Chasing waterfalls;

A method to detect natural barriers to salmon and trout migration

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Abstract

Fragmentation and habitat loss are major threats to present day biodiversity. Rivers are fragmented by high or low flow, shallow water and long steep falls that create barriers. Such barriers can occur naturally or as a result of human infrastructure. Effects caused by natural barriers on fish migration are understudied compared to the effects caused by man-made barriers. Even so, natural barriers affect connectivity, which is an important factor to consider in studies of man-made barriers. Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) are anadromous salmonids that undertake extensive migration back to important spawning habitat, where barriers can obstruct their migration. In Norwegian rivers, escaped Atlantic salmon of farmed origin are common. Escaped salmon have shown different migration patterns compared to its wild conspecific as escapees lack natal imprinting needed to locate spawning ground and reduced physiology.

In this study, natural barriers as steep gradients and drops were remotely detected from fine scale elevation data (1 m resolution) using ArcMAP. The number of barriers passed were compared among the three salmonids and size classes of wild and escaped salmon. The barrier characteristics height, length, distance from river mouth and number of downstream barriers were tested on the number of fish passing a barrier as well as on passability and cumulative passability values. The highest number of barriers passed was by wild salmon (Mean = 1.3), followed by trout (Mean = 1.1) and last escaped salmon (mean = 0.3). All barrier characteristics had a negative effect on the numbers of fish upstream of a barrier. Only height and distance from river mouth had a statistically clear effect on barrier passability and cumulative passability for all fish combined. No effect of characteristics other than distance to mouth were found. This might be explained by salmonids stopping at spawning areas or by lack of motivation, as opposed to being stopped by barriers, and affecting the calculation of passabilities. Several detected natural barriers in this study showed high passage for salmonids, all barriers below 1.5 m height show passability above 66 % for all salmonids and wild salmon has higher passability when gradient is greater than 50 %.

Clear definitions of what type of river topography to consider as a natural barrier could result in more exact detection of natural barriers. Incorporation of natural barriers in future efforts to conserve wild salmonid populations will help focus efforts to areas without natural fragmentation. Natural barriers can also be a way to exclude escapees from wild salmonid spawning areas and mitigate hybridization.

1   Introduction

Fragmentation and habitat loss are major threats to the persistence of terrestrial and aquatic biodiversity (Kemp & O'Hanley 2010, Bunt et al. 2012, Noonan et al. 2012). Habitat connectivity is the ability to freely move between and within areas to make use of different habitats. This concept is commonly used when discussing fragmentation and loss of habitats (O'Hanley & Tomberlin 2005, Cote et al. 2009, Kemp & O'Hanley 2010, Fuller et al. 2015). Movement between habitats within the river can be viewed as one dimensional, only occurring upstream or downstream within the channel (Fuller et al. 2015). This makes river systems highly vulnerable to fragmentation as one impassable area can result in large parts of the river being inaccessible to organisms in the river (Cote et al. 2009).

Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) (hereby also referred to as salmon and trout) are two of the most well studied species of migrating fish (Birnie-Gauvin et al. 2019). These anadromous species undertake extensive migrations from sea and upwards through rivers to reach their spawning grounds, often displaying iteroparity and spawning multiple times in a life cycle (Thorstad et al. 2008). Wild Norwegian populations of Atlantic salmon and brown trout are under multiple threats, one of the biggest being production of hydropower (Skaala et al. 2014, Forseth et al. 2017). To accommodate power demands, flows are regulated and hydropeaking is used, which in turn can reduce habitat, obstruct migration and isolate sections of the rivers (Skaala et al. 2014, Forseth et al. 2017). It is also the major cause of migration barriers, which fragments rivers and severely affect the distribution of Atlantic salmon and brown trout (Klemetsen et al. 2003, Thorstad et al. 2008). In addition, escaped salmon can cross breed with both wild salmon and brown trout which can affect populations negatively by reducing smolt production and potentially lead to maladaptive traits in (Gausen & Moen 1990, Webb et al. 1993, Fleming et al. 2000, Forseth et al. 2017).

Much research on the effects and mitigation of man-made barriers have established that anthropogenic barriers can delay or stop migrating Atlantic salmon and brown trout (Rivinoja et al. 2001, Ovidio & Philippart 2002, Thorstad et al. 2003, Roscoe & Hinch 2010, Noonan et al. 2012). In addition to man-made structures hindering migration, delays and stops also occur at natural migration barrier such as waterfalls (Kennedy et al. 2013, Lennox et al. 2018). Natural barriers are a part of nature and therefore also part of the desired river morphology from an ecological perspective (Degerman 2008). But if we are to fully understand the effect of river fragmentation by anthropogenic structures, research on river connectivity need to consider natural barriers (Finstad et al. 2005, Cote et al. 2009). Even so, knowledge about natural barriers and standardized methods of recognition are low if not completely non-existent today (Thorstad et al. 2008, Kennedy et al. 2013).

