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Spawning migration of salmon and sea trout in the Tornionjoki river

Riina Huusko, Gustav Hellström, Mikko Jaukkuri, Stefan Palm and Atso Romakkaniemi

LUONNONVARAKESKUS

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Abstract

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In this collaborative project between the Natural Resources Institute (Luke) and the Swedish Agricultural University (SLU), the migratory behaviour and survival of Tornionjoki (Torneälv in Swedish) salmon and sea trout were studied between 2018–2021 by the means of radiotelemetry. Altogether, 227 and 92 salmon were tagged at the Tornionjoki estuary and in the river, respectively. 114 sea trout were tagged in the river. Scale samples and fin clips for ageing and genetic identification were taken from all the tagged specimens. The external condition of the tagged specimen was also documented (wounds, skin colour, degree of haemorrhage etc.). Moreover, a separate follow-up of the external condition of salmon caught in trap nets was conducted in 2020–2021 at sea near the river mouth.

The post-release behaviour of salmon tagged at the estuary was markedly different from that normally expected: a large majority (61% and 83% in 2018 and 2019, respectively) of the salmon which ascended the river after tagging aborted their riverine migration on the lower river and returned to the sea during the summer (i.e., before spawning season). Those salmon which stayed in the river until spawning time predominantly stayed on the lowermost 100 km of the river. More varying migration patterns were observed among the salmon tagged in the river. All specimens caught and tagged during the early summer of 2018 and 2019 started to drift downstream after their release and none of them was alive in the river at spawning time. However, about half of the specimens tagged in the river in early summer 2020 and 2021 continued their upstream migration and were alive in the river at spawning time. Salmon tagged in late summer 2018–2020 stayed alive in the river and almost half of them also moved further upstream by spawning time. A large majority of salmon overwintered in the river after spawning and returned to the sea in spring. The majority of the salmon caught in the estuary had various external damages (wounds, scale losses, fin damages, and skin haemorrhage). Most of the damages, however, were regarded as minor. No correlation between the occurrence of damages and the post-tagging behaviour of salmon could be detected.

Based on the data obtained from tagged sea trout, two distinct groups of trout were recognised: (1) non-mature trout which ascended the river in autumn and returned to the sea in spring after overwintering in river, and (2) maturing trout which ascended the river in autumn, overwintered in the river, and continued their upstream spawning migration the following summer. Specimens belonging to either of these groups typically overwintered in the same short lowermost stretch of the river, although some of the maturing trout overwintered further upstream. At spawning season, tagged trout were located both on the main stem (Tornionjoki and Muonionjoki rivers) and in several tributaries (Naamijoki, Äkäsjoki, Parkajoki, Pakajoki and Merasjoki rivers). After spawning time, trout which were observed in the tributaries usually moved back to the main stem where they overwintered and descended to the sea the next spring. Both the immature and the maturing overwintering trout descended to the sea at almost the same time in spring.

The results of the project highlight the sensitivity of salmon to handling at/around the time of their river ascent in early summer. This sensitivity is likely linked to the recent health problems observed among Tornionjoki salmon and may have induced the unexpected (and seemingly maladaptive) migratory behaviour of salmon observed in the study. The in-river and sea to river movements observed for the Tornionjoki sea trout provides very useful information for efforts to protect this species and strengthen its stock status. In general, mature Tornionjoki sea trout have a two year in-river migratory cycle in connection with spawning, and hence spend a large majority of their life in the river, which underlines the need for good management of the riverine environment and river fisheries.

Keywords: Spawning migration, salmon health, overwintering, anadromous trout, Baltic salmon, arctic river

Abstract in Finnish

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Radiotelemetriamenetelmällä selvitettiin lohen ja meritaimen vaelluskäyttäytymistä ja eloonjääntiä Tornionjoessa vuosina 2018–2021 Luonnonvarakeskuksen (Luke) ja Ruotsin maataloustieteellisen yliopiston (SLU) yhteisessä hankkeessa. Tutkimuksen aikana merkittiin lohia joen edustan merialueella (n=227) ja joella (n=92). Meritaimenia merkittiin joella yhteensä 114. Kaikilta radiolähettimellä merkityiltä kaloilta kerättiin näytteet iänmääritystä ja geneettistä määritystä varten. Merkittyjen kalojen ulkoista kuntoa arvioitiin ja luokiteltiin merkinnän yhteydessä. Lisäksi vuosina 2020–2021 seurattiin lohien kuntoa joen edustan merialueella.

Tornionjoen edustalla merkittyjen lohien käyttäytyminen poikkesi voimakkaasti odotetusta, sillä suurin osa (61 % vuonna 2018 ja 83 % vuonna 2019) jokeen merkinnän jälkeen nousseista lohista palasi kesän aikana, siis ennen kutuaikaa, takaisin merelle. Jokeen jääneistä lohista suurin osa oli syksyllä kutuaikaan Kattilakosken kaikuluotainpaikan alapuolisella jokialueella. Joella merkittyjen lohien käyttäytyminen vaihteli vuosien ja vuodenaikojen välillä. Vuosina 2018–2019 kaikki keväällä merkityt lohet lähtivät merkinnän jälkeen liikkumaan alavirtaan, eikä yksikään keväällä merkitty lohi ollut elossa joella enää syksyn kutuaikana, kun puolestaan vuosina 2020–2021 keväällä merkityistä lohista lähes puolet jatkoivat vaellustaan ylävirtaan. Syyspuolella joella merkityt lohet sen sijaan pysyivät joella kutuajan yli kaikkina merkintävuosina (2018–2020), ja osa niistä vaelsi vielä huomattaviakin matkoja ylävirtaan merkinnän jälkeen. Suurin osa lohista talvehti kudun jälkeen joessa ja palasi merelle kutua seuraavan kevään aikana. Enemmistöllä Tornionjokisuulla tutkituista lohista havaittiin eriasteisia ja -tyyppisiä ulkoisia vaurioita. Vauriot olivat kuitenkin pääosin lieviä. Merkityillä lohilla ei ilmennyt yhteyttä ulkoisten vaurioiden esiintymisen ja vaelluskäyttäytymisen välillä.

Merkittyjen taimenten perusteella Tornionjokeen nousevat meritaimenet jakautuvat kahteen käyttäytymismalliin: (1) joen alajuoksulle syksyllä talvehtimaan tulevat, ei-sukukypsät taimenet, jotka palaavat keväällä takaisin merelle, sekä (2) jokeen syksyllä (tai paljon harvinaisemmin vasta keväällä) tulevat yksilöt, jotka jatkavat vaellustaan kutualueille. Molempien ryhmien syksyllä jokeen nousevat kalat talvehtivat yleensä samalla alueella joen alajuoksulla. Kutemaan nousevista taimenista kuitenkin osa vaeltaa talvehtimaan ylemmäs joelle. Talven jälkeen kudulle nousevat taimenet jatkavat matkaansa lisääntymisalueille touko-kesäkuun vaihteessa. Merkittyjä taimenia havaittiin kutuaikana vesistön pääuomien (Tornionjoki, Muonionjoki) lisäksi Naamijoessa, Äkäsjoessa, Parkajoessa, Pakajoessa ja Merasjoessa. Kudun jälkeen taimenet siirtyvät useimmiten sivujoista pääuomaan ja talvehtivat pääuomassa ennen merelle vaellustaan seuraavana keväänä. Kudulta palaavat ja joella vain talvehtimassa käyneet taimenet lähtevät joelta merelle lähes samaan aikaan.

Projektin tulokset korostavat lohien herkkyyttä niiden vaelluskäyttäytymisen voimakkaaseenkin häiriintymiseen erityisesti keväällä jokeen nousun yhteydessä, mikä luultavasti kytkeytyy

Tornionjoen lohilla viime vuosien kuluessa havaittuihin terveysongelmiin. Tornionjoen meritaimenen jokivaellukset sekä vaellukset meren ja joen välillä saatiin määriteltyä hyvin, mikä tieto on hyödyllistä taimenten suojelussa kantojen vahvistamiseksi. Sukukypsät meritaimenet viettävät joessa hyvin suuren osan elinajastaan, mikä korostaa jokiympäristöstä huolehtimisen ja jokikalastuksen säätelyn tärkeyttä meritaimenkantojen hoidossa.

Asiasanat: Kutuvaellus, lohen terveys, talvehtiminen, anadrominen taimen, Itämeren lohi, arktinen joki

Abstract in Swedish

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I detta samarbetsprojekt mellan Naturresursinstitutet (Luke) och Sveriges lantbruksuniversitet (SLU) studerades vandringsbeteende och överlevnad hos Torneälvens lax och havsöring under 2018–2021 med hjälp av radiotelemetri. Totalt märktes 227 laxar i älvens mynning, och 92 laxar och 114 havsöringar i älven. Fjällprover för åldersbestämning och fenklipp för genetisk identifiering togs från alla märkta individer. En yttre kroppsbesiktning avseende prevalens av till exempel sår och blödning genomfördes på alla märkta laxar. Detta gjordes också på lax som fångats i fällor under 2020–2021 i havet nära flodmynningen, men som inte märktes.

Beteendet efter utsättning hos lax märkt i älvmynningen/estuariet skiljde sig markant från det förväntade beteendet för lekvandrande lax: en stor majoritet (61 % 2018, och 83 % 2019) avbröt sin vandring i nedre delen av älven och återvände tillbaka till havet under sommaren (dvs. före leksäsongen). De laxar som stannade i älven fram till lektid höll sig i de nedersta 100 kilometrarna. Ett mer varierat vandringsmönster observerades för de laxar som märktes i älven. Här började alla individer som fångades och märktes under försommaren 2018 och 2019 drifta nedströms efter att de släppts ut, och ingen av dessa laxar var vid liv i älven vid lektid. Ungefär hälften av de individer som märktes i älven under försommaren 2020 och 2021 fortsatte dock sin vandring uppströms och var vid liv i älven vid lektid. Lax märkt i älven under sensommaren 2018–2020 var vid liv i älven under lektid, och ca. hälften vandrande också längre uppströms i samband med lek. En stor majoritet av laxarna övervintrade i älven efter leken och återvände till havet på våren. Majoriteten av de laxar som fångades i estuariet hade olika yttre skador (sår, fjällförluster, fenskador och blödningar). De flesta av skadorna ansågs dock vara lindriga. Det gick inte att fastställa något samband mellan förekomsten av skador och laxens beteende efter märkningen.

Studien identifierade två olika grupper av öring: 1) icke-könsmogna öringar som vandrade upp i älven på hösten och återvände till havet på våren efter att ha övervintrat i älven, och 2) könsmogna öringar som vandrade upp i älven på hösten, övervintrade, fortsatte sin uppströms lekvandring påföljande sommar. Individer som tillhörde någon av dessa grupper övervintrade vanligtvis på en specifika relativt kort sträcka i nedersta delen av älven, även om en del av de könsmogna öringarna även övervintrade längre uppströms. Under lekperioden hittades märkta öringar både i huvudfåran (Torneälven och Muonionjoki) och i flera biflöden (Naamijoki, Äkäsjoki, Parkajoki, Pakajoki och Merasjoki). Efter lekperioden flyttade de öringar som observerades i biflödena vanligtvis tillbaka till huvudfåran där de övervintrade och tog sig ner till havet på våren. Både den icke-könsmogna och den könsmogna öringen vandrade ner till havet vid nästan samma tidpunkt på våren.

Resultaten av projektet visar hur känslig laxen är för hantering då den stiger upp i älven på försommaren. Denna känslighet är sannolikt kopplad till de hälsoproblem som nyligen obser-

verats bland Torneälvens laxar, och som kan ha orsakat det oväntade (och till synes maladaptiva) vandringsbeteende hos den lax som ingick i studien. Kunskapen om havsöringens förflyttningar inom älven, och mellan älv och hav, som denna studie producerat är värdefull för den fortsatta förvaltningen och bevarandet av Torneälvens havsöringsbestånd. I allmänhet har den vuxna havsöringen i Torneälven en tvåårig lekvandringscykel och den tillbringar därför en stor del av sitt liv i älven, vilket understryker behovet av en god förvaltning av älvsmiljön och fisket.

Nyckelord: Lekvandring, laxhälsa, övervintring, anadrom öring, Östersjölax, arktisk flod

Contents

1. Background 10

1.1. Study objectives 10

2. Material and methods 12

2.1. Salmon and sea trout of the Tornionjoki river 12

2.1.1. River discharge and water temperature 14

2.2. Catching, tagging, and tracking of fish 16

2.2.1. Catching and tagging at the Tornionjoki estuary 16

2.2.2. Catching and tagging in the Tornionjoki river 16

2.2.3. Radio-tagging and tracking of fish 18

2.3. Data analysis 20

2.3.1. Genetic analysis 20

2.3.2. Ageing of fish 21

2.3.3. Visual condition monitoring of salmon 21

2.3.4. Radio-tracking data 21

3. Results 23

3.1. Salmon 23

3.1.1. Sea-age structure and genetic origin 25

3.1.2. Visual condition 26

3.1.3. Behaviour and migration speed of salmon tagged at the estuary 27

3.1.4. Behaviour of C&R salmon 29

3.1.5. Spawning areas and behaviour after spawning 32

3.2. Sea trout 34

3.2.1. Sea-age structure and genetic origin 35

3.2.2. Behaviour 36

3.2.3. Spawning areas and behaviour after spawning 40

3.3. Trout-salmon hybrids 42

3.4. Radio-tagged fish vs. echo sounding at Kattilakoski 43

4. Discussion 44

4.1. Salmon 44

4.2. Sea trout 47

4.3. Limitations of the data 51

References 52

1. Background

The Tornionjoki river (Torneälven in Swedish) is the largest free-flowing river in western Europe, and the river system produces half of all wild salmon in the Baltic Sea (ICES 2021). The river system also hosts several wild anadromous trout populations, the status of which is deemed so weak that sea trout have been fully protected from harvest since 2013 (https://www.finlex.fi/fi/laki/alkup/2013/20130313). Thus, efficient and sustainable management of the salmon as well as recovery actions targeting sea trout populations in the river is of utmost importance.

The Tornionjoki salmon stock is closely monitored. Annually upstream migrating fish are counted by echo sounders in Kattilakoski (about 100 km from the river mouth) and salmon catches in the river are estimated by annual surveys with catch samples collected for monitoring of the stock demography. Moreover, the production of juvenile salmon is monitored annually by electrofishing and smolt trapping. However, in-river migratory behaviour and survival of both pre- and post-spawning salmon, as well as the distribution of spawning sites, are not well known. Additionally, recent observations of sick and dying salmon in many Baltic rivers, including the Tornionjoki river system, and declining returns reported in connection with such observations, are concerning (ICES 2021).

The status of sea trout populations in the Gulf of Bothnian rivers has been a concern for decades. However, there is less biological knowledge about sea trout than about salmon because sea trout has a more complex life history and a larger individual variation in e.g., migration and spawning areas. Moreover, smolt trapping and adult counting are challenging for sea trout in the environmental conditions of the Gulf of Bothnian rivers. Thus, despite some data obtained about the sea trout in conjunction with the annual salmon monitoring in Tornionjoki, there are considerable knowledge gaps about the migration behaviour, spawning sites, survival, and in-river movements between the sea and the river. To understand the effects of fishing regulations, as well as to further improve the management and conservation of Tornionjoki sea trout populations, more detailed biological information is needed.

1.1. Study objectives

This 4-year project focused on obtaining more knowledge about in-river migrations of salmon and sea trout in the Tornionjoki river. The project used radio telemetry and genetic stock identification methods to collect detailed data on the migration, behaviour, and population structure of these species. More specifically, the project aimed to answer nine main questions:

1. Where in the Tornionjoki river system do salmon and sea trout with different local genetic origins and biological characteristics (run timing and age) spawn?
2. What kind of upstream migration behaviour do salmon and sea trout display in terms of migration speed, directional movements and holding sites?
3. How do salmon spawners disperse along the river system during spawning time, and how do they utilize the main stem and the tributaries?
4. Where do sea trout spawn: in which tributaries and where in these tributaries?

5. How many of the tagged fish that pass the Kattilakoski counting site can be detected by the fish counter?
6. What kind of in-river migrations do immature (sub-adult) sea trout exhibit?
7. How does catch and release (C&R) angling affect the behaviour and survival of fish?
8. Do apparently sick salmon display different migration than salmon which appear healthy?
9. How do post-spawned salmon and sea trout overwinter, when do they return to the sea and what is their survival to the next spawning?

2. Material and methods

2.1. Salmon and sea trout of the Tornionjoki river

The Tornionjoki catchment flows into the Bothnian Bay, and it is the northernmost of the catchments in the Baltic Sea basin. The river system has a catchment area of 40 157 km^2, a river length of 520 km, and a mean annual flow of 400 m^3/s (Fig. 1). The catchment is in sparsely populated terrain ranging from the boreal zone in its lower and middle reaches to the headwater subarctic zone, 400 to 500 meters above the sea level. Headwater sources form three main stems (Swedish Torneälven and Lainioälven and Swedish-Finnish Muonionjoki), which all join 150–200 km upstream from the sea. Before the confluences, about half of the discharge of the Swedish Torneälv flows into a bifurcation river which runs to the neighbouring river Kalixälven.

Tornionjoki salmon seems to utilize basically all suitable spawning habitats in the river system along both the main stems and the headwater tributaries, ranging from 0.5–500 km upstream from the estuary (Fig. 1). Salmon spawning in the upper reaches of the river system differ genetically from salmon in the lower and middle reaches (Miettinen et al. 2021). Furthermore, out-migrating smolts genetically assigned to upper river reaches are older and tend to leave the river later in the season than smolts from the lower-middle reaches, while ascending spawners originating from the upper reaches return to the river earlier in the season than spawners originating from the lower-middle reach (Miettinen et al. 2021).

