure along the coast outside the studied rivers appears to have been lower in 2020 compared to 2019 (Norwegian Institute of Marine Research, 2021). Yet, the proportion of brown trout with detected salmon lice in Fjæreelva was higher in 2020. In addition, brown trout, as well as Arctic char, with detected lice were registered later than conspecifics without detected lice. Late in the season in Fjæreelva in 2020, reduced video quality led to a higher number of fish being registered with an "impossible" quality for salmon lice registration, and therefore deemed unfit for the sub-dataset used for analysis on salmon lice. The skewed observations due to the riverine conditions could explain the earlier registration of brown trout and Arctic char with detected lice in Fjæreelva in 2020. Whether premature migration was the reason for the earlier timing of recordings of fish with detected lice in the present study remains unclear as other factors might have contributed to the observed differences. In general, individuals within each species with detected lice had a greater body length than those without visible salmon lice. Moore *et al.* (2018) found that the probability of salmon lice being present increased with the size of the host, indicating a size-dependent risk of being infected. However, this might not always hold true (Bjorn & Finstad, 2002). Moreover, larger individuals can tolerate higher number of salmon lice, as lice related mortality and compromised reproduction depends on fish size (Taranger *et al.*, 2015). It is unknown whether smaller individuals might have suffered from higher mortalities, leading to fewer shorter individuals being detected migrating upstream through the video tunnel. In addition, differences

between various size-groups in time spent in freshwater and brackish water prior to passing the tunnel could have resulted in less delousing for larger fish prior to recording, and therefore a higher likelihood of larger fish being registered with visible lice. It is also possible that differences in within-river migrations between different size-groups may have led to less delousing for larger fish prior to being registered at video, causing a higher likelihood of larger fish being registered with visible lice. Due to the limits of the method used for detection, the number of lice on each fish was uncertain and underestimated. Hence, the relationship between size and lice burden experienced in the marine environment remains unclear in the present study. Davidsen *et al.* (2019) reported a higher number of anadromous brown trout with damages caused by salmon lice (75%) compared to the number of fish with attached adult lice (53%) caught in a fish trap in Botnelva in 2017, suggesting lice fell off during the upstream migration. To what extent fish stayed downstream in the rivers or in brackish water at the river outlets prior to being registered through the video tunnels was not investigated in the present study. Salmon lice detected through the video analysis were adult lice, and not distinguishable by gender. As salmon lice development is greatly influenced by sea temperature (Hamre *et al.*, 2019), fish registered with detected lice must have been infested at least two weeks, likely more, prior to registration at the video tunnel. In addition, adult stages of salmon lice may survive on the host for as long as eight days while in freshwater (Wright *et al.*, 2016). Some degree of delousing prior to registration through the video tunnels seems likely to have happened during the present study, but to what extent would require data on within-river migrations prior to being registered at the video tunnels in the given rivers.

Few anadromous Arctic char were recorded with detectable salmon lice compared to brown trout and Atlantic salmon. The salmon lice infestation rate, and a potential premature return, would depend on the habitat usage during the marine migration. In the Botn watercourse in 2017, fewer anadromous Arctic char had lice inflicted wounds or attached adult lice compared to brown trout (Davidsen *et al.*, 2019), which concurs with the findings in the present study. The authors emphasized that the observed difference likely arose from the difference in marine area usage: while Arctic char mainly utilized brackish water and areas in the inner part of the fjord, brown trout utilized a larger part of the fjord system, making it more prone to infestation. Atlantic salmon with detected salmon lice were registered on average ~27 – 51 days earlier than salmon with no detected lice in the present study. In addition, the Atlantic salmon with detected lice generally had a significantly longer body length. As larger Atlantic salmon may utilize different ocean areas than smaller conspecifics during their feeding migration, fish of different sizes may return from different directions at different times (Ulvan *et al.*, 2018). If larger Atlantic salmon were to return earlier to coastal areas without ascending the river at once, as observed by Jonsson *et al.* (1990), they may have been more prone to lice infestation.