1.1 Migration

Atlantic salmon and brown trout are commonly coexisting in Norwegian rivers and exhibit a great variation in upstream migration patterns (Finstad et al. 2005). Timing of ascent, behaviour and swimming capabilities differ between species and populations, as well as between the wild and farmed type of Atlantic salmon (Peake et al. 1997, Thorstad et al. 1998, Klemetsen et al. 2003, Finstad et al. 2005).

Wild Atlantic salmon and brown trout start their migration from sea towards spawning areas in Norway between April and November with a peak occurring in June-August (Finstad et al. 2005). In an undisturbed system, salmonids move towards spawning in three phases (Økland et al. 2001, Finstad et al. 2005). First, a direct or stepwise migration towards pre-smolt imprinted spawning area in the river. Second, up- and downstream movement close to search for a final spawning site and third, a stationary period of holding the spawning site until time of spawning (Økland et al. 2001, Finstad et al. 2005). These patterns differ in escaped Atlantic salmon where a lack of imprint makes them migrate aimlessly upstream, aggregate far up in the river and often stop below or close to barriers (Heggberget et al. 1993, Thorstad et al. 1998, Kennedy et al. 2013, Moe et al. 2016).

While migrating, Atlantic salmon and brown trout do not feed and energy reserves are diverted to gonad growth and movement (Thorstad et al. 2008). Due to a finite energy reserve, salmonids are vulnerable to man-made or natural barriers delaying or stopping movement and the energy spent passing barriers is highly dependent on water velocity and barrier elevation (Ovidio & Philippart 2002, Thorstad et al. 2003, Lennox et al. 2018). Timing of river entry has been observed to be later for escaped salmon compared to wild (Gausen & Moen 1990, Jonsson et al. 1990, Erkinaro et al. 2010). This late onset of migration reduces the time in river and the chance of experiencing water velocities allowing for migration beyond barriers in a system with strong fluctuations in flow (Reiser et al. 2006).

Close to spawning time, wild salmon and brook trout enters holding phase (Økland et al. 2001, Finstad et al. 2005). During this phase, escaped salmon has been shown to continue extensive upstream and downstream movement instead of finding a holding spot (Gausen & Moen 1990, Moe et al. 2016). Escaped salmon has also been found to be less probable to be at spawning site at the time of spawning (Kennedy et al. 2013). Nevertheless, some cross breeding occur between escaped salmon and both wild salmon and brown trout, posing a problem of competition during spawning and introduction of genes less adapted to nature (Adams et al. 2014, Forseth et al. 2017, Sylvester et al. 2018)

1.2 Swimming and jumping capabilities in Atlantic salmon and brown trout

The swimming speeds and jumping heights of Atlantic salmon and brown trout have been examined by multiple studies which have produced varying results (Peake et al. 1997, Scruton et al. 1998, Ovidio et al. 2007, Taugbøl et al. 2019). Swimming speeds are classified by the energy cost and how long the speed can be maintained, commonly categorized as sustained, prolonged or burst speed (Thorstad et al. 2008, Bourne et al. 2011, Calles et al. 2013). To avoid exhaustion and to ensure successful passage when swimming against water flow, sustained or prolonged speed should ideally be used (Colavecchia et al. 1998).

Sustained swimming speed (approximately 1 m/s for Atlantic salmon and 0.7 m/s for brown trout) has low energy cost and can be sustained for more than 200 minutes (Peake et al. 1997, Calles et al. 2013). Prolonged swimming speed (approximately 3.6 m/s for salmon and 1.9 m/s for trout) has an intermediate energy cost and can be sustained from 15-20 seconds up to 200 minutes (Peake et al. 1997, Calles et al. 2013, Taugbøl et al. 2019). Burst speed (8 m/s for salmon and 3.8 m/s for trout) is the maximal swimming speed and can only be maintained up to 15-20 seconds (Peake et al. 1997, Calles et al. 2013). Experiments have been made using farmed Atlantic salmon to determine its prolonged swimming speed. These trails that prolonged swimming speed for farmed salmon varies between 0.9 m/s and 1.25 m/s (Hvas et al. 2017, Hvas & Oppedal 2017), which is lower than both its wild conspecifics and to brown trout. Wild salmon are known to be able to jump 2 m in height and in extreme cases clear up to 4 m high waterfalls (Rivinoja et al. 2001, Degerman 2008, Baudoin et al. 2015). Brown trout is able to pass falls of at least 0.5 m by jumping but has also been observed jumping up to 1.89 m (Ovidio et al. 2007, Baudoin et al. 2015). Although farmed salmon has been observed to jump, no measurements of jumping height is present today (Furevik et al. 1993).