Like all other Gulf of Bothnian salmon, the Tornionjoki salmon migrates to the southern Baltic Sea during its first marine phase (e.g., Jacobson et al. 2020). These salmon are exposed to various commercial and recreational sea fisheries, both in the open sea and along the coast, pursued by many countries. During the latter half of the last century, the total fishing mortality in this mixed-stock sea fisheries increased and resulted in substantial overfishing, which pushed many wild salmon stocks to the verge of extinction (Romakkaniemi et al. 2003). This was the case also with the Tornionjoki salmon, with very few salmon escaping the fishery to spawn, resulting in less than 100 000 wild smolts annually leaving the river during the 1980s. To mitigate this decline, hatchery juveniles of the river's own genetic strain were stocked in the river during this period. Since the mid-1990s, stricter regulations for the fishery have been enforced, which has led to a rapid and strong recovery of the Tornionjoki salmon stock (Romakkaniemi et al. 2003; Michielsens et al. 2006; ICES 2021). During the last ten years, 50 000–100 000 salmon have been annually spawning in the Tornionjoki river, and this spawning results in approx. 1.5 million smolts produced annually. This abundance level is considered to attain the national and international management targets (ICES 2021; Palm et al. 2022) and Tornionjoki river is currently by far the largest producer of wild Atlantic salmon in the Baltic Sea region (e.g., ICES 2021).

Trout occur almost everywhere in the river system, but the anadromous form of trout (sea trout) is known to predominantly spawn in about a dozen tributary river systems located on the middle reach of the catchment, 100–300 km upstream from the estuary (Palm et al. 2019; Fig 1). Trout originating from different tributaries are genetically differentiated, but no phenological nor other specificities are known to exist between the local populations (Palm et al. 2019).

Tornionjoki sea trout spend their marine phase along the Bothnian Bay coast, although some individuals have been found to migrate as far as the Bothnian Sea (Vähä et al. 2010). Similar to other Gulf of Bothnian sea trout, Tornionjoki sea trout are caught as a bycatch in the coastal whitefish net fisheries (e.g., ICES 2021). Due to the high net fishing effort, fishing mortality of sea trout is believed to have been considerable for many decades (e.g., Whitlock et al. 2017). This together with various human activities (forestry, draining, agriculture, timber floating with river dredging, migration barriers) detrimental to the nursing and the reproduction habitats of trout are believed to have caused a severe decline in many of the Gulf of Bothnian sea trout stocks (Jutila et al. 2006). In the recent two decades, however, the status of sea trout has somewhat improved in the Tornionjoki and several other Gulf of Bothnian rivers. Currently, the annual sea trout spawning runs into Tornionjoki is estimated to range between hundreds to about one thousand individuals, and the smolt production is estimated to be about 20 000 trout smolts (e.g., Palm et al. 2022).

Fishing for salmon in the Tornionjoki river system mainly consists of various types of recreational fisheries with rod and reel (‘trolling’ by rowing boats, fly fishing, spinning etc.). During the fishing season (1st June–31st August) recreational fishing is prohibited one day a week along the border river reach of Tornionjoki, and along the whole Muonionjoki and Könkämäeno rivers, and there is a bag limit of one salmon per day/fisherman. The bulk of the salmon catch is caught by these recreational fisheries. However, on the lower reach of the river, net fishing of salmon is allowed periodically over the fishing season, and the so-called hoop net fishing (catching mainly migratory whitefish) also catches some salmon. Historically, in-river net fishing and especially fishing with large weirs was common, but this was banned by the mid-1990s. As mentioned above, all trout fishing has been banned in the border river and in the estuary since 2013.

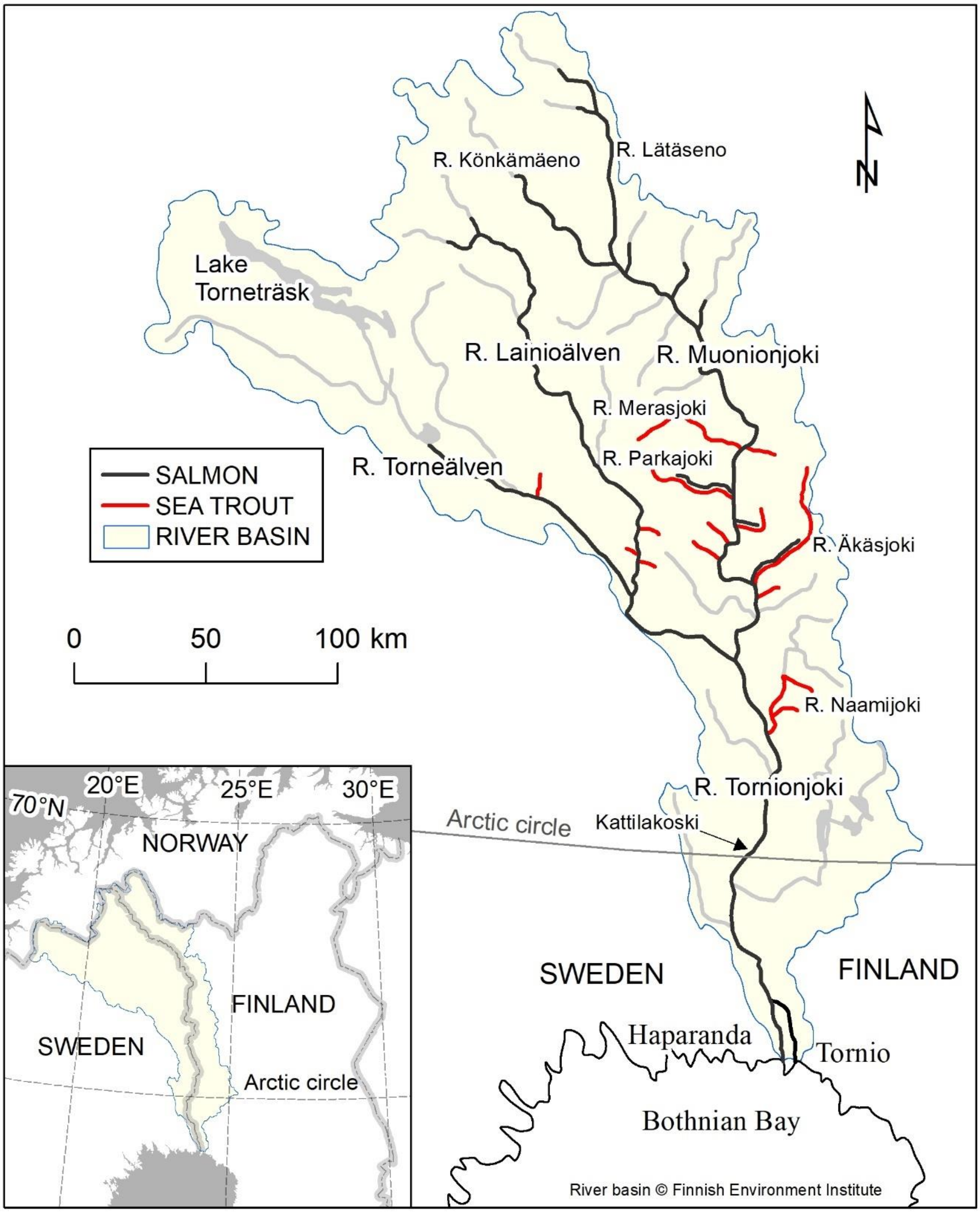

Figure 1. The Tornionjoki river is located on the northernmost edge of the Baltic Sea catchment. The river stretches with salmon (black) and sea trout (red) spawning sites, as currently known, are indicated. The catchment area of Tornionjoki river is highlighted with light yellow.

2.1.1. River discharge and water temperature

The Tornionjoki river has a large spring flood caused by melting waters of ice and snow. The highest flood usually occurs between mid-May to mid-June (Fig. 2). After the spring flood, discharge decreases and stays relatively stable during the summer. Water temperature increases concurrent with the decreasing discharge and is usually the warmest at the end of July (Fig. 2–3). In autumn, discharge often increases following autumn rains. Water temperature starts to decrease typically in mid-August, and the ice cover forms in October–November. During winter, discharge is usually low and water temperature is stable at approx. zero degrees.

The discharge during the study years 2018, 2019 and 2021 was exceptionally low during summer (long period <500 m^3/s), while the summer discharge during 2020 was higher than normal (>500 m^3/s during the summer and peaked at >1 500 m^3/s at the end of July; Fig. 2). During all study years, the water temperature was higher than normal in July, often exceeding 20°C (Fig. 3).

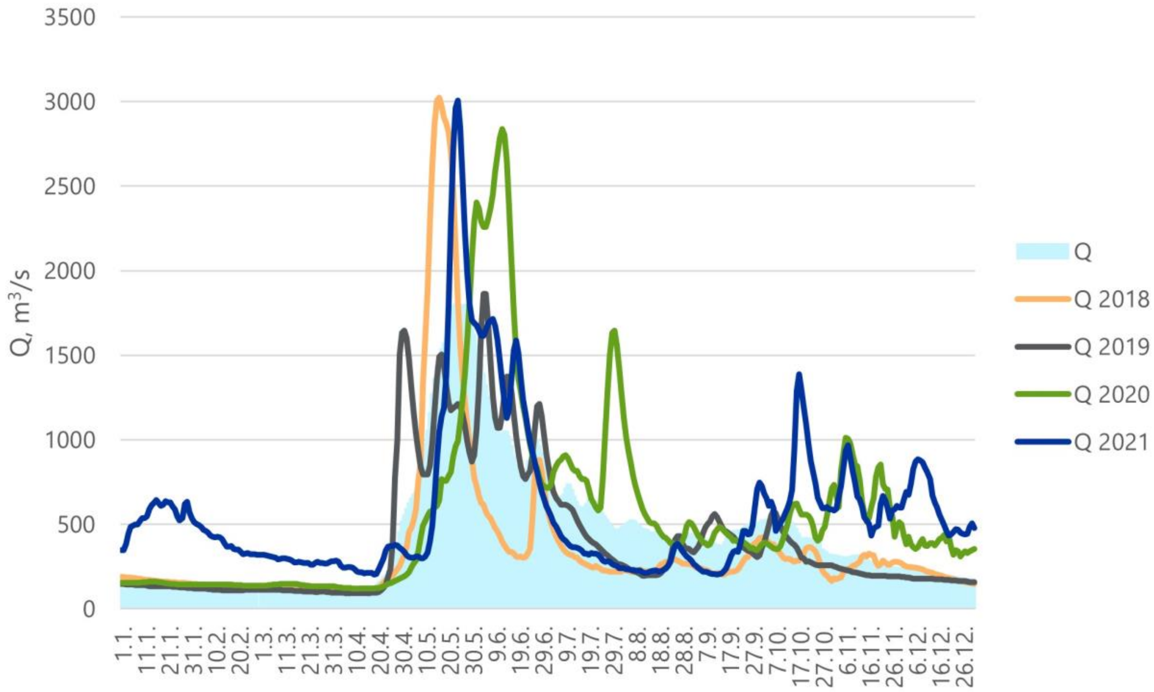

Figure 2. Discharge (Q, m^3/s) in Tornionjoki river (observation from Kukkolankoski, about 20 km upstream from the estuary) during the study years 2018–2021. The light blue area represents the average discharge during 2010–2020. Data: Hydrology observation/SYKE, open data.

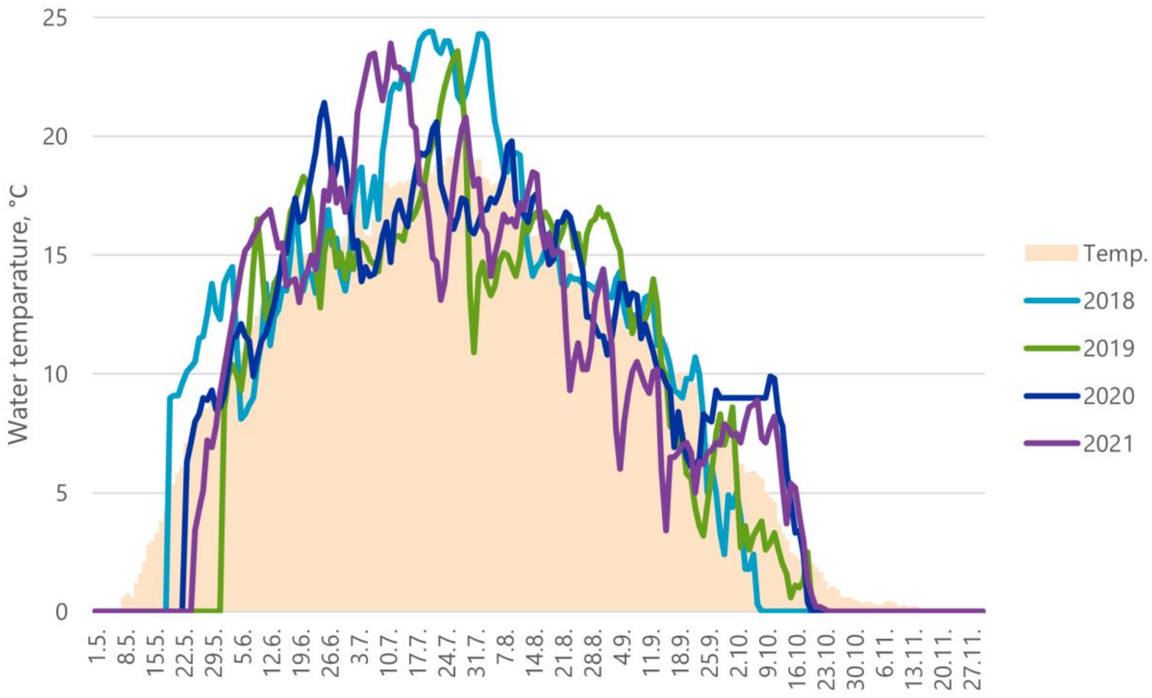

Figure 3. Water temperature (°C) in Tornionjoki river (observation from Kukkolankoski, about 20 km upstream from the estuary) during the study years 2018–2021. The light orange area represents the average water temperature during 2010–2020. Data: Hydrology observation/SYKE, open data.

2.2. Catching, tagging, and tracking of fish

2.2.1. Catching and tagging at the Tornionjoki estuary

In the years 2018 and 2019 salmon were caught by trap nets at the estuary close to the river mouth (Fig. 4) and tagged with radio transmitters. The trap nets had a special keep-net to prevent salmon from physical injuries during the emptying of the gear. The fish selected for tagging were moved directly from the trap to an aerated water tank on board a boat. In total, 227 salmon and 2 sea trout were tagged at the estuary during June–August (see below for details of the tagging procedure). Following observations of weak and sick fish in 2018–2019, a detailed visual inspection of salmon caught along the coast was done during 2020 and 2021 (see below for details of the visual inspection procedure). These years, a total of 338 salmon were inspected from the trap nets during June–July.

All sampling of fish at the estuary was performed in collaboration with commercial fishermen in the area. Fishing outside the regular fishing season was needed to better cover the whole migration period of salmon; for this, a special permit was applied from the Swedish Agency for Marine and Water Management (HaV) and the Finnish Lapland's Centre for Economic Development, Transport, and the Environment (ELY).

2.2.2. Catching and tagging in the Tornionjoki river

In the years 2018–2021, fish were caught by rod-and-reel angling at up to 10 sites along the river 15–220 km upstream from the river mouth (Fig. 4, Table 1). Fishing took place in two periods: during early summer (May–June) and during autumn (August–October). The exact locations of sites varied between years, but anyhow the same river stretches were used over two successive years as much as possible, to get comparable data between years.

Three angling methods were used to catch the fish: trolling/harling using a rowing boat (the most common type of rod fishing in Tornionjoki river), fly fishing from the riverbank, and spinning using a weight and a fly (so-called "spinnfluga"). Salmon were caught using all these methods, whereas sea trout were caught only by trolling/harling. The tagging of sea trout was mostly carried out near the river mouth (Table 1) and most of the trout were caught in autumn (August–October).

Fishing was performed mainly by local collaborating recreational fishermen. Fishing outside the regular fishing season was conducted with a special permit from Finnish Lapland's Centre for Economic Development, Transport, and the Environment (ELY).

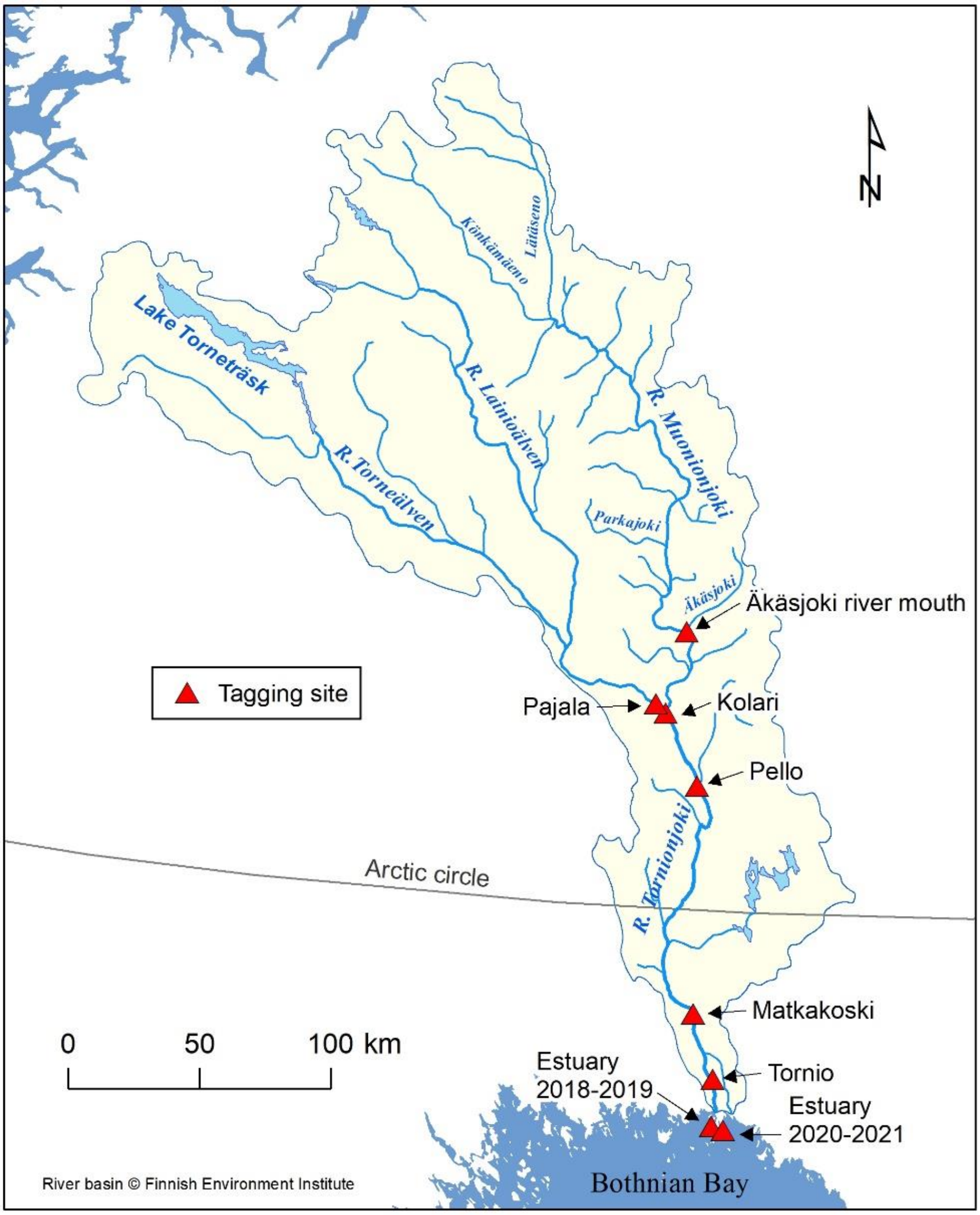

Figure 4. Locations of the catching and tagging sites during the study.