In the present study, returning Atlantic salmon with detected salmon lice generally had few ($\leq$ 10) visible lice (91%, *n* = 79) at the time of registration, and an estimated body length of 66 ± 11 cm (mean ± SD, *n* = 87). Meaning, the observed lice numbers likely were lower than the problematic limits described by Taranger *et al.* (2015). Thus, the earlier return of Atlantic salmon infested with salmon lice appears to be a result of area use and/or time of migration, rather than premature return. The coastal marine area usage of brown trout suggests they would

be more prone to infection (Moore *et al.*, 2018), and therefore more likely of commencing on a premature homing migration to freshwater. Still, brown trout with detected salmon lice had few (≤ 10) visible lice (97%, *n* = 1687) and an estimated body length of 48 ± 16 cm (mean ± SD, *n* = 1732), suggesting below problematic lice burdens for most of the lice infested brown trout. Halttunen *et al.* (2018) suggested that anadromous brown trout may suffer from lost growth opportunities as the use of freshwater habitats become more frequent in years of high infestation pressure. In addition, high lice density may lead to a more than 50 times higher mortality risk of Atlantic salmon posts molt (Bøhn *et al.*, 2020). Knowledge on the degree of delousing prior to registration through the video tunnel, and more accurate counts of salmon lice, would be necessary to determine to what extent salmonids residing in the watercourses Fjære and Botn are prone to premature homing migration. Nonetheless, reduced growth, and potentially survival, of individuals in the studied populations were plausible effects due to the observed salmon lice infestations. Reduced benefits from marine migration may over time lead to loss of the anadromous trait in local populations (Thorstad *et al.*, 2015).

The present study further demonstrates the potential of video analysis in the use of gathering data on entire anadromous fractions of populations. It provided important details on size and structure of the populations, as well as the timing of river ascent without any substantial interaction, thereby improving welfare and potentially limiting bias caused by different catchment methods. However, there were limits with the presented method. Salmon lice counts would be more accurate with physical handling of fish. In addition, monitoring of seaward migration could be a problem as spring/summer floods might lead to a rapid and disorderly dismantling of equipment installed in the river. Thorstad *et al.* (2008) emphasized that seemingly easily passable obstacles may prove difficult, and vice versa, for upstream migrating Atlantic salmon. Based on observations during fieldwork and from video analysis, few fish were observed in the areas during daytime and most fish passed through the video tunnel without any apparent difficulties. In addition, fish were commonly observed passing through at periods when the video tunnels would have been easily avoidable due missing or incomplete guiding-fences. A more thorough study of within-river migration would be necessary to determine if the video tunnel and guiding-fences itself altered the migration of the populations examined in the present study.

In conclusion, the present study demonstrates significant differences in the timing of homing migration between anadromous brown trout, Arctic char and Atlantic salmon. Upstream migration took place earlier for each of the three species in river Fjæreelva compared to Botnelva, independent of year. Allover, Arctic char was the first species to migrate upstream, followed by brown trout and Atlantic salmon, respectively, within each river and year. Earlier upstream migration with increasing body length was observed for all three species in both rivers in 2019, and for brown trout and Arctic char in Botnelva in 2020. However, the significance of body length as a controlling factor in the timing of homing migration was not uniform in the present study. As individuals of all three species passed the video tunnels at all levels of water temperature, light intensity and water runoff, within their respective migratory period, the measured environmental factors did not appear to pose absolute restrictions on the timing of upstream migration. However, there appeared to be a preference for migration during lower

light intensities and a slight change in preferred brightness for brown trout during a time period with increased runoff, suggesting an altered behavior in response to increased water level and turbidity. Moreover, measured river temperatures indicated that individuals of all three species, in both rivers, might have experienced temperatures previously reported to have caused physiological impairment. However, the potential for acclimation prior to registration at the video tunnel might have mitigated such effects. Brown trout with salmon lice visible through video analysis migrated upstream earlier than individuals without in both rivers in 2019, likewise for Atlantic salmon in both rivers both years. However, the potential for delousing prior to registration at the video tunnel makes for uncertainties regarding lice burdens while in the marine environment, and whether the observed earlier return was associated with increased physiological stress due to salmon lice infestations. Anadromous salmonid populations are in decline. High salmon lice infestation pressure and increasing temperatures have the potential to negatively influence wild salmonid populations in Northern Norway. The data provided in this thesis have shown that video monitoring during river ascent can provide information crucial for evaluating inter-annual population trends needed to implement effective conservation measures. Increased knowledge on within-river migrations and potential delousing prior to registration at the video tunnel would increase accuracy and further expand the potential of video analysis in salmonid management and research. The present study contributes to knowledge on a local scale, providing valuable information for local fisheries management. Combining surveying methods, such as video/PIT/acoustic telemetry, will provide new insight on the population dynamics and their response to human activity, both on regional and national scales. Through increased insight, we can better understand how these, and other, populations might be affected by the ever-changing world in which we all have to share.