Both jumping and swimming capabilities in Atlantic salmon and brown trout varies with temperature and fish size and optimum seem to differ between populations (Furevik et al. 1993, Jensen et al. 1998, Ovidio et al. 2007, Baudoin et al. 2015, Taugbøl et al. 2019). A positive correlation has been observed between size and swimming speed in both Atlantic salmon and brown trout (Peake et al. 1997, Castro-Santos 2006, Remen et al. 2016).

1.3 Barriers

A barrier is a man-made or natural structure that has the potential to disrupt migration between habitats in a river (Atkinson et al. 2018). Most commonly regarded in fresh water biology is anthropogenic barriers as dams and weirs but a barrier can also occur naturally as waterfalls and rapids (Thorstad et al. 2008, Cote et al. 2009, Kennedy et al. 2013). Water velocities that exceeds swimming capabilities or elevation changes that forms insurmountable drops are usually the direct reason of

disrupted migration, while barriers are cause of such conditions (Castro-Santos 2006, Kemp et al. 2008, Thorstad et al. 2008).

Successful passage of barriers is dependent on multiple conditions, and mainly three barrier characteristics. First, slope of the barrier cannot create water flow higher than critical swim speed for a longer stretch than a fish is capable of swimming at than speed. Second, water depth downstream a barrier must be sufficient for a fish to accelerate to maximum speed and water depth within and above barrier must be deep enough to swim. Third, the height of a barrier only passable by jumping cannot exceed the maximum jumping capability of a fish (Meixler et al. 2009, Baudoin et al. 2015). In addition other factors such as bottom roughness (Baudoin et al. 2015), temperature dependent swimming and jumping capabilities (Baudoin et al. 2015) and variations in discharge and light can affect motivation in salmonids to pass a barrier (Erkinaro et al. 1999, Ovidio et al. 2007, Kennedy et al. 2013). Passing of multiple consecutive barriers can also result in an extra energy cost and a cumulative negative effect on ability to pass successive barriers or to a further extent to successfully spawn (Booth et al. 1997, Colavecchia et al. 1998, Cote et al. 2009, Kemp & O'Hanley 2010)

Swimming and jumping abilities differs among species of fish, which makes it important to assess barrier impact in view of abilities of the target species (Castro-Santos 2006, Baudoin et al. 2015). Atlantic salmon and brown trout are capable of jumping and swimming at great speeds and barrier passage need to address both jumping barriers and swimming barriers (Glover et al. 2008, Meixler et al. 2009, Baudoin et al. 2015). Studies have shown that wild salmon possess a greater ability to migrate upstream barriers than farmed conspecifics (Gausen & Moen 1990, Moe et al. 2016, Lennox et al. 2018), which seem to be an effect of eroded fins and reduced muscle mass due to the conditions in fish farms (Gausen & Moen 1990). Interbreeding between wild and escaped Atlantic salmon has also been shown to decrease by the number of barriers between mouth and spawning habitat, indicating a lesser ability to pass multiple barriers by escaped Atlantic salmon compared to wild (Sylvester et al. 2018). Methods to classify barrier passage also predict a lower passage by brown trout compared to wild salmon due to differences in swim speed (Peake et al. 1997, Glover et al. 2008, Baudoin et al. 2015).

1.4   Passability of barriers

The ICE-protocol (Information sur la Continuité Écologique) grade barrier passability in French rivers based on barrier height, slope and water depths (Baudoin et al. 2015). SNIFFER-protocol (Scotland and Northern Ireland Forum for Environmental Research) is used for barriers in UK rivers and assigns passability based on the same measurements as ICE-protocol but also considering hydrology (SNIFFER 2010, Barry et al. 2018) Both protocols defines passability of a barrier into four classes (plus indeterminate impact in the ICE-protocol) (SNIFFER 2010, Baudoin et al. 2015, Barry et al. 2018). Glover

et al. (2008) suggested Norwegian standards for barrier passability to be made based on barrier heights and slope. These standards considers any fall higher than 0.5 m and slopes steeper than 10% lasting 6 m without resting stops a potential barrier (Glover et al. 2008). This lower limits was set using potadromous brown trout as target species and barriers are further classified into five classes depending on barrier height (Glover et al. 2008).

Another method to classify the effect of a barrier is by defining its passability based on successful passages instead of barrier characteristics (Kemp & O'Hanley 2010). Passability can either be viewed as a binary value (pass or no pass) (Kemp & O'Hanley 2010), as the proportion of a fish population that is able to pass a barrier (O'Hanley & Tomberlin 2005) or as the proportion of successful passages out of all attempts to pass a barrier (Haro et al. 2004). The effect of passing multiple barriers can be considered as the product of all passabilites (Kemp & O'Hanley 2010).