Table 1. Fishing locations of salmon and trout during the study.

Location	km from the river mouth	Salmon	Trout
		Year	Year
Estuary 1	-	2018–2019	2018
Estuary 2	-	2020–2021	-
Tornio	15	2018–2019	2018–2020
Matkakoski	40	2019–2021	2019
Pello	150	2018–2019	2018–2019
Kolari	180	2019–2020	-
Äkäsjoki river mouth	230	-	2019
Pajala	190	2018	-

2.2.3. Radio-tagging and tracking of fish

Fish were surgically tagged internally with a radio transmitter. Before tagging, all fish were anaesthetised with buffered MS-222 solution (100 mg/l), one fish at a time. During the anaesthesia, scale and tissue samples were taken, and the fish was measured (total length, cm) and photographed. The anaesthetised fish was moved into a custom-made tagging cradle and a coded radio transmitter (model MCFT2-3A, Lotek Wireless Inc., Canada) was placed into the body cavity via a 30 mm longitudinal incision made on the ventral side posterior to the pectoral fins. The antenna wire was inserted through the skin with a hypodermic needle (1.5x50 mm/17Gx2´´) pricked caudally from the incision. The incision was closed with two stitches using monofilament sutures (Ethilon 1671H, Ehticon, USA). The fish head was kept under the water and checked for ventilation during the tagging. Tagging operation took on average 2 min 56 sec per fish. After tagging, the fish was weighed (kg) and moved to a recovery cage. All fish were released following visual inspection to ensure that they had fully recovered from the anaesthesia.

Automatic data logging stations were installed at multiple sites along the main river, the main tributaries along the catchment and in the river mouths of the neighbouring rivers Kalixälven and Kemijoki (Fig 5.). An automatic data logging station consisted of a radio receiver (model SRX-DL or SRX800, Lotek Wireless Inc., Canada) connected to a four-, six-, or nine-elements Yagi-antenna. The detection area of each automatic data logging site covered the whole river width.

In addition to the continuous passive tracking by automatic data logging stations, manual tracking was done by car using a portable radio receiver (SRX800, Lotek Wireless Inc., Canada) and six-element Yagi antenna. Manual tracking was conducted weekly during spring (from mid-May to the end of June) and autumn (from mid-August to the end of October). In July and during winter, manual tracking was done on one or two occasions per month. Tracking by car was done in areas where roads follow alongside the riverbank. Additionally, manual tracking by boat was carried out during autumn in 2018–2020 to find lost radio-tagged fish (i.e., fish that had not been detected for a long time by the passive tracking stations) and/or to get a more precise location for the fish. In 2018 and 2019, boat tracking was conducted from the estuary to approx. 15 km upstream from the river mouth. In autumn 2018, tracking by boat was also conducted around Pello, and along the river from Muonio to Tornio to find fish that had been detected earlier either from manual tracking or from the passive tracking stations. In autumn 2020, boat tracking was done in the tributary Naamijoki to find trout which had ascended the tributary but had not been detected via manual tracking by car. A small aeroplane was also used in the autumns of 2018 and 2021 to detect fish along the main river and the biggest tributaries of the Swedish Torneälven (mouth to the village Junosuando) and the Muonionjoki river (from the river mouth to the village Karesuando).

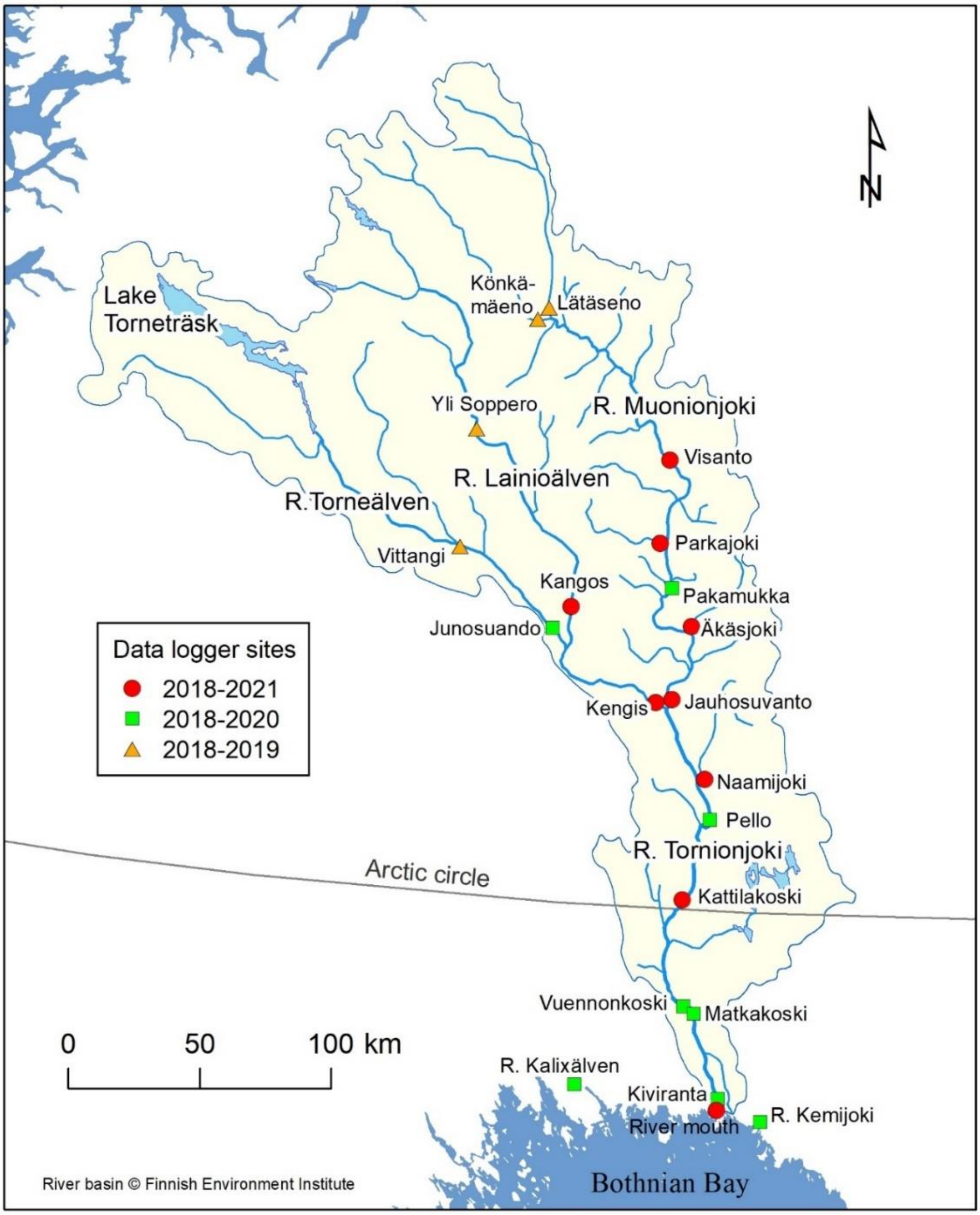

Figure 5. Locations of the automatic data logging stations during the study years 2018–2021.

2.3. Data analysis

2.3.1. Genetic analysis

For salmon, 18 microsatellite markers were analysed. The same markers were used by Miettinen et al. (2021) in their genetic study of salmon in the Torne-Kalix river system, and 17 of the 18 markers are also common to the "pan-Baltic genetic baseline" used for mixed-stock-analyses (MSA) of off-shore and coastal catches of Baltic salmon (e.g., Whitlock et al. 2018; ICES 2021). So-called 'genetic reporting groups' were used in statistical analyses (MSA/IA; below) to handle cases with several spatially and/or temporally separated samples from the same river stock (Fig 6).

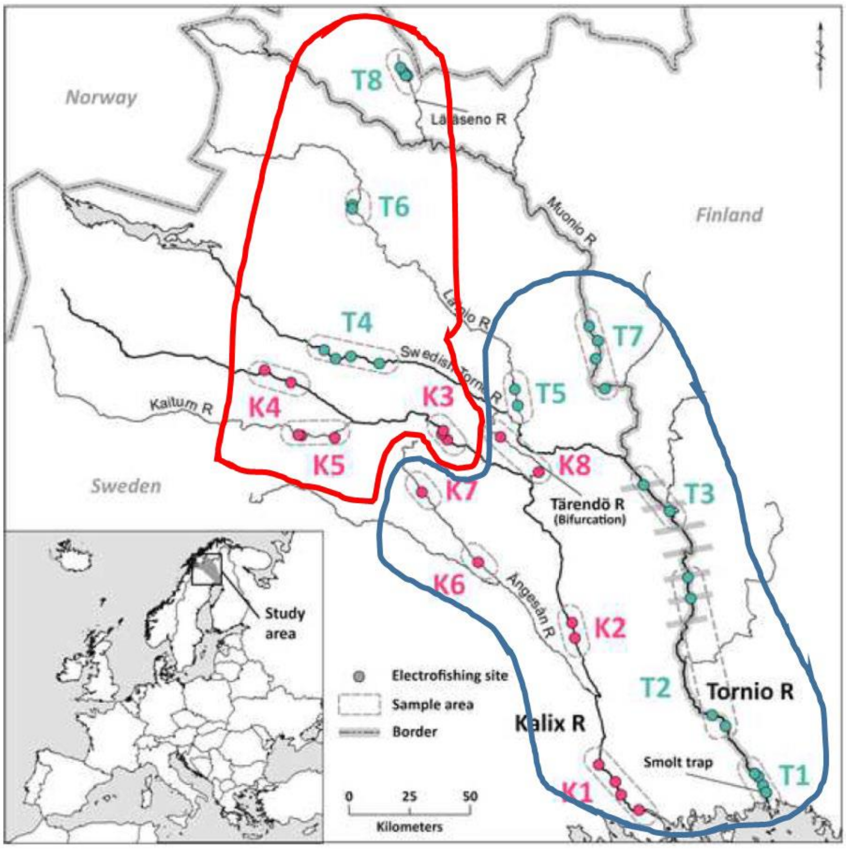

Figure 6. Map of the Torne-Kalix river system (modified from Miettinen et al. 2021) showing 16 local areas (K1–K8 and T1–T8) where parr for genetic analysis (18 microsatellites) were sampled using electrofishing in 2012. The zones marked with red and blue lines depict the headwater (hereafter called "Upper") and the lower-middle reach (hereafter called "Lower") groups of more genetically similar sampling areas (used as a basis when defining four genetic reporting groups: Torne-upper, Torne-lower, Kalix-upper, Kalix-lower). Note that the bifurcation, Tärendö river (K8), is considered as a part of Kalixälven.

For trout, 10 microsatellites were analysed. The same panel was used in a previous genetic study of trout from Tornionjoki river (Palm et al. 2019), and raw data for parr included in that study served as river baseline (with 17 tributaries/areas used as genetic reporting groups; for details, see Palm et al. 2019). The same 10 markers have been used in previous studies of a relatively large number of Swedish wild and hatchery-reared sea trout populations analysed at SLU Aqua. However, there is currently no 'baseline' data from Finnish wild and hatchery-reared populations, and there is no data from many of the smaller tributaries on the Swedish side and as well as from the neighbouring river Kalixälven. Therefore, the geographic 'coverage' of the genetic baseline data for sea trout was not as comprehensive as for salmon.

In total, 300 salmon and 115 sea trout were genotyped during the present study. In addition, four salmon-trout hybrids were genotyped, but these were removed from the statistical analyses and not included the total number of analysed fish. Statistical analyses of data (mixed stock analyses, MSA, and individual assignments, IA) was performed using the ONCOR software (Kalinowski et al. 2008).

2.3.2. Ageing of fish

Ageing was based on annual growth increments recorded from scales with the standard ageing methods (the Finnish scale reading manual edited by Raitaniemi, Nyberg & Torvi 2000). Based on scale reading the 'sea-age' of salmon or trout is determined by the number of winters the fish spend at sea, i.e., sea-winters (SW). Also, spawning migration to the river affects the growth of fish and makes it possible to determine from scales the number of earlier spawning events, and the time spent at sea between spawning events. All ageing was made by an experienced specialist and conducted using prepared scales under microscopes.

2.3.3. Visual condition monitoring of salmon

Salmon was photographed for documentation of their apparent health status and external body condition. Systematic monitoring of the body condition at the estuary covered the years 2020–2021. In addition, most of the salmon tagged at the estuary in 2018–2019 (76% of the salmon in 2018, and 100% in 2019) were photographed and could hence be evaluated for health status at any later time by investigating photos. However, due to incomplete documentation and the fact that tagged salmon had no damage or had only minor damage, the results from 2019 and 2018 are not directly comparable to the health status data collected in the systematic condition monitoring in 2020–2021.

Visual classifications were based on the presence and magnitude of fresh skin damage, including haemorrhage ("redness") located mainly on the skin of the belly and the fins. The severity of skin damage was divided into three groups: (D1) no fresh damage; (D2) minor damage; and (D3) severe damage. In addition, the damages were divided in four types: scale loss, fin damages, marks around the head, and open wound. A single salmon could have damage belonging to multiple categories. Salmon were similarly divided into three groups based on the degree of haemorrhage ("redness"): (R1) no redness; (R2) small amount of redness (redness in the base of fins or small patch on skin); and (R3) severe redness (one or several large red areas on the skin).

2.3.4. Radio-tracking data

Data from both the automatic data logging stations and the manual tracking were combined to create a database containing individual-level location history using Microsoft Office Excel. For each observation, the distance from the river mouth (km; the starting point was the lower-most data logging station, see Fig. 5) was measured using GIS software.

Migration time and average migration speed were calculated based on detection data from the automatic data logging stations. Time spent in the river (hours) was calculated using the first and the last observations from the lowermost automatic data logging station. The detection with the highest signal power of each fish at each data logging station was used for calculating the average migration speed (MS; km/day). In cases there were many detections with the same signal power present, the first detection time was selected.

3. Results

3.1. Salmon

Altogether, 319 salmon were radio-tagged during 2018–2021 (Table 2). The average size of the tagged salmon decreased over time within each year.

The proportion of females among the tagged salmon was higher at the start of tagging in early June (70–90% females) and decreased during the summer, however, the magnitude of the decrease varied between years (Fig. 7). All the salmon tagged in August were males (week 32, Table 2).

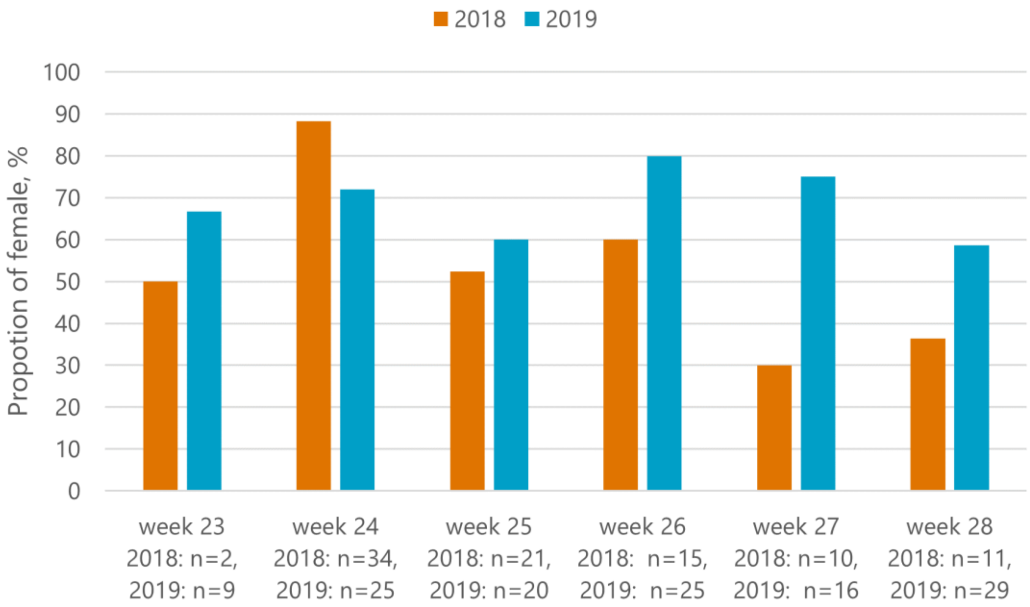

Figure 7. The proportion of females among the radio-tagged salmon 2018-2019 at the estuary by calendar week. In addition, all salmon tagged week 32 in 2019 were males.