5 References

Abrahams, M. V. & Kattenfeld, M. G. (1997). The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behavioral Ecology and Sociobiology* **40**, 169-174.

AMS (2012a). Astronomical Twilight. https://glossary.ametsoc.org/wiki/Astronomical_twilight. 28.03.2021.

AMS (2012b). Civil Twilight. https://glossary.ametsoc.org/wiki/Civil_twilight. 28.03.2021.

AMS (2012c). Nautical Twilight https://glossary.ametsoc.org/wiki/Nautical_twilight. 28.03.2021.

Anon. 2019. Klassifisering av tilstanden til 430 norske sjøørretbestander.

Temarapport fra Vitenskapelig råd for lakseforvaltning nr 7, 150 s.

Banks, J. (1969). A review of the literature on the upstream migration of adult salmonids. *Journal of Fish Biology* **1**, 85-136.

Bendall, B., Moore, A. & Quayle, V. (2005). The post-spawning movements of migratory brown trout *Salmo trutta* L. *Journal of Fish Biology* **67**, 809-822.

Berg, O. K. & Jonsson, B. (1990). Growth and survival rates of the anadromous trout, *Salmo trutta*, from the Vardnes River, northern Norway. *Environmental Biology of Fishes* **29**, 145-154.

Birkeland, K. (1996). Consequences of premature return by sea trout (*Salmo trutta*) infested with the salmon louse (*Lepeophtheirus salmonis* Krøyer): migration, growth, and mortality. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 2808-2813.

Birkeland, K. & Jakobsen, P. J. (1997). Salmon lice, *Lepeophtheirus salmonis*, infestation as a causal agent of premature return to rivers and estuaries by sea trout, *Salmo trutta*, juveniles. *Environmental Biology of Fishes* **49**, 129-137.

Bjorn, P. A. & Finstad, B. (2002). Salmon lice, *Lepeophtheirus salmonis* (Kroyer), infestation in sympatric populations of Arctic char, *Salvelinus alpinus* (L.), and sea trout, *Salmo trutta* (L.), in areas near and distant from salmon farms. *ICES Journal of Marine Science* **59**, 131-139.

Bjørn, P., Finstad, B. & Kristoffersen, R. (2001). Salmon lice infection of wild sea trout and Arctic char in marine and freshwaters: the effects of salmon farms. *Aquaculture Research* **32**, 947-962.

Bøhn, T., Gjelland, K. Ø., Serra-Llinares, R. M., Finstad, B., Primicerio, R., Nilsen, R., Karlsen, Ø., Sandvik, A. D., Skilbrei, O. T., Elvik, K. M. S., Skaala, Ø. & Bjørn, P. A. (2020). Timing is everything: Survival of Atlantic salmon *Salmo salar* postsmolts during events of high salmon lice densities. *Journal of Applied Ecology* **57**, 1149-1160.

Clark, C. W. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology* **5**, 159-170.

Connell, S. D. (2000). Is there safety-in-numbers for prey? *Oikos* **88**, 527-532.

Davidsen, J. G., Svenning, M.-A., Orell, P., Yoccoz, N., Dempson, J. B., Niemelä, E., Klemetsen, A., Lamberg, A. & Erkinaro, J. (2005). Spatial and temporal migration of wild Atlantic salmon smolts determined from a video camera array in the sub-Arctic River Tana. *Fisheries Research* **74**, 210-222.

Davidsen, J. G., Eldøy, S. H., Meyer, I., Halvorsen, A. E., Sjursen, A. D., Rønning, L., Schmidt, S. N., Præbel, K., Daverdin, M., Bårdsen, M. T., Whoriskey. F. & Thorstad, E. B. 2019. Sjøørret og sjørøye i Skjerstadfjorden - Marine vandringer, områdebruk og genetikk– NTNU Vitenskapsmuseet naturhistorisk rapport 2019-5:1-80.

Ebel, J. D., Leroux, S. J., Robertson, M. J. & Dempson, J. B. (2015). Ontogenetic differences in Atlantic salmon phosphorus concentration and its implications for cross ecosystem fluxes. *Ecosphere* **6**, art136.

Eldøy, S. H., Bordeleau, X., Crossin, G. T. & Davidsen, J. G. (2019). Individual repeatability in marine migratory behavior: a multi-population assessment of anadromous brown trout tracked through consecutive feeding migrations. *Frontiers in Ecology and Evolution* **7**.