1.5   Aims and hypothesis

Anthropogenic barriers have been the subject of research and mitigation efforts for several years and metrics affecting passability are well investigated (Roscoe & Hinch 2010, Noonan et al. 2012). Natural structures can potentially act as barriers and disrupt fish migration (Erkinaro et al. 1999, Kemp et al. 2008) and several authors have pointed out the possible negative effect of natural barriers on fish migration (Finstad et al. 2005, Thorstad et al. 2008, Cote et al. 2009). Even so, the effects of a natural barrier on migration of brown trout, wild and escaped Atlantic salmon are understudied and mostly unknown (Thorstad et al. 2008, Kennedy et al. 2013) but an important source of knowledge in efforts to increase connectivity in rivers (Lennox et al. 2018).

Mitigation of anthropogenic barriers and restoration of rivers is an key part of river management that increases the success of fish migration (Roni et al. 2002, Kemp & O'Hanley 2010, Silva et al. 2017). However, as efforts are both expensive and time consuming, it is important to be able to allocate mitigation of barriers where it will yield maximum effect on river connectivity (Bourne et al. 2011). Cote et al. (2009) showed that the presence of a natural barrier in a river can counteract the improvement of river connectivity gained from removing anthropogenic barriers. Therefore, there is a need to consider the connectivity of a river relative to a baseline including limiting effects of natural barriers to effectively prioritize mitigation efforts (Finstad et al. 2005, Cote et al. 2009). In the same way as Atkinson et al. (2018) proposes methods for remotely detecting anthropogenic barriers, it is important to develop methods to efficiently and cost effective detect natural migration barriers.

This project aims to develop a method for remote detection of potential natural migration barriers for Atlantic salmon and brown trout. By investigating the metrics of detected barriers I aim to define what structures constitutes a barrier, as well as define values by which migration barriers can

be classified and detected in nature. I hypothesize that migration barriers depend on elevation changes in the river and can be detected by analysis of gradient changes derived from digital terrain models. Sudden changes in elevation can indicate high drops and steep gradients and indicate areas of high water velocities which is key factors to river connectivity (Glover et al. 2008, Kemp et al. 2008).

In addition, I hypothesize that any escaped salmon is motivated to migrate as far as it is physically able in the river and will show a lesser ability to proceed migration than its wild conspecific when reaching a natural barrier. By using wild salmon as reference, a low passage rate in escaped salmon is expected to be an effect of a natural barrier and thus confirm the presence of such.

2 Materials and methods

2.1 Study sites

Study sites include seven rivers located in the Hardangerfjord in Hordaland, western Norway (Figure 1). Steep gradients and alpine environment dominate upper parts of the rivers, whereas the lower reaches are dominated by farming landscape, urban communities and lower gradient. All rivers contain reproducing populations of Atlantic salmon and brown trout (Hauer & Pulg 2018). The Hardangerfjord has a high concentrations of salmon farms (Skaala et al. 2014) and escaped farmed Atlantic salmon is present in all of the studied rivers. Long time series of spawning counts have been made in all of the study rivers (Skoglund et al. 2018). The anadromous reach in the rivers ranges from 14 km to 78 km and hydropower is present in four of the rivers (Skaala et al. 2014, Hauer & Pulg 2018).