Table 2. Weekly amounts of radio-tagged salmon, 2018–2021, and their size (average weight (kg) and average total length (cm) and their ranges (min–max) in parentheses) presented separately for each catch location. Catch locations are shown on the map in

Location	Time	2018		2019		2020		2021	
		n	Size	n	Size	n	Size	n	Size
Estuary									
	Week 23	2	14.8 (14.3-15.3) kg 117 (116-118) cm	9	10.6 (5.0-14.2) kg 98 (81-108) cm				
	Week 24	34	10.1 (5.8-17.3) kg 97 (80-115) cm	25	9.7 (5.0-19.0) kg 95 (80-114) cm				
	Week 25	21	8.9 (5.3-14.5) kg 92 (75-107) cm	20	9.6 (5.5-17.2) kg 95 (79-113) cm				
	Week 26	15	8.5 (6.0-12.4) kg 91 (82-107) cm	25	7.8 (4.0-13.0) kg 91 (73-110) cm				
	Week 27	10	5.2 (1.7-10.1) kg 76 (57-97) cm	16	6.7 (2.4-8.9) kg 87 (62-95) cm				
	Week 28	11	4.2 (1.2-8.8) kg 71 (53-94) cm	29	6.5 (1.3-14.8) kg 84 (52-109) cm				
	Week 32			10	2.2 (1.6-2.4) kg 62 (56-69) cm				
	TOTAL	**93**	8.5 (1.2-17.3) kg 90 (53-118) cm	**134**	7.8 (1.3-19.0) kg 89 (52-114) cm				
River									
Pajala	Early summer	5	9.5 (5.3-13.3) kg 98 (80-113) cm						
Matkakoski	Early summer			4	9.9 (5.5-15.1) kg 99 (84-112) cm	15	10.2 (4.1-16.8) kg 100 (79-116) cm	20	8.5 (4.9-17.3) kg 92 (79-115) cm
Tornio	Autumn	6	5.1 (2.5-8.9) kg 82 (65-98) cm	15	5.2 (2.4-9.0) kg 79 (64-95) cm				
Pello	Autumn	5	3.1 (1.4-6.8) kg 67 (55-89) cm	2	8.0 (7.9-8.0) kg 93 (92-94) cm				
Pajala	Autumn	1	6.6 kg 86 cm						
Kolari	Autumn			9	5.1 (1.8-11.4) kg 77 (58-103) cm	10	7.2 (1.4-15.7) kg 91 (59-115) cm		
	TOTAL	**17**	5.9 (1.4-13.3) kg 83 (55-113) cm	**30**	6.0 (1.8-15.1) kg 81 (58-112) cm	**25**	9.0 (1.4-16.8) kg 96 (59-116) cm	**20**	8.5 (4.9-17.3) kg 92 (53-115) cm

3.1.1. Sea-age structure and genetic origin

Of the salmon tagged in the estuary, most were 2 sea-winter (2SW) old, and the proportion of 3SW salmon was c. 20% in both years (Fig. 8). Among salmon tagged in the river, the proportion of the 3SW salmon was lower in 2018 and 2019 (12 % and 7 %, respectively) than in 2020 and 2021 (20% in both years). This was probably due to different tagging times (early summer vs. autumn) between the years because older salmon migrate earlier: 60% of the salmon (n=15) in 2020 and all salmon in 2021 were tagged in early summer (June). No 1SW salmon were tagged in 2021 as tagging took place only in June. Tagging bias towards spring in 2020 could be the reason for most of the tagged salmon being repeat spawners (Fig. 8). Two salmon tagged at the estuary in 2018 had spent 4 winters at sea before their first spawning migration (Fig. 8).

At the estuary, the first 1SW salmon was caught at the beginning of July in both study years (2018–2019). In the river, 1SW salmon were not caught until autumn (2018–2020).

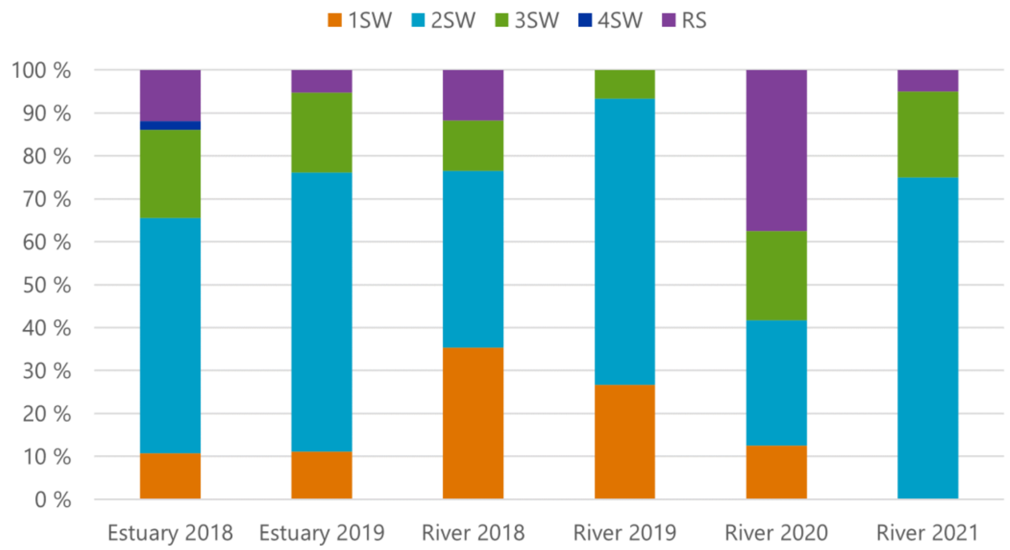

Figure 8. Proportions of sea-ages (1SW–4SW virgin spawners) and repeat spawners (RS) among the radio-tagged salmon.

According to the genetic analyses (MSA and IA using the pan-Baltic baseline), all the tagged salmon most likely originated from the Torne-Kalix river system. Tornionjoki and Kalixälven salmon do not substantially differ from each other genetically, therefore assignment of individuals to specific river origin (Tornionjoki or Kalix river) is rather uncertain. However, within both rivers, salmon from lower and middle reaches (here called ‘lower’) differ genetically from salmon originating from the upper reaches (called ‘upper’) (Miettinen et al. 2021). Using the local Torne-Kalix baseline, the majority of the radio-tagged salmon were assigned to the ‘lower’ river genetic reporting groups (Fig. 6, 9), and among those, most were assigned to the sub-group ‘Torne lower’ (rather than ‘Kalix lower’; Fig. 9). In total, only c. 14% of the tagged salmon were assigned to the ‘upper’ genetic reporting groups, i.e., they most likely originate from the headwater rivers of the Tornionjoki-Kalix river system (Fig. 6, 9).

The results from IA showed that most of the tagged salmon had a low individual assignment score (highest probability of belonging to the respective groups). Only 103 (c. 34%) of the 300 radio-tagged salmon had an assignment probability >0.9. Of those, 87 (84.5%) were assigned to the 'Torne lower', whereas only 7 (6.8%) were assigned to the 'Torne upper'. Nine salmon (8.7%) were assigned with a higher probability (>0.9) to the two 'Kalix groups'.

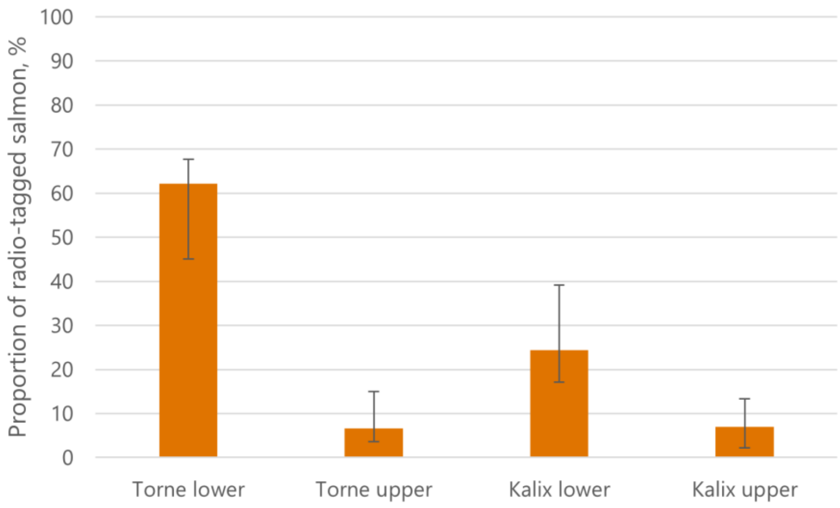

Figure 9. Estimates from genetic mixed stock analysis (MSA) of the relative origin (proportions with 95% confidence intervals) of radio-tagged salmon (n=300) using a division into four genetic reporting groups (for details, see text and Miettinen et al. 2021).

3.1.2. Visual condition

In 2020 and 2021, on average 42% of the salmon had external visual damages (Table 3). Fin damages and scale losses were the most common damage categories in both years. The extent of redness differed between years; 29% and 19% of the monitored salmon had redness in 2020 and 2021, respectively (Table 3). In both years, redness covered most often only small areas of the head/belly or fins (redness group R2, Table 4). 27% of salmon in 2020 and 20% of salmon in 2021 salmon had both visual damage and redness (Table 4).

Table 3. Number and average size (average total length, cm, average weight, kg, and their ranges) of monitored salmon in 2020–2021, and number and percentage of salmon which had redness (R, groups R2 and R3) or damage (D, groups D2 and D3).

	2020				2021			
	n	Size	R	D	n	Size	R	D
Week 23-24	10	93 cm (72-113) 9.2 kg (3.2-16.7)	4 (40%)	4 (40%)	74	88 cm (74-110) 7.0 kg (4.0-14.5)	11 (15%)	33 (45%)
Week 25	29	87 cm (68-108) 7.0 kg (3.1-12.2)	7 (24%)	9 (31%)	40	90 cm (78-111) 7.3 kg (4.2-14.3)	8 (20%)	22 (55%)
Week 26	23	86 cm (60-107) 7.0 kg (2.1-14.0)	8 (35%)	10 (43%)	85	87 cm (50-112) 6.7 kg (1.1-13.0)	20 (24%)	30 (35%)
Week 27	35	76 cm (56-93) 5.1 kg (1.9-9.6)	7 (20%)	11 (31%)	6	90 cm (86-95) 7.6 kg (6.6-9.6)	1 (16%)	2 (33%)
Week 28	16	75 cm (56-115) 4.7 kg (1.8-16.5)	3 (19%)	10 (62%)	7	76 cm (51-95) 4.9 kg (1.5-9.6)	1 (14%)	2 (29%)
Week 29-30	13	62 cm (55-82) 2.4 kg (1.7-5.1)	8 (62%)	9 (69%)				
TOTAL	126	80 cm (53-115) 5.9 kg (1.7-16.7)	37 (29%)	53 (42%)	212	88 cm (51-112) 6.8 kg (1.1-14.5)	41 (19%)	89 (42%)

Table 4. The number of salmon (and percentage from all) divided into different redness groups (R1=no redness, R2 = minor, R3= redness) and damage groups (D1= no damage, D2= minor, D3= damage) in monitoring years 2020 and 2021.

2020					2021				
	R1	**R2**	**R3**			**R1**	**R2**	**R3**	
D1	70 (56%)	3 (2%)	0	**73 (58%)**	**D1**	123 (58%)	0	0	**123 (58%)**
D2	9 (7%)	17 (14%)	1 (1%)	**27 (21%)**	**D2**	22 (10%)	15 (7%)	0	**37 (17%)**
D3	10 (8%)	13 (10%)	3 (2%)	**26 (21%)**	**D3**	26 (12%)	25 (12%)	1 (1%)	**52 (25%)**
	89 (71%)	**33 (26%)**	**4 (3%)**	**126**		**171 (81%)**	**40 (19%)**	**1 (0%)**	**212**

3.1.3. Behaviour and migration speed of salmon tagged at the estuary

Most of the salmon tagged at the estuary (66% in 2018 and 85% in 2019) were detected by the lowermost automatic data logging station, located at the Tornionjoki river mouth (Fig. 5). The median detection time after the release at this data logger was 32 hours (range 4–839 h).

After entering the river, two rather distinct behaviour patterns could be observed: salmon either (1) stayed in the river only a short time and returned to sea during the summer (Fig. 10), or (2) migrated actively to the spawning areas and usually overwintered in the river (Fig. 11). Most radio-tagged salmon (61% in 2018 and 83% in 2019) displayed the first behaviour pattern, i.e., returned to the sea by the end of July (Fig. 10). However, in 2018, salmon stayed longer time in the river (on average 176 h; range 1–438 h) and migrated further upstream (on average 30 km; range 1–140 km) compared to 2019 (on average 90 h; range 9–525 h and migrated on average 10 km; range 1–100 km). In both years, most of the salmon displaying the first behaviour pattern were females (75 % in 2018 and 67 % in 2019). Salmon that stayed in the river until spawning time migrated further upstream in the year 2018 (on average 120 km) than in 2019 (on average 60 km; Fig. 11).

In 2018, nine salmon migrated above the Kattilakoski sonar counting site (which is located 100 km from the river mouth) and migration from the river mouth (lowermost automatic data logging station) to Kattilakoski took on average 15 days (median 8 days, range 4–90 days). Most of the salmon which migrated upstream from Kattilakoski in 2018 were 2SW–3SW males (67%) with a median migration time of 11 days (range 5–90 days) and a median migration speed 10 km/day (range 1–19 km/day). The large variation in migration times of these males was due to two males who stayed on the lowermost part of the river over summer and finally migrated upstream to the spawning areas in August–September. In 2018, only one 1SW salmon migrated upstream from Kattilakoski. This individual displayed the fastest migration of the entire study (4 days from the river mouth to Kattilakoski, 25 km/day). In 2019, no multi-sea-winter salmon migrated above Kattilakoski, however, three 1SW salmon did. The migration time of these fish from the river mouth to the Kattilakoski was between 14–36 days (average migration speed 5 km/day).

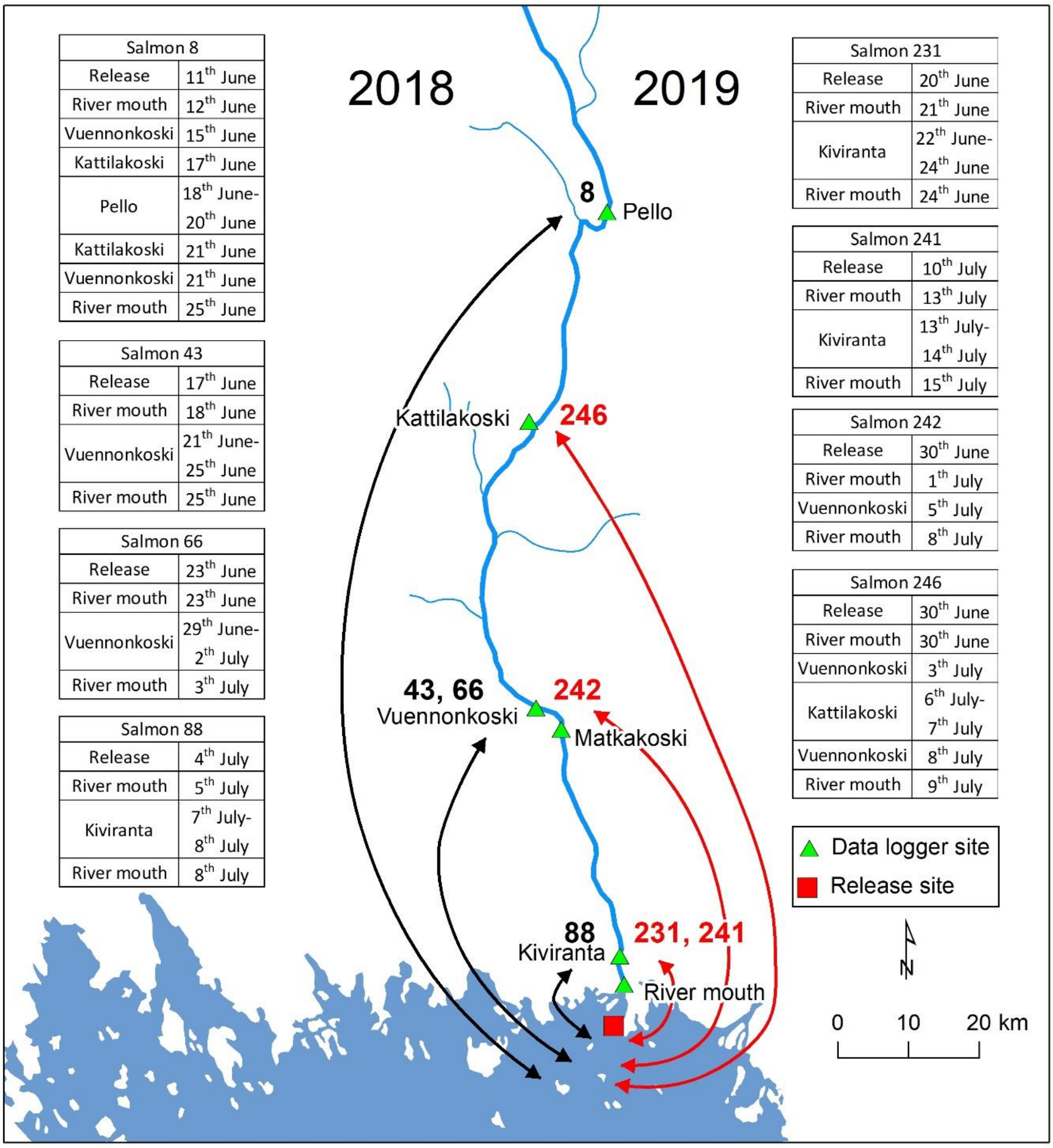

Figure 10. Examples of salmon tagged at the estuary in 2018–2019 and displaying a typical category 1 migration behaviour (i.e., staying in the river for only a short time and returning to sea during the summer).