Eldøy, S. H., Bordeleau, X., Lawrence, M., Thorstad, E., Finstad, A., Whoriskey, F., Crossin, G., Cooke, S., Aarestrup, K., Rønning, L., Sjursen, A. & Davidsen, J. (2021). The effects of nutritional state, sex and body size on the marine migration behaviour of sea trout. *Marine Ecology Progress Series* **665**, 185-200.

Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., Gale, M. K., Patterson, D. A., Hinch, S. G. & Farrell, A. P. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science* **332**, 109-112.

Elliott, J. (1976). The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *The Journal of Animal Ecology* **45**, 923-948.

Elliott, J. M. & Elliott, J. A. (2010). Temperature requirements of Atlantic salmon *Salmo salar*, brown trout *Salmo trutta* and Arctic charr *Salvelinus alpinus*: predicting the effects of climate change. *Journal of Fish Biology* **77**, 1793-1817.

Elliott, J. M. (2011). A comparative study of the relationship between light intensity and feeding ability in brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*). *Freshwater Biology* **56**, 1962-1972.

Enders, E. C., Boisclair, D. & Roy, A. G. (2005). A model of total swimming costs in turbulent flow for juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1079-1089.

Erkinaro, J., Okland, F., Moen, K., Niemela, E. & Rahiala, M. (1999). Return migration of Atlantic salmon in the River Tana: the role of environmental factors. *Journal of Fish Biology* **55**, 506-516.

Farrell, A. P., Eliason, E. J., Sandblom, E. & Clark, T. D. (2009). Fish cardiorespiratory physiology in an era of climate change. *Canadian Journal of Zoology* **87**, 835-851.

Feunteun, E. & Marion, L. (1994). Assessment of grey heron predation on fish communities: the case of the largest European colony. *Hydrobiologia* **279-280**, 327-344.

Finstad, A. G. & Hein, C. L. (2012). Migrate or stay: terrestrial primary productivity and climate drive anadromy in Arctic char. *Global Change Biology* **18**, 2487-2497.

Finstad, B., Staurnes, M. & Reite, O. B. (1988). Effect of low temperature on sea-water tolerance in rainbow trout, Salmo gairdneri. *Aquaculture* **72**, 319-328.

Finstad, B. & Heggberget, T. (1993). Migration, growth and survival of wild and hatchery-reared anadromous Arctic charr (*Salvelinus alpinus*) in Finnmark, northern Norway. *Journal of Fish Biology* **43**, 303-312.

Finstad, B., Bjørn, P. & Nilsen, S. (1995). Survival of salmon lice, *Lepeophtheirus salmonis* Krøyer, on Arctic charr, *Salvelinus alpinus* (L.), in fresh water. *Aquaculture Research* **26**, 791-795.

Fjelldal, P., Hansen, T., Karlsen, Ø. & Wright, D. (2019). Effects of laboratory salmon louse infection on Arctic char osmoregulation, growth and survival. *Conservation Physiology* **7**, coz072.

Fleming, I. A., Jonsson, B., Gross, M. R. & Lamberg, A. (1996). An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *The Journal of Applied Ecology* **33**, 893.

Forseth, T., Barlaup, B. T., Finstad, B., Fiske, P., Gjøsæter, H., Falkegård, M., Hindar, A., Mo, T. A., Rikardsen, A. H., Thorstad, E. B., Vøllestad, L. A. & Wennevik, V. (2017). The major threats to Atlantic salmon in Norway. *ICES Journal of Marine Science* **74**, 1496-1513.

Gilbert, M. J. & Tierney, K. B. (2018). Warm northern river temperatures increase post-exercise fatigue in an Arctic migratory salmonid but not in a temperate relative. *Functional Ecology* **32**, 687-700.

Gilbert, M. J. H., Donadt, C. R., Swanson, H. K. & Tierney, K. B. (2016). Low annual fidelity and early upstream migration of anadromous Arctic char in a variable environment. *Transactions of the American Fisheries Society* **145**, 931-942.

Gilbert, M. J. H., Harris, L. N., Malley, B. K., Schimnowski, A., Moore, J.-S. & Farrell, A. P. (2020). The thermal limits of cardiorespiratory performance in anadromous Arctic char (*Salvelinus alpinus*): a field-based investigation using a remote mobile laboratory. *Conservation Physiology* **8**, coaa036.