These rivers were chosen because of available counts of spawning Atlantic salmon and brown trout and absence of anthropogenic barriers in the anadromous reach (Skaala et al. 2014, Skoglund et al. 2018). For this study, counts made between 2006 and 2014 were used. Counts were not made in all of the rivers for entire time series and counts performed later than start of 2013 in river Etne was omitted due to presence of a trap designed to remove escaped salmon.
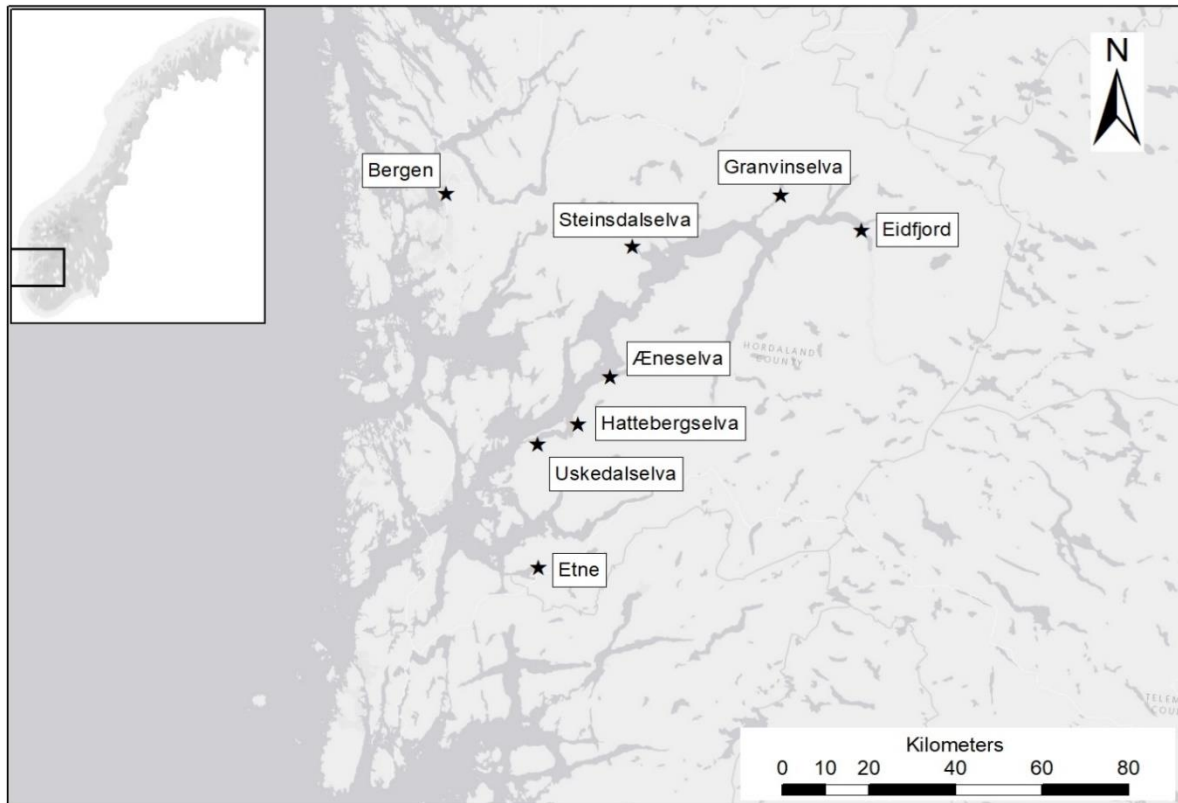
Figure 1: Map of study area with Bergen city and locations of the seven river systems included in the study. Eidfjord river system consist of rivers Eio, Veig and Bjoreio and Etne river system consist of rivers Etne and Sørelva.

2.2 Biological sampling

Spawning count data on Atlantic salmon (including wild and escaped farmed salmon) and brown trout was collected all in October or November from 2006 to 2014 by drift diving by NORCE according to Norwegian standards (NS 9456). During drift dives, one to four divers equipped with snorkelling gear started at the upmost extent of the anadromous reach of the river and drifted down to the river mouth. All fish that passed upriver of the dive team were counted, positions in river were noted and fishes were categorised by origin (wild salmon, escaped salmon or brown trout) and into size classes (small <3kg, medium = 3-7kg and large > 7kg for salmon and <1kg, 1-2kg, 2-3kg and >3kg for brown trout). Escaped salmon were distinguished by body shape, pigmentation, behaviour and fin erosion (Jonsson & Jonsson 2006, Orell & Erkinaro 2007, Svenning et al. 2017).

When performed by experienced personnel, drift diving has been shown to be an effective method to estimate the total abundance of fish in rivers (Orell et al. 2011, Mahlum et al. 2019) and detection of escaped Atlantic salmon (Orell et al. 2011, Skoglund et al. 2018, Mahlum et al. 2019).

2.3 Remote barrier identification

Potential migration barriers in the rivers are mapped using two methods. An experienced drift diver with first-hand knowledge of the rivers marked possible natural barriers on a map (hereby referred to

as "expert barriers") and steep gradients or abrupt elevation changes along the river stretch was identified in ArcMap (hereby referred to as "remote sensed barriers"). All mapping work and detection of remote sensed barriers was made using ArcMap version 10.7.1.

Expert barriers were identified by marking spots and areas in the study rivers that were considered barriers to salmon and trout migration or dangerous to pass during drift dives. Possible barriers were identified with high acceptance to minimize exclusion of any true barriers.