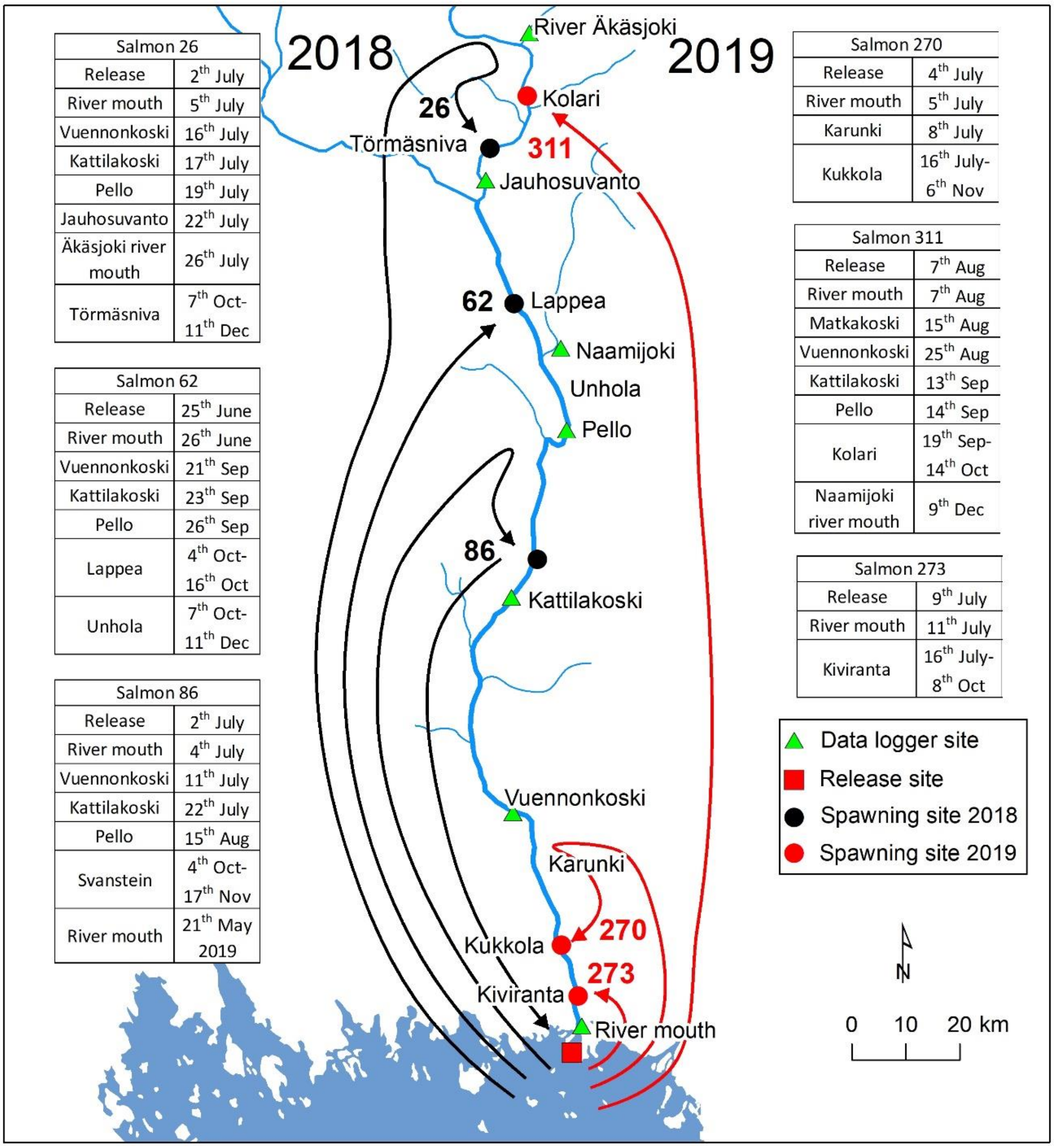

Figure 11. Examples of salmon tagged at the estuary in 2018–2019 and displaying a typical category 2 migration behaviour (i.e., migrating actively to the spawning areas and typically overwintering in the river).

3.1.4. Behaviour of C&R salmon

Salmon which were caught in the river by recreational fishing methods potentially enable evaluation of the post-release effects of ‘catch-and-release’ (C&R) type of fishing. The results of the behaviour and survival of these salmon can increase our understanding of the sustainability of C&R fishing. However, as the salmon in the study also were exposed to radio-tagging and related extra handling, estimates of survival and behaviour of these fish should be considered as comparable to salmon released normally in the C&R fishing.

Salmon tagged in the river after being caught by angling displayed highly varying post-release behaviour. In 2018 and 2019, all the salmon tagged during early summer (n = 9; Table 2) moved downstream after release (Fig. 12). Most of these salmon descended to the sea

(70%), however, three salmon (30%) died during the downstream movement. The results from the early summer tagging in 2018 and 2019 were similar, although the tagging locations and the fishing methods differed between years. A large percentage of salmon tagged in spring 2020 and 2021 also descended downstream after tagging (2020: 40% and 2021: 65%), however in both these years some of the tagged salmon also moved upstream after release. Only three salmon in 2020 and five salmon in 2021 stayed alive until the spawning period (Table 5, Fig. 12). The remaining salmon either disappeared from the detection range or died (as determined by being detected at the same location throughout the rest of the study). In contrast, most of the autumn-tagged salmon stayed near the release location, but some up- or downstream movements were also observed before the spawning period (Fig. 13).

In 2019, four of the salmon tagged in October had silvery colour, indicating that they had entered the river late in the season. Two of them migrated upstream in spring 2020 and two of them returned to the sea (Fig. 14). One of the upstream migrating individuals presumably spawned in the Lainio river during autumn 2020 (Fig. 14).

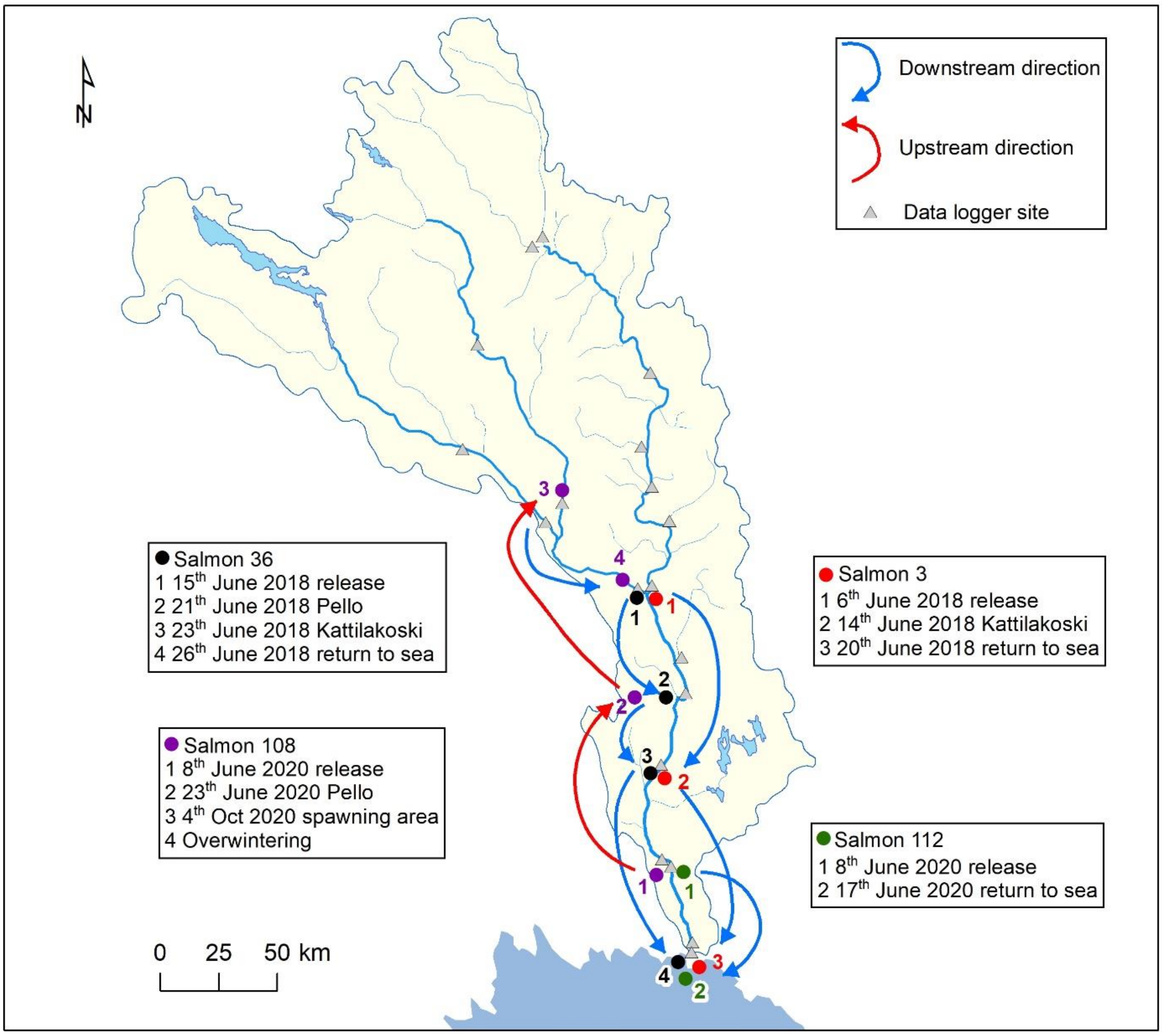

Figure 12. Examples of typical post-release migration behaviour of tagged salmon caught by angling in the river during early summer.

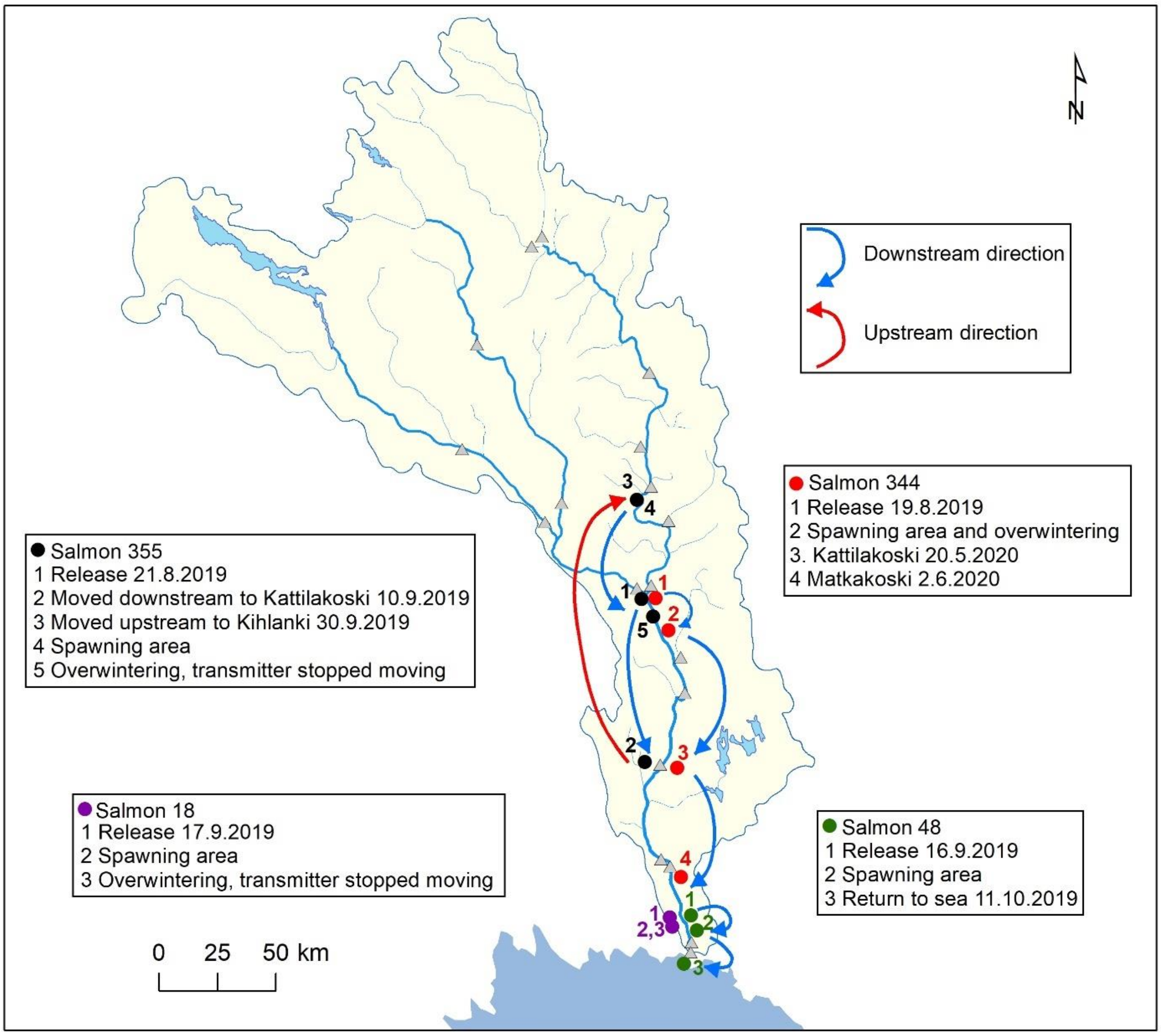

Figure 13. Examples of typical post-release migration behaviour of tagged salmon caught by angling in the river during autumn.

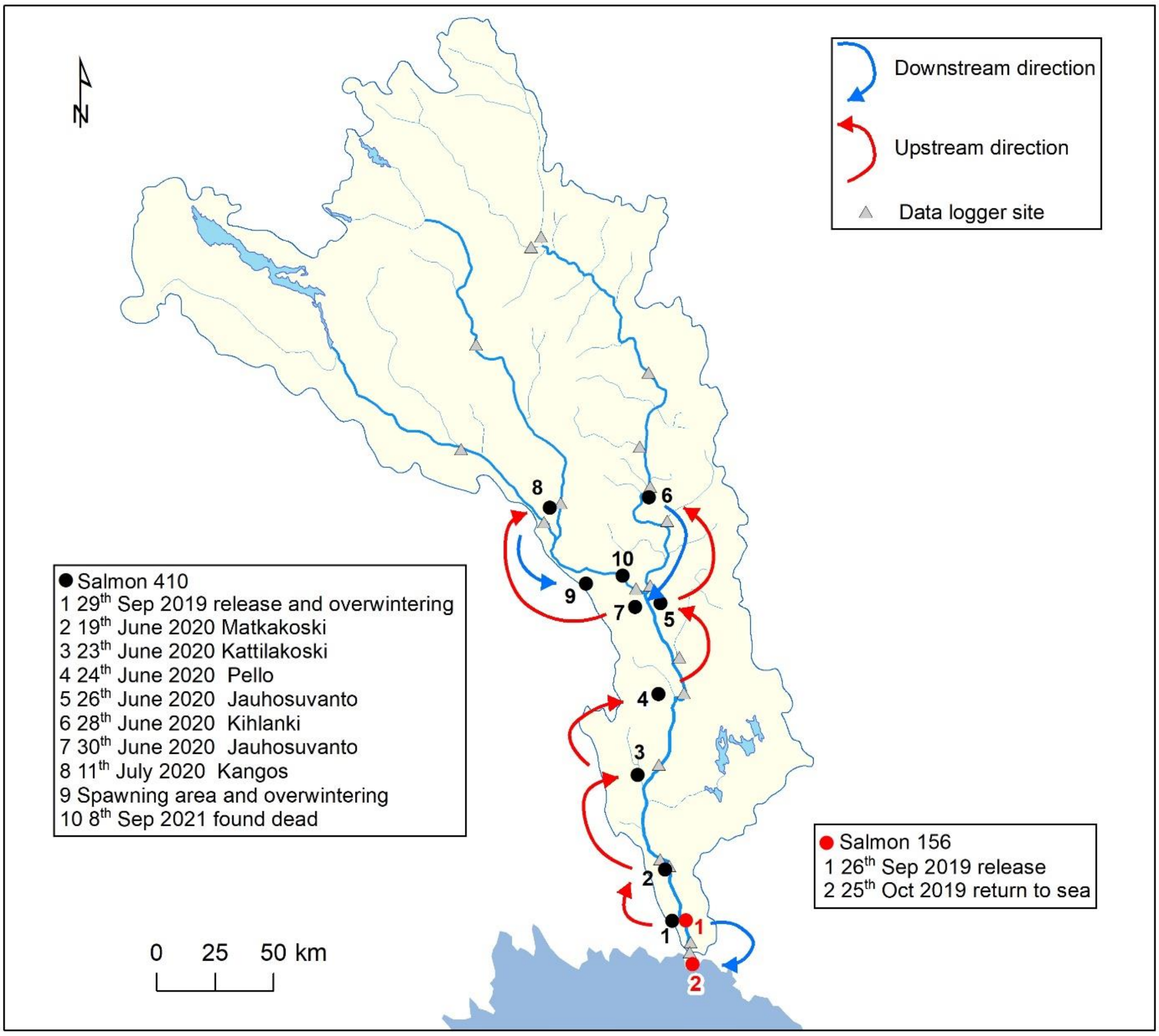

Figure 14. Examples of two migration behaviour displayed by the 'silvery' salmon (i.e., presumed to have entered the river late in the season) tagged in autumn 2019.

3.1.5. Spawning areas and behaviour after spawning

About half of all the tagged salmon was found on the lower part of the river during the spawning time (late September-early November) (Table 5). Most often they were found on the lowermost 50 km river stretch.

Only one-third of the salmon tagged at the estuary migrated upstream from Kattilakoski (Table 5, Fig. 15). Most of the salmon that passed Kattilakoski were detected around the Pello area at the spawning time (Fig. 15). No salmon tagged at the estuary were observed to enter the Swedish Torneälven. All salmon which were tagged at the estuary and migrated above Kattilakoski belonged most likely to the 'Torne lower' genetic reporting group (which extends relatively high upstream in the river; Fig. 6). The average sea age of these salmon did not differ from the average sea age of salmon which stayed on lowermost river until spawning time.