Gross, M. R., Coleman, R. M. & McDowall, R. M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science* **239**, 1291-1293.

Halttunen, E., Gjelland, K. Ø., Hamel, S., Serra-Llinares, R. M., Nilsen, R., Arechavala-Lopez, P., Skarðhamar, J., Johnsen, I. A., Asplin, L., Karlsen, Ø., Bjørn, P. A. & Finstad, B. (2018). Sea trout adapt their migratory behaviour in response to high salmon lice concentrations. *Journal of Fish Diseases* **41**, 953-967.

Hamre, L., Bui, S., Oppedal, F., Skern-Mauritzen, R. & Dalvin, S. (2019). Development of the salmon louse *Lepeophtheirus salmonis* parasitic stages in temperatures ranging from 3 to 24°C. *Aquaculture Environment Interactions* **11**, 429-443.

Hansen, A. K., Byriel, D. B., Jensen, M. R., Steffensen, J. F. & Svendsen, M. B. S. (2017). Optimum temperature of a northern population of Arctic charr (*Salvelinus alpinus*) using heart rate Arrhenius breakpoint analysis. *Polar Biology* **40**, 1063-1070.

Hansen, L. P., Jonsson, N. & Jonsson, B. (1993). Oceanic migration in homing Atlantic salmon. *Animal Behaviour* **45**, 927-941.

Heggenes, J., Krog, O. M. W., Lindas, O. R. & Dokk, J. G. (1993). Homeostatic behavioural responses in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. *The Journal of Animal Ecology* **62**, 295.

Hellawell, J. M., Leatham, H. & Williams, G. I. (1974). The upstream migratory behaviour of salmonids in the River Frome, Dorset. *Journal of Fish Biology* **6**, 729-744.

Hvidsten, N. A., Heggberget, T. & Jensen, A. J. (1998). Sea water temperatures at Atlantic salmon smolt enterance. *Nordic Journal of Freshwater Research*, 79-86.

Ibbotson, A. T., Beaumont, W. R. C. & Pinder, A. C. (2011). A size-dependent migration strategy in Atlantic salmon smolts: small smolts favour nocturnal migration. *Environmental Biology of Fishes* **92**, 151-157.

ICES. 2016. Report of the Working Group on North Atlantic Salmon (WGNAS), 30 March–8 April 2016, Copenhagen, Denmark. ICES CM 2016/ACOM:10. 323 pp.

Jackson, P. & Howie, D. (1967). The movement of salmon (*Salmo salar*) through an estuary and a fish-pass. *Irish Fisheries Investigations* **2**, 10-67.

Jensen, A. J., Heggberget, T. G. & Johnsen, B. O. (1986). Upstream migration of adult Atlantic salmon, *Salmo salar* L., in the river Vefsna, northern Norway. *Journal of Fish Biology* **29**, 459-465.

Jensen, A. J., Finstad, B. & Fiske, P. (2019). The cost of anadromy: marine and freshwater mortality rates in anadromous Arctic char and brown trout in the Arctic region of Norway. *Canadian Journal of Fisheries and Aquatic Sciences* **76**, 2408-2417.

Jensen, A. J., Finstad, B., Fiske, P., Diserud, O. H. & Thorstad, E. B. (2020). Repeatable individual variation in migration timing in two anadromous salmonids and ecological consequences. *Ecology and Evolution* **10**, 11727-11738.

Jensen, J. L. A. & Rikardsen, A. H. (2008). Do northern riverine anadromous Arctic charr *Salvelinus alpinus* and sea trout *Salmo trutta* overwinter in estuarine and marine waters? *Journal of Fish Biology* **73**, 1810-1818.

Jensen, J. L. A. & Rikardsen, A. H. (2012). Archival tags reveal that Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during winter. *Journal of Fish Biology* **81**, 735-749.

Jonsson, B. & Gravem, F. R. (1985). Use of space and food by resident and migrant brown trout, *Salmo trutta*. *Environmental Biology of Fishes* **14**, 281-293.

Jonsson, B., Jonsson, N., Brodtkorb, E. & Ingebrigtsen, P. J. (2001). Life-history traits of brown trout vary with the size of small streams. *Functional Ecology* **15**, 310-317.

Jonsson, B., Jonsson, N. & Hansen, L. P. (2003). Atlantic salmon straying from the river Imsa. *Journal of Fish Biology* **62**, 641-657.

Jonsson, B. & Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology* **75**, 2381-2447.