Remote sensed barriers were identified using Digital Terrain Models (DTM) from laser scans of 2 points / m^2 made between 2010 and 2015 (Blom Geomatics AS 2011, 2016, TerraTec AS 2013, COWI AS 2014). Points were created with 1 m intervals along the deepest point (thalweg) of each study river. Meter above sea level at each point was extracted from DTM and distance from river mouth at each point, was calculated in meters. Percent gradient between neighbouring points was calculated as the rise over run times 100. Points where the percent gradient was at least 50 % or 10 % for at least six consecutive meters was marked as potential natural barriers. These are values corresponding with Glover et al. (2008), where the lower limit of a possible barriers is defined as falls higher than 0.5 m and slope steeper than 10 % lasting at least 6 m without resting stops. These threshold values are adapted to Norwegian populations of small potadromous brown trout and is assumed to be conservative values considering Atlantic salmon and brown trout (Ovidio & Philippart 2002, Degerman 2008, Glover et al. 2008, Calles et al. 2013, Baudoin et al. 2015). To avoid barrier duplications, potential barriers occurring less than 100 m apart were grouped as one. The distance from river mouth to barrier, or top most barrier in groups, was calculated. Using elevation above sea level extracted from DTM, barrier height was calculated as the difference in elevation between downstream pool and upstream pool water surfaces. The length of a barrier was calculated as the distance between downstream- and upstream pools. Each barrier was assigned an ID number of first two letters in the river name followed by the order of the barrier counted from river mouth to top, method of detection (expert barrier, remote sensed barrier or both methods) was noted for each barrier and the position of the barrier was noted.

2.4   Barrier verification

Each expert barrier and remote sensed barrier was visited in field. GPS points with measurements of elevation above sea level were recorded using a differential GPS (Trimble model TSC3, Trimble antenna R6 model 4) according to methods described by Ovidio et al. (2007) and Baudoin et al. (2015). The topography of a barrier was mapped by GPS points along the thalweg from 50 m below the barrier to 50 m above the barrier. When passing through the barrier, measurements were intensified to every 0.3 m or more if needed to fully map the topography of the barrier. GPS-points recorded elevation above sea level at 0.5 m intervals along three cross sections of the downstream pool and the same was

done in the upstream pool. GPS points were also taken in line with water surface in both of the pools and in the middle of the barrier which were used to calculate depths at each location.

Manual measurements were made when the conditions made it unsafe to walk in the rivers using measuring tape. The vertical distance between the water surface levels above- and below a barrier was measured as height and the horizontal distance between start and stop of the barrier was measured as length. Depth in downstream pool was measured 0.5 – 1 m from the barrier. Depth in a barrier was measured at the shallowest part of the barrier. Upstream pool depth was measured directly above the barrier crest. All depths were measured as close to the thalweg as possible.

The barrier was classified as a waterfall, rapid, threshold, riffle or run based on dominating characteristics. A waterfall was classified as having a vertical drop (greater than 150 % gradient) of at least 1 m height and presenting a jumping barrier to migrating fish. A rapid was classified as a stretch with high water velocity (indicated by foaming, or whitewater), presenting high turbulence and velocity barriers. Threshold was classified as a vertical drop of less than 1 m height, riffle was defined as a stretch of less than 0.2 m depth and low water velocity and runs was defined as a stretch with water depth greater than 0.2 m and low water velocity (Powers et al. 1985, Baudoin et al. 2015).

2.5   Passability

Passability of a barrier is defined as a fractional number representing the proportion of a population able to pass the barrier. The cumulative passability of a barrier is defined as the product of all passabilities up to and including the barrier (O'Hanley & Tomberlin 2005). In this project, individuals are considered to have passed all barriers downstream of their position at observation but none of the barriers upstream. Passability of a barrier was calculated as:

1. $P_{(x)} = 1 - \dfrac{nstopped}{npassed + nstopped}$

where $P_{(x)}$ = Passability of barrier x, *nstopped* = numbers of individuals that have passed all barriers before x and *npassed* = number of individuals that have passed barrier x. Cumulative passability of a barrier was calculated as:

2. $cumP_{(x)} = \prod_{n=1}^{x}(P_n)$

where *cumP$_{(x)}$* = cumulative passability of barrier x, *x* = the number of the barrier counted from river mouth and P_n = Passability of nth barrier. Barriers detected at the end of the presumed anadromous reach were considered to have a passability of 0.

Passability and cumulative were calculated at every detected natural barrier in all of the study rivers using data from all spawning counts performed within the study period. Both values were

calculated using counts of wild salmon, escaped salmon and brown trout as well as a global value using counts of all three groups combined.

2.6   Statistical analysis

All statistical analyses were performed using R-studio 1.2.1335 (R Core Development Team 2019) with additional packages tidyverse (Wickham 2017), glmmTMB (Brooks et al. 2017), multcomp (Hothorn et al. 2008), survival (Therneau & Grambsch 2000) and survminer (Kassambara et al. 2019). Stepwise forward selection was used to find significant predictor variables and AIC was used to select the best fitted model. To account for overdispersion, generalized linear models were fitted using negative binomial distribution. No assumptions of distribution is made by survival models and ties in cox proportional hazards model are handled by exact partial likelihood as it is most suitable when response steps are small and of discrete value.