A majority of the salmon tagged in the river during autumn stayed relatively close to their catching and tagging site over the spawning period (Table 5, Fig. 15). Most of these salmon were found between Pello and Kolari or near Tornio. Five salmon tagged in Matkakoski during early summer 2020–2021 migrated to the Swedish Torneälven or its tributary Lainio in autumn (Fig. 15). According to genetic IA-analysis, one of these salmon belonged most likely (assignment prob.=0.48 to the 'Kalix upper' reporting group and the rest belonged most likely to the 'Torne lower' group (assignment probs. ranging from 0.35 to 0.79). One silver-coloured salmon tagged in the autumn (2019) was detected in the Lainio river in autumn 2020 (Fig. 14–15). This salmon belonged most likely to the 'Torne lower' reporting group (assignment prob.=0.75) and was a 2SW virgin spawner. Thus, despite its extraordinary migration behaviour (spawning migration extended over two migration seasons), this individual did not appear to differ in these respects from most other Tornionjoki salmon.

After the spawning period, most of the salmon (kelts) started to move slowly downstream but stayed in the river until the next spring. In spring, these kelts arrived at the river mouth between mid-May to mid-June. However, 50% of the salmon which had their potential spawning sites in the lowermost reach of the river returned to sea already before April. Altogether, 27% (range between years 7–36%) of the tagged salmon, which were assessed to be alive during the spawning period, survived back to the sea after spawning. The proportion of the surviving salmon varied between years (Table 5).

Table 5. Number of salmon in the river during the spawning period and the number of salmon returning (surviving) to the sea after spawning, years 2018–2021.

	Year			
	2018	**2019**	**2020**	**2021**
Presumed spawning				
Tagged at estuary	16	11		
Tagged in river	12	21	14	4
TOTAL	28	32	14	4
Returning to sea				
Tagged at estuary	5 (31%)	0		
Tagged in river	5 (42%)	9 (43%)	1 (7%)	?
TOTAL	10 (36%)	9 (28%)	1 (7%)	?

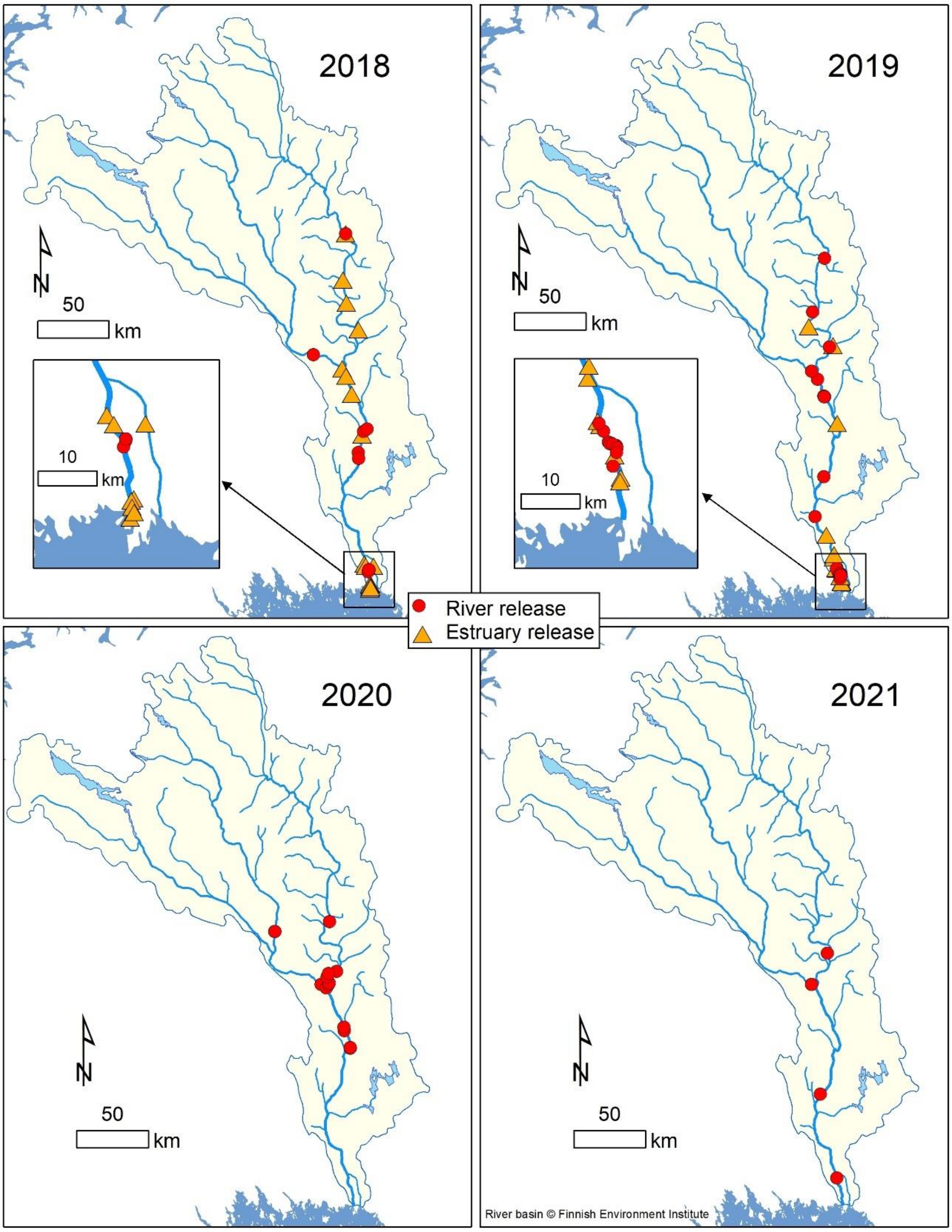

Figure 15. Locations of salmon during spawning time 2018–2021 (tagging sites are shown by different colour symbols).

3.2. Sea trout

Altogether, 113 trout were tagged in the river during 2018–2020 (Table 6). In addition, two sea trout were tagged at the estuary in 2018 (29th June: 62 cm, 3.3 kg, and 9th July: 54 cm, 1.8 kg), but they were not detected in the river during the study. The average size of tagged sea trout was similar between years (average weight 2.3 kg, 2.5 kg, 2.2 kg and average length 58 cm, 60 cm and 59 cm in 2018, 2019 and 2020, respectively).

Table 1. The number and average size (weight and total length, range min-max in parenthesis) of tagged trout in the river in 2018–2020 by location and tagging period (Early summer = May-June, Autumn = August-October).

Location	Tagging time	2018		2019		2020	
		n	Size	n	Size	n	Size
Tornio	Early summer			25	2.2 kg (2.2-5.7 kg) 59 cm (48-82 cm)	13	2.1 kg (1.1-3.3 kg) 59 cm (49-70 cm)
	Autumn	14	2.0 kg (1.1-4.7 kg) 56 cm (48-74 cm)	41	2.5 kg (1.1-5.5 kg) 60 cm (50-74 cm)	10	2.4 kg (1.4-3.5 kg) 59 cm (52-67 cm)
Matkakoski	Early summer			2	2.2 kg (2.0-2.3 kg) 61 cm (59-62 cm)		
Pello	Early summer	3	3.5 kg (1.5-5.2 kg) 68 cm (54-79 cm)				
	Autumn			1	2.2 kg 61 cm		
Äkäsjokisuu	Early summer			4	3.5 kg (1.9-6.5 kg) 70 cm (62-85 cm)		
	TOTAL	17	2.3 kg (1.1-5.2 kg) 58 cm (48-79 cm)	73	2.5 kg (1.1-6.5 kg) 60 cm (48-85 cm)	23	2.2 kg (1.1-3.5 kg) 59 cm (49-70 cm)

3.2.1. Sea-age structure and genetic origin

Scale analysis showed that 27 (24%) of the tagged sea trout were repeat spawners and 70% of these had spawned once before tagging. 46 of the tagged trout were observed to return for spawning at least one time in the following years after tagging. When one combines the scale analysis results and the observed spawning times after the tagging, a few trout in the study could be concluded to have likely spawned as many as four times. The average length of the repeat spawners was 66 cm, but the variation was large (range 51–85 cm). Trout, which had not spawned before tagging (average length 57 cm, range 48–72 cm), were mostly caught and tagged near the river mouth (Tornio). Most of the trout (63%), which were tagged further up in the river were repeat spawners.

Genetic analysis (MSA and IA) using the geographically larger baseline showed that all the radio-tagged sea trout originated from the Tornionjoki river system with high probability. According to MSA and using the river-specific baseline, around 40% of the tagged trout originated from the Äkäsjoki tributary, followed by Parkajoki (c. 23%) and Naamijoki (c. 19%), whereas the remaining groups had lower point estimates (<10%) with confidence intervals including zero (Fig. 16). Also, the individual assignment results (IA) showed that about half of the individuals most likely originated from the Äkäsjoki tributary (57 out of 115 individuals), followed by the Parkajoki and Naamijoki tributaries. A few trout were assigned to Yl. Kihlankijoki, Niesajoki and Pakajoki. However, most of the tagged sea trout had a low individual assignment score (probability of belonging to a certain group); only 30 (c. 26%) of them had a probability >0.9 of being assigned correctly to their group. Of these individuals with a high assignment probability, 13 were assigned to Äkäsjoki, 8 to Naamijoki, 5 to Parkajoki, 3 to Yl. Kihlankijoki and 1 to Niesajoki tributary, which is in line with MSA-results (Fig. 16).

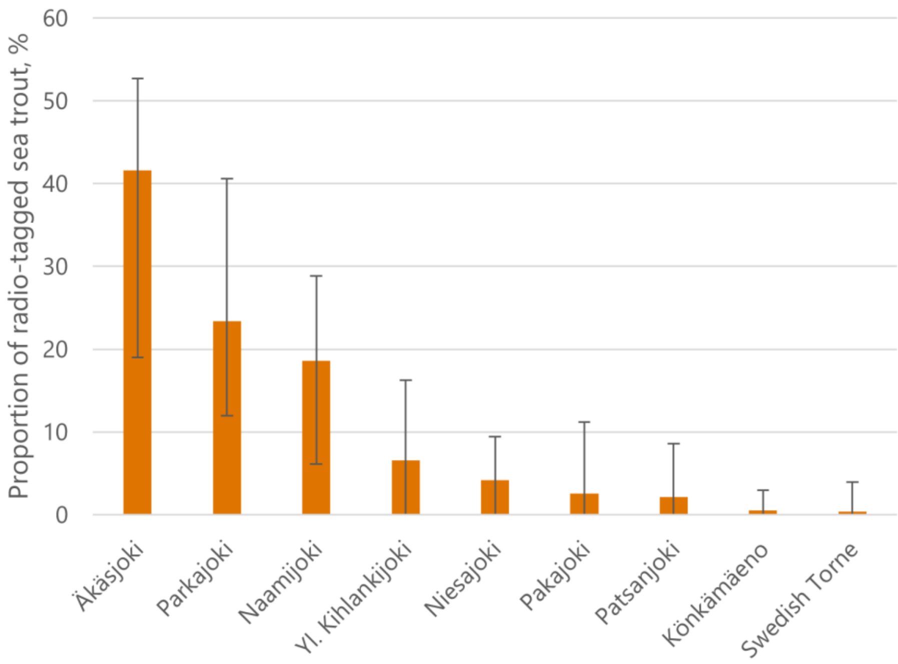

Figure 16. Estimates from genetic mixed stock analysis (MSA) of the relative origin (proportions with 95% confidence intervals) of radio-tagged sea trout (n=115) using 17 genetic reporting groups (for details, see text and Palm et al. 2019). Only results for the nine groups with point estimates >0 is shown.

3.2.2. Behaviour

Based on the data, sea trout in the river can be categorized into two main groups: 1) non-mature trout overwintering in the lowermost reach of the river, and 2) 'maturing trout' ascending the river for spawning (i.e., trout did not leave freshwater until they spawned).

The overwintering area of immature trout is located in the lowermost part of the river 10–20 km upstream from the sea. The average size of non-mature tagged sea trout was 56 cm (range 48–68 cm) and 1.8 kg (range 1.1–3.5 kg). However, it is important to note that many sea trout too small to be tagged were caught at the lowermost reach of the river during the fishing for tagging; these individuals were likely also non-mature and overwintering in the river. Minor movements of trout were observed within the overwintering area during the winter. After overwintering, trout returned to the sea typically between the end of May and mid-June (range 13th April–24th June) (Fig. 17–18). The median date of returning to the sea was slightly different between the springs (25th May in 2019 vs. 3rd June in 2020; Fig. 17). Some of these individuals returned to the river the next autumn and returned to the sea again or continued upstream for spawning after the second overwintering.

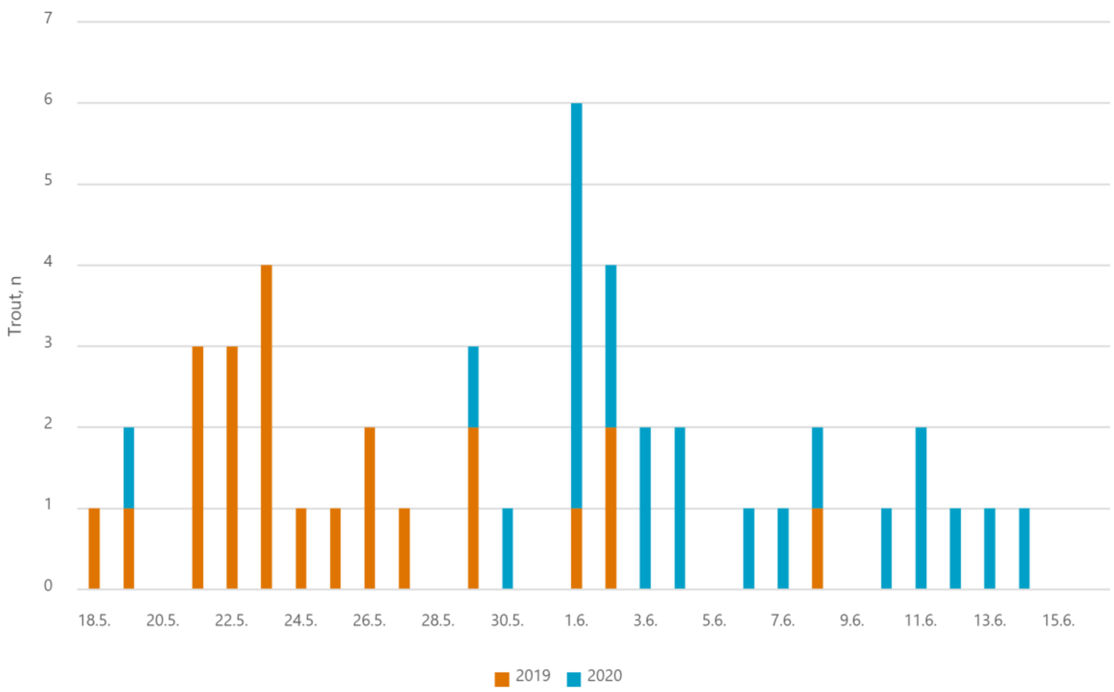

Figure 17. Returning days to the sea after overwintering of immature trout during the springs 2019 and 2020.

The average size for the maturing trout was 62 cm and 2.7 kg. As a rule, maturing trout migrated to the river during autumn one year before spawning, stayed on the lowermost section of the river or moved some distance further upstream for overwintering, continued the migration to spawning areas in the following spring, assumingly spawned (the telemetry data as such does not indicate, however, if spawning took place) in the autumn, overwintered in the river after the spawning, and returned to the sea in the spring (Figs. 18–20).

The maturing trout which overwintered in the river normally dwelled in the same spots on the lowermost river section as the overwintering immature trout. Only five trout migrated above Kattilakoski for overwintering. After winter they continued their spawning migration between late May and mid-June. Some of the trout swam directly to a spawning tributary, but others spent their summer near the mouth of a tributary and visited the tributary only for a short period in autumn (Fig. 18). Five trout were observed to return to spawn a second time within the lifetime of the transmitter. All these trout migrated to spawn in the same tributary in which they had spawned the first time (Figs. 18–20).

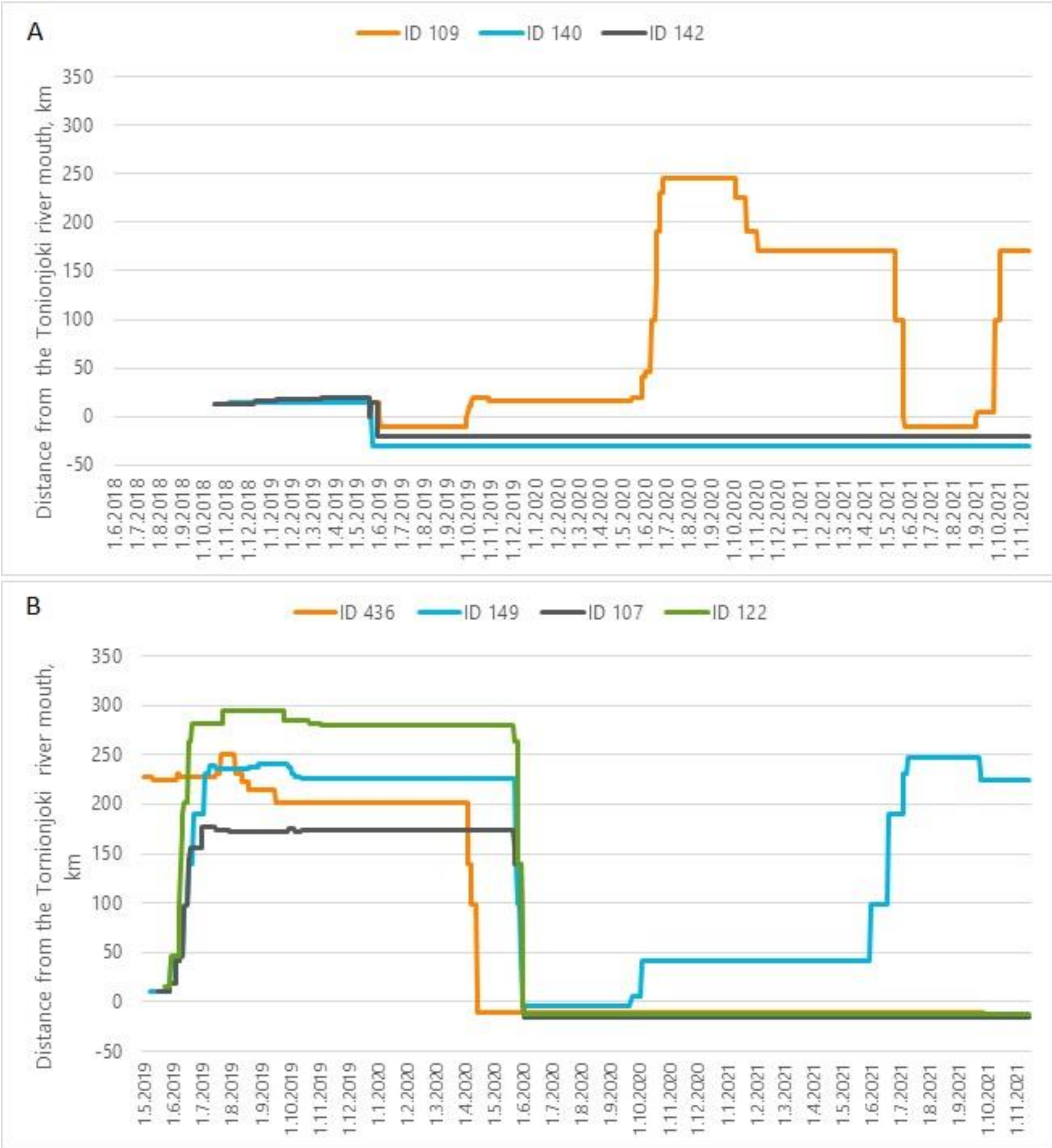

Figure 18. Sea trout movements visualized by the distance from the Tornionjoki river mouth. A) examples of two immature trout that overwintered in the lowermost reach of the river after tagging (blue and black lines), and one individual (orange line) which overwintered, returned to the sea in spring 2019, returned to the river following au-tumn, again overwintered, and then migrated into the Äkäsjoki tributary and spawned in 2020, overwintered in the river, and finally descended to the sea in the springtime, and ascended to the river again in autumn 2021; B) typical examples of spawning migrations of maturing trout. The straight lines below value 0 of the Y axis represent the period when the trout have been staying at sea (without any spatial data of their locations at sea).