Jonsson, B. & Jonsson, N. (2011). *Ecology of Atlantic Salmon and Brown Trout: Habitat As a Template for Life Histories*, Fish & Fisheries Series, Volume 33. Springer, New York.

Jonsson, B. & Jonsson, N. (2014). Naturally and hatchery produced European trout *Salmo trutta*: do their marine survival and dispersal differ? *Journal of Coastal Conservation* **18**, 79-87.

Jonsson, B., Jonsson, N. & Jonsson, M. (2018). Water level influences migratory patterns of anadromous brown trout in small streams. *Ecology of freshwater fish* **27**, 1066-1075.

Jonsson, N., Jonsson, B. & Hansen, L. P. (1990). Partial segregation in the timing of migration of Atlantic salmon of different ages. *Animal Behaviour* **40**, 313-321.

Jonsson, N. (1991). Influence of water flow, water temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research* **66**, 20-35.

Jonsson, N., Hansen, L. P. & Jonsson, B. (1991). Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. *The Journal of Animal Ecology* **60**, 937.

Jonsson, N. & Jonsson, B. (2002). Migration of anadromous brown trout *Salmo trutta* in a Norwegian river. *Freshwater Biology* **47**, 1391-1401.

Karppinen, P., Erkinaro, J., Niemela, E., Moen, K. & Okland, F. (2004). Return migration of one-sea-winter Atlantic salmon in the River Tana. *Journal of Fish Biology* **64**, 1179-1192.

Klemetsen, A., Amundsen, P. A., Dempson, J., Jonsson, B., Jonsson, N., O'connell, M. & Mortensen, E. (2003). Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecology of freshwater fish* **12**, 1-59.

Knutsen, J., Knutsen, H., Olsen, E. & Jonsson, B. (2004). Marine feeding of anadromous *Salmo trutta* during winter. *Journal of Fish Biology* **64**, 89-99.

Moore, A., Potter, E., Milner, N. & Bamber, S. (1995). The migratory behaviour of wild Atlantic salmon (*Salmo salar*) smolts in the estuary of the river Conwy, North Wales. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1923-1935.

Moore, I., Dodd, J. A., Newton, M., Bean, C. W., Lindsay, I., Jarosz, P. & Adams, C. E. (2018). The influence of aquaculture unit proximity on the pattern of *Lepeophtheirus salmonis* infection of anadromous *Salmo trutta* populations on the isle of Skye, Scotland. *Journal of Fish Biology* **92**, 1849-1865.

Moore, J. (1975). Distribution, movements, and mortality of anadromous arctic char, *Salvelinus alpinus* L., in the Cumberland Sound area of Baffin Island. *Journal of Fish Biology* **7**, 339-348.

Mottola, G., Kristensen, T. & Anttila, K. (2020). Compromised thermal tolerance of cardiovascular capacity in upstream migrating Arctic char and brown trout—are hot summers threatening migrating salmonids? *Conservation Physiology* **8**, coaa101.

Norwegian Institute of Marine Research (2021). Lakseluskartet. https://www.hi.no/forskning/marine-data-forskningsdata/lakseluskart/html/lakseluskart.html. 19.03.2021.

Ojanguren, A. F. & Branta, F. (2000). Thermal dependence of swimming endurance in juvenile brown trout. *Journal of Fish Biology* **56**, 1342-1347.

Olsen, E. M., Knutsen, H., Simonsen, J. H., Jonsson, B. & Knutsen, J. A. (2006). Seasonal variation in marine growth of sea trout, *Salmo trutta*, in coastal Skagerrak. *Ecology of freshwater fish* **15**, 446-452.

Penney, C. M., Nash, G. W. & Gamperl, A. K. (2014). Cardiorespiratory responses of seawater-acclimated adult Arctic char (*Salvelinus alpinus*) and Atlantic salmon (*Salmo salar*) to an acute temperature increase. *Canadian Journal of Fisheries and Aquatic Sciences* **71**, 1096-1105.

Quinn, N. L., McGowan, C. R., Cooper, G. A., Koop, B. F. & Davidson, W. S. (2011). Identification of genes associated with heat tolerance in Arctic charr exposed to acute thermal stress. *Physiological genomics* **43**, 685-696.

Quinn, T. P., McGinnity, P. & Reed, T. E. (2016). The paradox of "premature migration" by adult anadromous salmonid fishes: patterns and hypotheses. *Canadian Journal of Fisheries and Aquatic Sciences* **73**, 1015-1030.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

RStudio Team (2021). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. http://www.rstudio.com/.