For each observed salmon, the numbers of barriers passed was given based on the number of barriers detected downstream its position in the river. The effect of salmon origin (wild or escaped) and size on numbers of barriers passed were tested for all study rivers and the entire study period combined, using a generalized mixed effect model (glmmTMB):

3.   glmmTMB(Pass ~ Group*Size + offset (log(total)) + (1|River) + (1|Year))

Where *Pass* = numbers of barriers passed by the individual, *Group* = origin of individual, *Size* = Size class of individual, *offset(log(total))* = an offset to account for the total number of barriers in the river where the subject was observed, *(1|River)* = random of river of observation and *(1|Year)* = random effect of year of observation. A post hoc Tukey HSD (multcomp) was used to compare average number of barriers passed among size classes in wild and escaped Atlantic salmon.

Testing for presence of natural barriers in rivers was done by comparing probabilities of passing barriers by wild and escaped salmon populations in each river separately. This was done with a survival analysis using a log rank test (survival):

4.   survfit(Surv(Pass) ~ Group)

Where *Pass* = number of barriers passed by the subject and *Group* = salmon origin.

In rivers where different probabilities of passage by wild and escaped salmon were found, the effect of size class and year of observation on probability of passing barriers was tested for each salmon origin individually using a Cox proportional hazard model (survival):

5.   Coxph(Surv(Pass ~ Size + Year), ties = "exact")

Where *Pass* = numbers of barriers passed by the individual, *Size* = Size class of the individual, *Year* = Year the individual was observed.

In rivers where different probabilities of passage by wild and escaped salmon were found, probability of passing barriers was tested between escaped salmon, wild salmon and brown trout using a cox proportional hazards model (survival):

6. Coxph(Surv(Pass ~ Group), ties = "exact")

Where *Pass* = numbers of barriers pass by the individual and *Group* = wild salmon, escaped salmon or brown trout.

At each of the potential natural barriers detected by remote sensing and expert knowledge, the numbers of salmons observed upstream within the study period were summarised. Barrier height, length, distance from river mouth and numbers of barriers downstream were tested for effect on number of salmons able to pass the barrier, using a generalized mixed effect model (glmmTMB):

7. glmmTMB(nPass ~ H * L + Distance + prev.barriers + offset(log(n.total)))

Where *nPass* = number of fish above a barrier, *H* = Barrier height, *L* = Length of the barrier, *Distance* = the distance from river mouth to the barrier, *prev.barriers* = the number of barriers located downstream in river and *offset(log(n.total))* = an offset to account for total number of fish in each river. Barrier height and length measured at field visits was used when such data was available and measured digitally when not available (as described in section "Remote barrier detection").

Each characteristic found to have an influence on number of fish above a barrier (as tested in model 7) was also tested for effect on barrier passability and cumulative passability. This was done for wild salmon, escaped salmon and brown trout individually as well as all groups combined. Testing was using a generalized linear model:

8. glm(passability ~ H * L + Distance + prev.barriers, family = "binomial")
9. glm(cum.passability ~ H * L + Distance + prev.barriers, family = "binomial")

Where *Passability* = passability, *Cum.passability* = cumulative passability of a barrier and all other predictors equal to function 3. A binomial distribution was used as passability is a proportion.

3 Results

Number of barriers passed were compared between brown trout, wild Atlantic salmon and escaped Atlantic salmon across all rivers. Sample sizes for each rivers are presented in table 1. Passability scores and cumulative passability scores for brown trout, wild salmon and escaped salmon were calculated

for each individual barrier in all of the rivers (Appendix 1). Values ranged from 0 (no chance of passage) to 1 (100 % chance of passage), barriers detected at top of anadromous reach were assigned a passability of zero for all species as no fish is expected above.

3.1 Barriers passed by species and size classes

Across all study rivers, wild salmon passed more barriers than its farmed conspecific (p < 0.001) and brown trout (p < 0.001). Brown trout passed more barriers than escaped Atlantic salmon (p = 0.004).

Comparing size classes within Atlantic salmon showed that medium sized escaped salmon passed more barriers than small sized escaped salmon (p < 0.001). No difference was found between large escaped salmon and the other two size classes of escaped salmon, or among the size classes of wild Atlantic salmon. Relationships between the salmon groups show that wild large salmon passed more barriers than medium escaped (p = 0.005) and small escaped (p < 0.001). Medium sized wild salmon passed more barriers than medium escaped (p < 0.001) and small escaped (p < 0.001). Small sized wild salmon passed more barriers than small sized escaped salmon (p < 0.001). Large escaped salmon did not differ from any size class of escaped and wild salmon (Figure 2). Final model included an interaction between size and salmon origin as predictors as well as random effects of both river and year of observation.