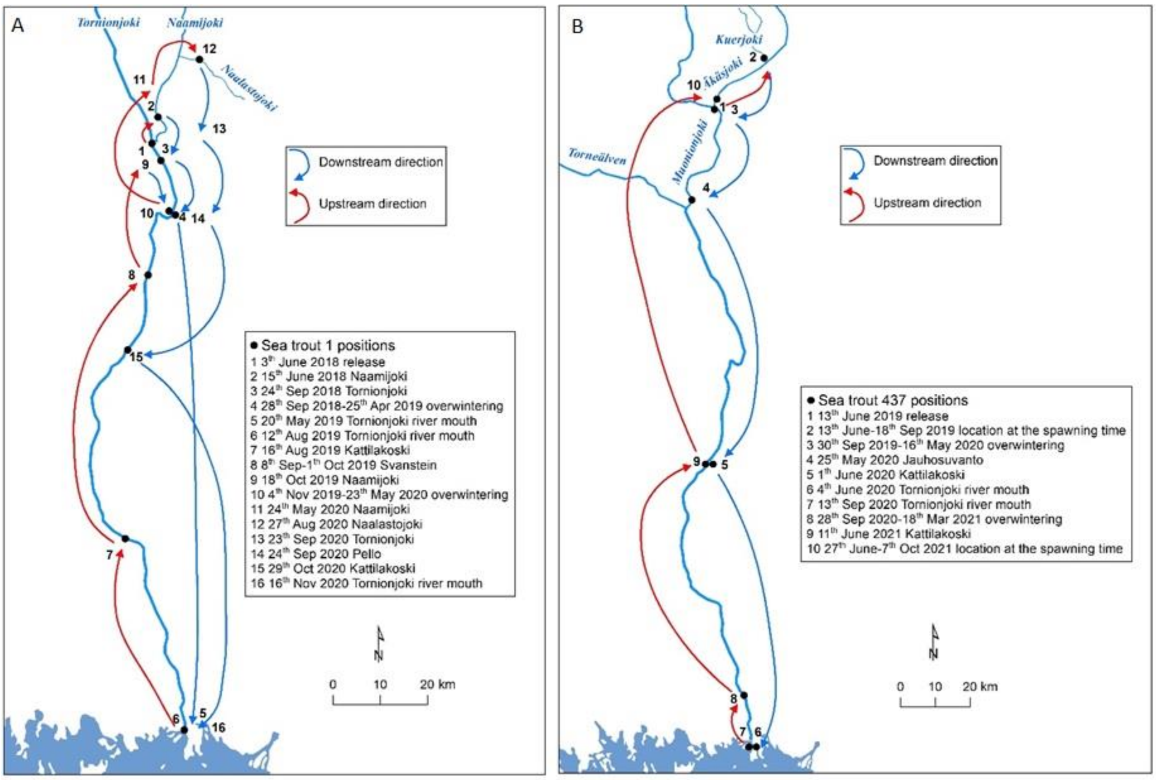

Figure 19. Examples of sea trout movements which tagged in spring around the Pello-Kolari. A) Movements of sea trout which tagged and released at the mouth of the Naamijoki tributary; B) movements of sea trout released at the mouth of the Äkäsjoki tributary.

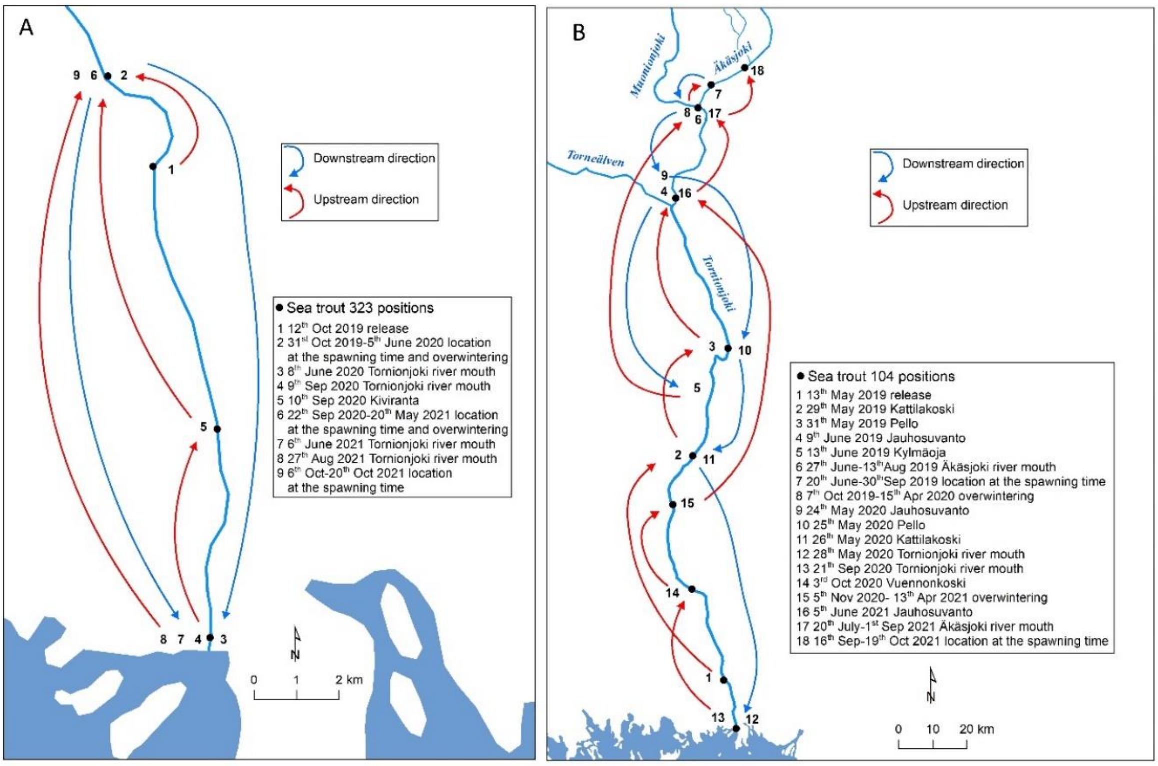

Figure 20. Movements of sea trout tagged in the lowermost section of the river Tornionjoki. A) Movements of immature sea trout which returned to the sea after overwintering; B) mature sea trout continued the spawning migration after overwintering.

3.2.3. Spawning areas and behaviour after spawning

During the spawning period (end of August to end of September) trout were found in the tributaries Naamijoki, Äkäsjoki, Pakajoki, Parkajoki and Merasjoki as well as in the main stems of Tornionjoki, Swedish Torne and Muonionjoki (Fig. 21). Many of the trout which were found in the main stems were residing near outlets of small tributaries. As these fish were tracked manually (there were no passive tracking stations next to these places), temporal gaps (typically 5–9 days long) in detections occurred. It is therefore possible that during these gaps the trout visited small tributaries for only a short period for spawning and therefore the visits did not become documented. One proof of this kind of behaviour was documented by a temporarily installed automatic receiver in the tributary Pakajoki, which recorded one sea trout making a brief trip (only a couple of days) to the tributary in the autumn of 2020. This sea trout spent time in the Muonionjoki main stem close to the Pakajoki river mouth both before and after its visit to the tributary.

After spawning, most of trout overwintered in the main stems within varying distances downstream from the spawning tributary. A minority stayed in the spawning tributary over the winter and this behaviour was documented to occur only in the largest tributaries (Naamijoki, Äkäsjoki and Parkajoki). Only one trout was observed to return to the sea during the same autumn as it spawned. A few individuals (a minority) likely died after spawning.

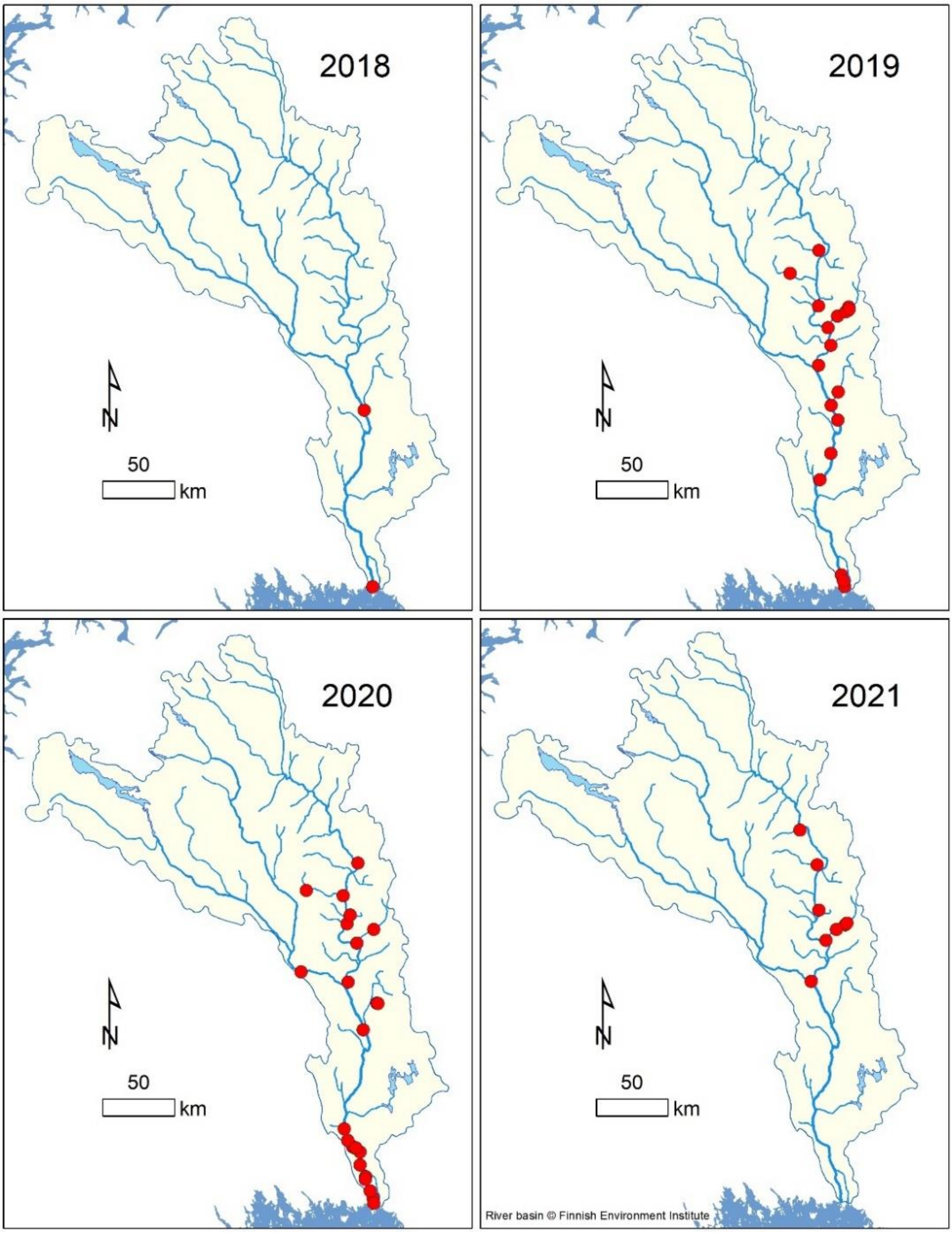

Figure 21. Locations (red circles) of sea trout during the presumed spawning period in years 2018–2021. Note that the individuals staying on the lowermost river (or in some cases further up in the main stem, see previous sections) were overwintering and presumably not spawning.

3.3. Trout-salmon hybrids

One fish tagged in spring 2019 and three fish tagged in autumn 2019 had visual characteristics of both trout and salmon (Fig. 22). The genetic analysis confirmed that these fish were trout-salmon hybrids. Their average size was 71 cm and 3.8 kg (Table 7).

One hybrid tagged in early summer returned to the sea after tagging (Table 7). All the hybrids tagged in autumn overwintered near Tornio in the same area as the overwintering sea trout and two of them returned to the sea in the spring of 2020 (Table 7). However, one hybrid migrated upstream and stayed in the tributary Lainio river during the autumn of 2020. The tag stopped moving during the winter of 2020–2021, indicating that the fish had likely died.

Figure 22. Photographs of two trout-salmon hybrids that were radio-tagged in 2019.

Table 2. Release days, sizes, and basic behaviour information of radio-tagged trout-salmon hybrids.

ID	Release day	Size	Return to sea	
120	24th May 2019	91 cm 6.9 kg	May 2019	August 2019: returned to the river and stopped moving during winter
423	20th September 2019	60 cm 2.3 kg		July 2020: Kattilakoski August 2020: Swedish Torne August 2020: Lainio river (Kangos) October 2020: returned to Swedish Torne and stopped moving during winter
407	1st October 2019	68 cm 3.5 kg	June 2020	
333	8th October 2019	64 cm 2.5 kg	spring 2020	

3.4. Radio-tagged fish vs. echo sounding at Kattilakoski

Data sets of the automatic listening station and the echo sounders at Kattilakoski were compared to examine if tagged fish became detected by the echo sounders when they passed the site. The alignment of the telemetry detection data and the echo sounder data proved challenging, as there were often many fish of approximately the same size passing the echo sounder site at the same time as the radio-tagged fish. Validating that a tagged fish was detected (because it was not known if one of the fish was the tagged one) on the echo sounder was hence difficult. However, in 13 cases, downstream migrating radio-tagged fish were concluded to have passed Kattilakoski at a specific time during which no downstream moving fish could be detected on the echo sounder. This result indicates that the echo sounding does not always detect downstream moving fish, and therefore the number of descending fish may become underestimated.

4. Discussion

In the following sections we discuss the results in light of the listed study objectives (see Section 1.1). We discuss salmon and sea trout separately, mainly because of the marked differences between the species-specific results.

4.1. Salmon

Do apparently sick salmon display different migration behaviour than salmon which appear healthy?

The salmon tracking results contain several very unexpected observations and to date, these observations cannot be explained in any other way than by concluding that most of the tagged salmon did not represent the normal spawning migration behaviour of Tornionjoki salmon. As discussed later, this abnormal behaviour may be best explained by the simultaneously occurring health problems among Tornionjoki salmon. Because of the essential influence of this factor in the salmon tracking results, we start the discussion by focusing on this topic.

A majority (61–83%) of the tagged salmon returned to the sea during the summers of 2018 and 2019, which is an abnormal behaviour for salmon. Most of these fish were tagged at the estuary and, concerningly, most of these were females. In both years, observations of abnormally behaving and dead salmon were also reported by fishermen in the Tornionjoki river which have been linked to health problems (Envira 2017). Thus, the abnormal behaviour of tagged fish observed in this study is likely also connected to the described health problems of salmon. The extra stress due to handling in conjunction with catching and tagging could further contribute to salmon giving up their spawning migration and reproduction. This appears evident because assuming that also among the untagged salmon a large majority of them would not have reached the Kattilakoski counting site, a calculation about the total spawning run of Tornionjoki salmon at the river mouth would result in an unrealistic high amount of salmon.

A similar type of behavioural change, salmon returning to the sea during summer, has been reported concurrently from River Umeälven, where the migration success of salmon through a fishway has been followed since the 1990's using telemetry (Vikström et al. unpublished). More details of the unusual behaviour of Tornionjoki salmon and the likely related health problem among salmon are discussed in the interim report of this study (Huusko et al. 2020), as well as in the annual stock status reports of Tornionjoki (e.g., Palm et al. 2022) and by ICES WGBAST (e.g., ICES 2021). The pathogenesis and aetiology of these health problems remain unknown, and their prevalence varies across salmon rivers (Weichert et al. 2020, ICES 2020). Redness in the skin has been reported as an early symptom, and in our study, 19–29% of the salmon caught at the estuary displayed such symptoms. Although no clear population-level effect has yet been reported (Palm et al. 2022), it is worrying that a considerable proportion of the tagged salmon in our study aborted migration and spawning, and hence did not contribute to the reproduction. Tracking the migration behaviour of salmon using telemetry may help managers to get an early warning of health problems in the population (Vikstrom et al. unpublished), and one should consider including telemetry in monitoring programs for the

Tornionjoki river at least in regular intervals to obtain comparative data from the river migration success of salmon and trout and to find out e.g., behaviour at sea.