Schlyter, P. (2017). Radiometry and photometry in astronomy. How bright are natural light sources? http://stjarnhimlen.se/comp/radfaq.html#10. 28.03.2021.

Serra-Llinares, R., Bøhn, T., Karlsen, Ø., Nilsen, R., Freitas, C., Albretsen, J., Haraldstad, T., Thorstad, E., Elvik, K. & Bjørn, P. (2020). Impacts of salmon lice on mortality, marine migration distance and premature return in sea trout. *Marine Ecology Progress Series* **635**, 151-168.

Shaw, A. K. (2016). Drivers of animal migration and implications in changing environments. *Evolutionary Ecology* **30**, 991-1007.

Sjursen, A. D., Rønning, L. & Davidsen, J. G. 2021. Overvåkning av anadrome laksefisk i Botnvassdraget i Nordland 2018-2020. – NTNU Vitenskapsmuseet naturhistorisk rapport 2021-2: 1-29.

Skilbrei, O. T., Finstad, B., Urdal, K., Bakke, G., Kroglund, F. & Strand, R. (2013). Impact of early salmon louse, *Lepeophtheirus salmonis* , infestation and differences in survival and marine growth of sea-ranched Atlantic salmon, *Salmo salar* L., smolts 1997-2009. *Journal of Fish Diseases* **36**, 249-260.

Svendsen, J. C., Koed, A. & Aarestrup, K. (2004). Factors influencing the spawning migration of female anadromous brown trout. *Journal of Fish Biology* **64**, 528-540.

Svenning, M. A. & Grotnes, P. (1991). Stationarity and homing ability of landlocked Arctic charr. *Nordic Journal of Freshwater Research* **66**, 36-43.

Taranger, G. L., Karlsen, Ø., Bannister, R. J., Glover, K. A., Husa, V., Karlsbakk, E., Kvamme, B. O., Boxaspen, K. K., Bjørn, P. A., Finstad, B., Madhun, A. S., Morton,

H. C. & Svåsand, T. (2015). Risk assessment of the environmental impact of Norwegian Atlantic salmon farming. *ICES Journal of Marine Science* **72**, 997-1021.

Tetzlaff, D., Soulsby, C., Youngson, A. F., Gibbins, C., Bacon, P. J., Malcolm, I. A. & Langan, S. (2005). Variability in stream discharge and temperature: a preliminary assessment of the implications for juvenile and spawning Atlantic salmon. *Hydrology and Earth System Sciences* **9**, 193-208.

Thomsen, D. S., Koed, A., Nielsen, C. & Madsen, S. S. (2007). Overwintering of sea trout (*Salmo trutta*) in freshwater: escaping salt and low temperature or an alternate life strategy? *Canadian Journal of Fisheries and Aquatic Sciences* **64**, 793-802.

Thorstad, E. B., Økland, F., Aarestrup, K. & Heggberget, T. G. (2008). Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries* **18**, 345-371.

Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., Kålås, S., Berg, M. & Finstad, B. (2015). Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta* a literature review. *Aquaculture Environment Interactions* **7**, 91-113.

Thorstad, E. B., Todd, C. D., Uglem, I., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., Kålås, S., Berg, M. & Finstad, B. (2016). Marine life of the sea trout. *Marine Biology* **163**, 47.

Tveiten, H., Bjørn, P. A., Johnsen, H. K., Finstad, B. & McKinley, R. S. (2010). Effects of the sea louse *Lepeophtheirus salmonis* on temporal changes in cortisol, sex steroids, growth and reproductive investment in Arctic charr *Salvelinus alpinus*. *Journal of Fish Biology* **76**, 2318-2341.

Ulvan, E. M., Foldvik, A., Jensen, A. J., Finstad, B., Thorstad, E. B., Rikardsen, A. H. & Næsje, T. F. (2018). Return migration of adult Atlantic salmon (*Salmo salar* L.) to northern Norway. *ICES Journal of Marine Science* **75**, 653-661.

Underwood, Z. E., Myrick, C. A. & Rogers, K. B. (2012). Effect of acclimation temperature on the upper thermal tolerance of Colorado River cutthroat trout *Oncorhynchus clarkii pleuriticus*: thermal limits of a North American salmonid. *Journal of Fish Biology* **80**, 2420-2433.

Vollset, K. W., Lennox, R. J., Davidsen, J. G., Eldøy, S. H., Isaksen, T. E., Madhun, A., Karlsson, S. & Miller, K. M. (2021). Wild salmonids are running the gauntlet of pathogens and climate as fish farms expand northwards. *ICES Journal of Marine Science* **78**, 388-401.

Winfield, I. J., Hateley, J., Fletcher, J. M., James, J. B., Bean, C. W. & Clabburn, P. (2010). Population trends of Arctic charr (*Salvelinus alpinus*) in the UK: assessing the evidence for a widespread decline in response to climate change. *Hydrobiologia* **650**, 55-65.

Wright, D. W., Oppedal, F. & Dempster, T. (2016). Early-stage sea lice recruits on Atlantic salmon are freshwater sensitive. *Journal of Fish Diseases* **39**, 1179-1186.

Appendix 1

Table A.1: Linear regression models for estimated date of registration during upstream migration for anadromous brown trout, Arctic char and Atlantic salmon in 2019 and 2020 in rivers Fjæreelva and Botnelva. Intercept is the Julian date of registration (DOY). Length is estimated body length (in cm) from video analysis. Values for statistical significance variable Length are in bold.

Coefficients	Estimate	*SE*	*t*-value	Pr(>|*t*|)
Fjæreelva 2019 Brown trout				
Intercept	244.84	2.24	109.22	< 0.001
Length	**-0.81**	0.05	-15.80	**< 0.001**
Fjæreelva 2019 Arctic char				
Intercept	175.25	1.74	100.55	< 0.001
Length	**-0.15**	0.05	-3.22	**< 0.01**
Fjæreelva 2019 Atlantic salmon				
Intercept	303.05	11.72	25.86	< 0.001
Length	**-1.39**	0.19	-7.24	**< 0.001**
Fjæreelva 2020 Brown trout				
Intercept	194.38	2.25	86.51	< 0.001
Length	**0.31**	0.05	6.31	**< 0.001**
Fjæreelva 2020 Arctic char				
Intercept	159.71	3.38	47.32	< 0.001
Length	**0.27**	0.10	2.67	**< 0.01**
Fjæreelva 2020 Atlantic salmon				
Intercept	237.85	18.42	12.91	< 0.001
Length	0.02	0.31	0.05	> 0.05
Botnelva 2019 Brown trout				
Intercept	264.75	1.15	230.97	< 0.001
Length	**-0.69**	0.03	-25.90	**< 0.001**
Botnelva 2019 Arctic char				
Intercept	228.56	1.90	120.41	< 0.001
Length	**-0.56**	0.06	-9.23	**< 0.001**
Botnelva 2019 Atlantic salmon				
Intercept	307.17	18.10	16.97	< 0.001
Length	**-0.78**	0.32	-2.40	**< 0.05**
Botnelva 2020 Brown trout				
Intercept	259.71	1.34	193.18	< 0.001
Length	**-0.22**	0.03	-7.27	**< 0.001**
Botnelva 2020 Arctic char				
Intercept	234.21	5.25	44.58	< 0.001
Length	**-0.37**	0.18	-2.09	**< 0.05**
Botnelva 2020 Atlantic salmon				
Intercept	290.12	21.26	13.64	< 0.001
Length	-0.46	0.35	-1.32	> 0.05

Table A. 2: Compared dates of registration between individuals with LiceS: NoneDetected and LiceS: Detected within the same species, the total number of compared registrations, W-value and *p*-value for performed Wilcoxon rank sum tests for anadromous brown trout, Arctic char and Atlantic salmon in rivers Fjæreelva and Botnelva in 2019 and 2020. * Notes that the exact *p*-value could not be computed, due to a small sample size.

Compared species groups	Total *n*	W	*p*
Fjæreelva 2019			
Brown trout	1443	241550	**< 0.001**
Arctic char	466	16598	> 0.05
Atlantic salmon	135	2933.5	**< 0.001**
Fjæreelva 2020			
Brown trout	996	97897	**< 0.001**
Arctic char	443	1988	**< 0.01**
Atlantic salmon	81	960.5	**< 0.01**
Botnelva 2019			
Brown trout	1946	519152	**< 0.001**
Arctic char	873	13102	> 0.05
Atlantic salmon	76	684.5	**< 0.001**
Botnelva 2020			
Brown trout	1085	113354	> 0.05
Arctic char	90	237.5	> 0.05
Atlantic salmon *	23	82.5	**< 0.01**