The widely observed abnormal migration behaviour in our study makes identification and description of ‘normal salmon migration’ difficult, as reflected in the discussion below. However, there were also seemingly normally behaving salmon which were tagged at the same time and with the same method, which indicates that not all the salmon had serious health problems.

We did not find any indices that ‘apparently sick’ salmon (individuals with skin lesions and/or poor performance in the holding tank at tagging) would have later behaved abnormally more often than the ‘apparently healthy’ salmon: many ‘apparently healthy’ individuals left the river before spawning, while several individuals with various external symptoms when tagged stayed in the river until spawning time. However, the individuals which had serious external lesions or were not able to orient themselves (keep an upright position) or otherwise appeared very tired, were not tagged. That is, our data is somewhat biased towards ‘apparently healthy’ salmon. Nevertheless, our results point towards an inability to detect salmon individuals with health problems based on their external qualities.

Where in the Tornionjoki river system do salmon with different genetic signatures and biological characteristics spawn?

Miettinen et al. (2021) found that Tornionjoki salmon genetically belonging to the ‘upper’ group ascend the river earlier than salmon belonging to the ‘lower’ group. Since the reproduction area of the ‘upper’ group is much smaller than that of the ‘lower’ group (which covers both the lower and the middle reaches of the river system; Fig. 6), it is expected, and also shown by the MSA results, that only a small proportion of the radio-tagged salmon belonged to the ‘upper’ group. A substantial proportion of these fish was caught and tagged in early summer in the river, at approximately the same time when trapnet fishing was started in the river mouth. Thus, it seems likely that a large proportion of the ‘upper’ Tornionjoki salmon had already entered the river before tagging was started at the river mouth.

The low spatial genetic resolution (only two genetic sub-groups in the river and generally low assignment probabilities), the low number of tagged fish most likely belonging to the ‘upper’ group and, finally, the widely aborted spawning migration undermined possibilities to properly describe how genetic origin is related to migratory behaviour (beyond the already known earlier migration among salmon belonging to the ‘upper’ group). Due to the same reasons, we could not get enough reliable data to study closer how migratory behaviour is linked to other biological characteristics (like sea age) of Tornionjoki salmon.

What kind of upstream migration behaviour do salmon display in terms of migration speed, directional movements and holding sites?

Most salmon did not abort the spawning migration, migrated upstream relatively fast. Most of these radio-tagged salmon arrived near presumed spawning areas by mid-July, i.e., they displayed a continuous directed ascent with few pauses. This is in accordance with Atlantic salmon migration behaviour reported from several other Scandinavian rivers and seem to represent a general strategy by ascending spawners of Atlantic salmon (Thorstad et al. 2011). Some of the tagged salmon ascended fairly large distances rapidly with an average swimming speed of up to 25 km/day. A few individuals showed a different behaviour by staying on the lower part of the river after entering and not continuing the migration towards the spawning area until August. Other studies have also shown increased migration activities of salmon closer to the spawning season, including longer migrations from holding sites to spawning sites (Thorstad et al. 2011).

Our study documented the first observation of a two-year spawning migration in Tornionjoki salmon. Four silvery-coloured salmon were caught and tagged in very late autumn (September) and two of them migrated upstream the next spring. Unfortunately, one stopped moving during the summer (fate unknown, but either it died or lost its tag or was caught and the tag was dropped into the river), whereas the other one migrated as far up as into Lainio river by spawning time. Two-year spawning migrations have not been commonly reported for Atlantic salmon; Nordqvist (1924) reports this kind of behaviour to be documented only in a few very large (long) rivers, like Vistula (Baltic Sea), Rhine (North Sea) and a few large Russian rivers flowing into the White Sea or Arctic Sea. He presents a hypothesis that the two-year spawning migration is an adaptation to the long upstream migration distance (close to or over 1000 km). In Tornionjoki the longest upstream migrations for salmon are about 500 km, i.e., clearly shorter. Perhaps the two-year spawning migration may occur as a rare behaviour in rivers of approx. the size of Tornionjoki. In any case, such migration behaviour is not commonly observed among Atlantic salmon and represents an interesting life history strategy for which little is known about its adaptive value and contribution to the population.

How do salmon spawners disperse along the river system during spawning time, and how do they utilize the main stem and the tributaries?

Major spawning areas were concluded to be in the lower 50 km of the river Tornionjoki, as well as around Pello and Kolari. Spawning areas were also observed in the Swedish Torneälven and the river Lainio. The extensive use of the lower parts of river Tornionjoki during spawning may be a reflection of the prevailing health problems during the present study; migration may not have been normal even among those salmon which stayed in the river until spawning time. Salmon seemed to use the main rivers for spawning, and we could see no indication that salmon spawned in tributaries (although based on the electrofishing results some salmon may spawn in certain tributaries). This is in line with results from other telemetry studies on Baltic salmon, where spawning is generally reported to occur in the main stem of rivers and seldom in smaller tributaries (Johnsson & Johnsson 2011). However, as the number of spawners increase, it is possible that such habitats also become more utilized over time.

How do catch and release (C&R) fishing affect behaviour and survival of salmon?

The behaviour and survival of in-river-tagged salmon differed between spring and autumn. Most of the salmon caught by sport fishing during spring did not participate in spawning after being released, either due to leaving the river or because of death in the river. However, the survival and potential participation in spawning were higher for salmon caught in the autumn. This indicates that salmon are more sensitive to handling-related stress during the early than during the late season. Again, some of these results may be affected by salmon being weakened by health problems. Also, the amount of the in-river-tagged salmon was small, and more research is needed to confirm these findings. Although the observed negative impact of C&R fishing on Tornionjoki salmon behaviour and survival is concerning, it is not likely to have an impact on the population dynamics given current catch rates, which indicates that about 15–20% of the spawning run is caught by rod fishing (Palm et al. 2022), and where only a minority of the caught salmon are released back (Luke, unpublished data). Studies from rivers in Norway, Canada and Ireland often report high survival of salmon in C&R fishery (>90%) as well as minor behavioural effects, especially if water temperatures are low (<15 °C) (Lennox et al. 2017, Johanssen et al. 2013).

How do post-spawned salmon overwinter, when do they return to the sea and what is their survival to the next spawning?

Most salmon overwintered in the river after spawning, and major overwintering locations were areas around Tornio, Pello and Kolari. Post-spawning overwintering in freshwater is a common behaviour of salmon and it has been observed in many rivers, including the Baltic Sea rivers such as river Vindel (Grandy-Rashap 2014). After overwintering, Tornionjoki kelts (i.e., post-spawning salmon) returned to the sea between mid-May and mid-June. Kelts started their downstream migration seemingly in connection with the spring flood. Those few salmon which returned to the sea directly after the spawning were readily located close to the river mouth (c. 20 km upstream from the river mouth). However, some salmon spawning in the same area close to the river mouth overwintered in the river and returned to the sea coming spring. These kelts left the river on average only a couple of days earlier than kelts which overwintered more upstream. Post-spawning survival out to the sea was 26% which is fairly low compared to other reported estimates from undammed rivers in Scandinavia (64–85% Jonsson et al. 1991; 80% Haltunen 2011). This could again be a reflection of the prevailing health problems and may hence not represent a valid estimate of natural post-spawning mortality.

4.2. Sea trout

Compared to salmon, sea trout showed no acute nor later signs of health problems. Sea trout seldom had external signs of injuries, and none had abnormal skin (like redness) when caught and tagged. Also, after tagging and release, sea trout displayed what could be assumed as normal behaviour and survival. This seems to be in line with the in general fewer observations of health problems among sea trout than salmon populations in the northern Baltic Sea.

Where in the Tornionjoki river system do trout with different genetic signatures and biological characteristics spawn?

There were no apparent differences in biological characteristics, including general migration behaviour, between sea trout individuals genetically assigned to different spawning tributaries. The large variation in the individual life histories typical for sea trout and relatively few individuals may mask any minor average differences between sub-populations, even if such existed. The sub-adult migration behaviour (which could only be studied when fish were in freshwater) also appeared similar regardless of the underlying genetic signature.

Tagged individuals often returned to spawn in the same tributary in which they were genetically assigned. However, exceptions to this were also common, especially between individuals assigned to Parkajoki, Pakajoki and Äkäsjoki. It is possible that the IA results in these cases were erroneous, which is supported by the often rather low assignment probability (p<0.9). Moreover, the genetic baseline of Tornionjoki sea trout populations may well be incomplete and thus lead to erroneous assignments. An interesting detail, which indicates a more exact homing than that based on IA, is that the five individuals which were found to spawn more than once in the river system always returned to spawn in the same tributary.

What kind of upstream migration behaviour do maturing sea trout display in terms of migration speed, directional movements and holding sites?

The two migration behaviours reported in our study appear to be attributed to the maturation status of the fish. For maturing trout, spawning migration, in general, lasts two years: trout ascend the river in autumn, overwinter in the (typically lowermost) river, continue upstream migration in spring, spawn in autumn (mainly in smaller tributaries of the middle reaches of catchment), overwinter again after spawning before descending to sea in the spring. Such two-year migration cycle has also been observed from sea trout in the Teno river (Kanniainen et al. 2014) and river Vindel (Östergren 2012). However, it is noteworthy that such seemingly complex migration behaviour is the dominating strategy in Tornionjoki sea trout. Hence, the maturing Tornionjoki trout have two major upstream migration periods: initial river ascent in autumn and further upstream migration in spring/early summer. Similarly, the downstream migration can be seen as a two-step process where the trout first descend from the tributary to the main stem for overwintering after spawning, followed by a second migration to the sea in the spring (see below for more about post-spawning behaviour).

Upstream migration from overwintering areas towards the spawning areas started between mid-May and mid-June, i.e., somewhat earlier than the major salmon run. The 150–300 km long migration towards spawning areas was typically highly directional and lasted normally 3–5 weeks. Based on observation data from automatic data logging sites in Matkakoski and Vuennonkoski rapids, trout often stayed a couple days below the rapid before continuing the migration. However, no major resting sites could be identified on the migration route, but this may be due to a lack of detailed enough tracking data along the route.

Contrary to the fast and directional approach to spawning areas, sea trout seemed to select a holding site in the vicinity of the spawning site. These holding sites varied; in some cases, the site was in the tributary in which the spawning occurred but sometimes the site was in the main stem (Tornionjoki/Muonionjoki) near the confluence of the spawning tributary. Trout spent on average two months (July–August) in these holding sites until the spawning season and the last (short) movement to the exact spawning location.

Where do sea trout spawn: in which tributaries and where in these tributaries?

Spawning areas of the radio-tagged sea trout reaffirmed earlier knowledge and assumptions of important spawning tributaries (Fig. 1). Äkäsjoki tributary was the most used spawning area for the tagged sea trout. Except for one trout, which entered the river Palojoki (located in the upper reach of the Tornionjoki catchment), all tagged trout entered the tributaries which have been assumed to be the most important for sea trout reproduction. Another important observation in the results is that only a couple of the tagged sea trout entered the Swedish main stems (Swedish Torne, Lainio), which suggests that there are no major spawning areas of sea trout in this part of the Tornionjoki catchment. Indeed, there is indirect evidence of the contribution of some (smaller) Swedish rivers in this catchment area to the whole Tornionjoki sea trout stock (Palm et al. 2019) and also a couple of the tagged trout were assigned to most likely originate from this part of the catchment (Fig. 6).

Interestingly, many sea trout were in the main stem during the spawning time, although the prior assumption was that trout do not spawn there (for instance, trout parr are rarely caught in the electrofishing of the main rivers). However, the manual tracking was conducted only once or twice a week, and it is hence possible that these trout briefly visited a spawning tributary between the tracking events. This is supported by observations that many of these trout were dwelling in the main river near some tributary, and also that in autumn 2020 one sea trout was documented visiting the tributary Pakajoki only for a couple of days during spawning season.

The exact spawning sites in the tributaries probably remained largely unidentified. During the spawning season, the locations of the tagged trout could be tracked only once a week, which leaves good opportunities for trout to visit the exact spawning site from its holding site. This is the case especially if it is common for sea trout to perform only brief visits to the spawning site (as indicated by the above observation from Pakajoki). A few of the tagged trout in our study were found rather high up in a tributary catchment, indicating that these individuals spawned in the small rivers/streams flowing into the main river of the tributary. Perhaps the spawning sites among the rest of the tagged individuals were also in smaller streams but as noted above, this cannot be confirmed from our data.

What kind of in-river migrations do immature (sub-adult) sea trout exhibit?

Sub-adult sea trout overwintering behaviour has been documented earlier studies (e.g., Kanniainen et al. 2014), and similar migrations have been thought to take place also in river Tornionjoki. However, actual data confirming this behaviour has lacked. This study shows that the overwintering area of the sub-adult Tornionjoki sea trout is located below Kukkolankoski rapid, 10–20 km from the sea. These trout seemed to arrive in the river as late as September to October; fishing of trout for tagging was started every year in August, but the first trout were caught not until about mid-September. During winter these trout moved very little and stayed within about a 10 km river section below the Kukkolankoski. The overwintering area of these sub-adult trout is very similar to that found in Teno river, where the sea trout overwintered below the lowermost notable rapid (Kanniainen et al. 2014).

Overwintering in the river, rather than at sea, appeared to be the predominant behavioural pattern in our data. Some individuals which were tagged in the river returned to the sea and were not observed to return to the river for the next winter (Fig. 18). However, no later observations of these individuals were made and therefore we could not confirm that these fish were still alive. It is good to note that no smaller than about 50 cm long individuals could be tagged in our study and therefore we did not obtain any migration data from them. The length range from the smolting size (15–20 cm) to 50 cm normally corresponds to at least one full year of growth after smoltification. Therefore, our study does not tell whether also the post-smolts after their first summer at sea return to the river for overwintering.

How do catch and release (C&R) fishing affect behaviour and survival of sea trout?

All the tagged sea trout were caught by trolling/harling using a rowing boat and therefore no reference group of tagged sea trout existed with a different type of catching and handling. Fishermen used barbless hooks and knotless dipnets, and in the boat, they had a water basin into which the caught specimen was immediately placed. Therefore, handling of the tagged sea trout was remarkably more tender than the usual handling of sea trout caught as a bycatch of salmon fishing are exposed to. Because of these reasons, the possible effects of C&R fishing could not be properly studied. However, indicative of potentially minor effects of C&R fishing on sea trout is that no signs of abnormal post-tagging behaviour of sea trout were observed. Moreover, no post-tagging mortality was documented, either. Some sea trout, however, got damages (e.g., bleeding) when caught (despite the above-described protocols applied in fishing and handling) and these individuals were not tagged. Bleeding has been recognised among the most important factors influencing the mortality of angler-caught fish (e.g., Gargan et al. 2015). Consequently, there are several reasons why our findings of no apparent harmful effects of C&R fishing on trout are too optimistic.

How do post-spawned sea trout overwinter, when do they return to the sea and what is their survival to the next spawning?

Post-spawning overwintering areas are rather widespread in the river system and therefore somewhat differed from those of before spawning. Post-spawned trout kelts often utilized the same overwintering areas as ascending spawning trout, both around Kattilakoski and Pello but also close to the river mouth (i.e., the same area used by immature trout and by maturing trout in winter before spawning), as excepted based on common knowledge about trout's life history strategies (Jonsson & Jonsson 2002, Klemetsen et al. 2003). Some kelts are also overwintered close to the mouth of the spawning tributary or even in the tributary. These observations differed from the observations from the Teno system, where all trout kelts returned to the main steam and moved downstream close to the river mouth after spawning (Kanniainen et al. 2014).

Several (n=5) trout were observed to complete two spawning migrations during the battery life of the transmitter. Between spawning migrations, these trout spent only one short summer at sea (1–3 months). Such behaviour was unexpected and suggests that contrary to their 'species' designation, maturing Tornionjoki sea trout spend a very large majority of their life in freshwater. Earlier it has been assumed that trout would spend more time at the sea between the spawning migrations by, for instance, staying at sea also over the winter following the descent from the previous spawning and ascending to the river in springtime before repeating spawning in the next autumn. However, in our data, we have no individuals with such behaviour. Also, we observed only one individual that ascended the river from the sea in springtime and continued its migration directly to the spawning area. This specimen, however, was likely a first-time spawner because of its young sea age (2SW) when tagged.

The extensive time spent in freshwater may make mature trout potentially vulnerable to recreational river fishing and highlights the importance of river fishing regulations specifically (space, time) targeted in protecting sea trout. Our study clearly shows the 'hotspot' times and places into which protective management measures could be directed. On the other hand, the long periods in freshwater protect sea trout from sea fisheries, which so far have been considered to be the main source of fishing mortality of the Gulf of Bothnian sea trout (e.g., Jutila et al. 2006, Whitlock et al. 2018). Especially the repeat spawners spend most of their time in freshwater and thus are largely protected from sea fisheries (and other sources of mortality at sea). As we could not tag smolts with long-life transmitters, we did not get good information about how much sea trout stay at sea before maturation. If they do spend more time at sea, then protective measures at sea would be most effective if specifically directed to the protection of the young (small) sea trout.

4.3. Limitations of the data

The number of spawned fish was eventually relatively small, although the fishing effort for tagging was notable. Even though the tracking data is reliable and accurate at the individual level, the limited number of tagged fish warrants some caution when making population-level generalizations from the results. This holds especially for salmon because the abnormal behaviour of salmon seemingly linked to the prevailing health problems largely corrupted the accumulated data. There have been no previous studies about salmon or trout in river Tornionjoki using radiotelemetry. Thus, there is no reference available from Tornionjoki salmon against which to relate the observed unexpected behaviour of salmon to return to the sea after a brief river ascent. It, therefore, remains unproven, whether this behaviour timely coinciding with observations about salmon health problems has a causal link. Seemingly 'normal' behaviour of salmon was also observed every year indicating that there was a difference to sustain handling and tagging between the individuals, whether this is related to their health status or not.

The results of genetic analysis based on microsatellites showed that most salmon had a low assignment score (probability of belonging to the respective groups), which reflects the relatively low level of genetic differentiation between salmon originating from different river sections (especially between lower Torne and lower Kalix). Similarly, there is a relatively low level of genetic differentiation between trout from different tributaries.

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