River	SeaTrout				EscAS			WildAS		
	<1 kg	1-2 kg	2-3 kg	>3 kg	Large	Medium	Small	Large	Medium	Small
Steinsdalselva	529	442	229	163	11	57	9	67	222	84
Granvinselva	2404	1615	829	408	12	46	9	71	313	113
Eio	254	279	216	155	0	4	0	53	75	22
Veig	38	90	123	63	0	7	0	18	18	7
Bjoreio	829	830	433	290	1	19	3	103	206	48
Æneselva	391	230	87	13	1	12	8	13	55	50
Hattebergselva	76	44	9	2	6	27	12	32	115	52
Uskedalselva	390	201	60	19	12	12	16	36	335	171
Etne	655	786	242	225	18	213	109	482	1474	558
Sorelva	290	328	155	37	2	15	2	200	819	320

Table 1: *Sample sizes in each of the study rivers for entire study period*
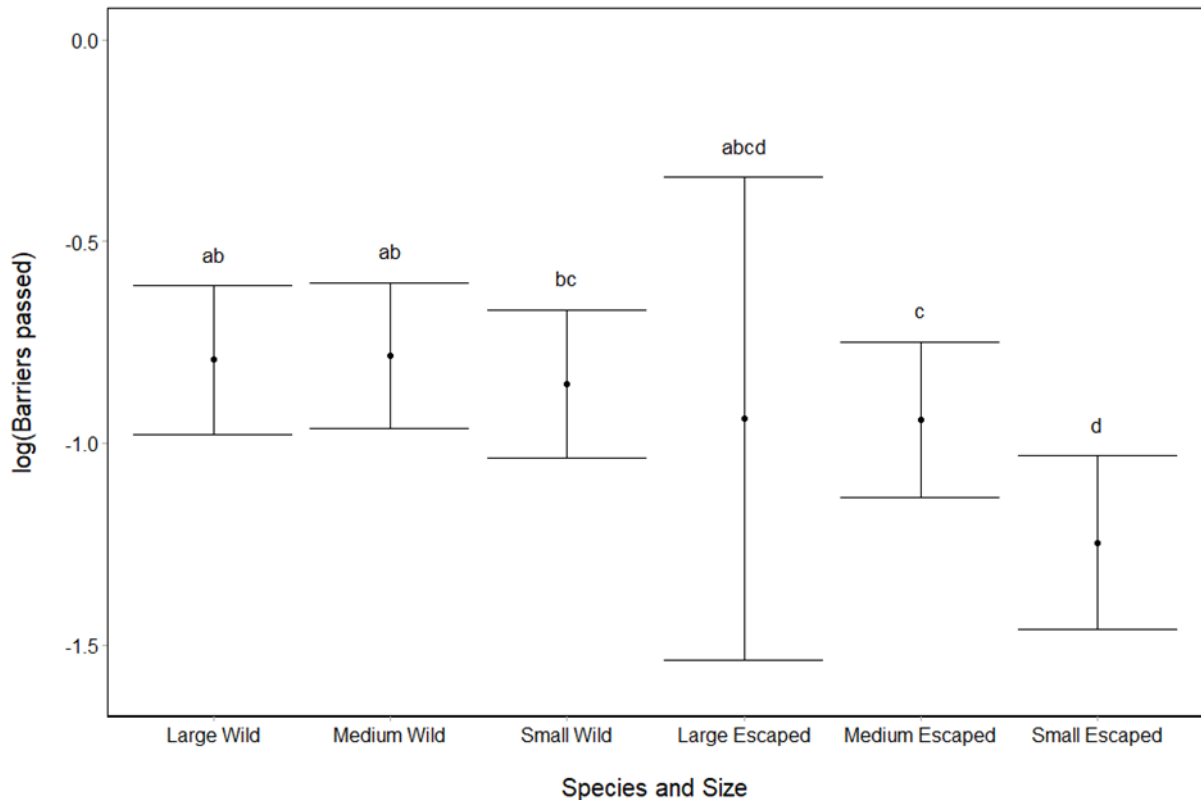
Figure 2: *Plot showing log values of predicted barriers passed for each size class and salmon group. Error bars represent 95 % confidence interval, points represent estimated mean log barriers passed by size groups in each salmon class. Letters a-c show relationship between groups where two groups are significantly different if they have no letter in common and not different if they share at least one common letter.*

3.2 River- specific testing

Testing the probability of passing barriers within the rivers showed a significant difference for Æneselva (p < 0.001), Uskedalselva (P = 0.023), Etne (p < 0.001) and Sørelva (p= 0.021) but no other river (Appendix 2). Wild Atlantic salmon showed higher probability of passing barriers than escaped Atlantic salmon and brown trout (Figure 3). Brown trout had higher probability of passing barriers than escaped Atlantic salmon in the rivers Æneselva (p = 0.002), Uskedalselva (p = 0.036) and Etne (p = 0.017) (Figure 3).

Comparing passage rates of wild and escaped Atlantic salmon across individual barriers show 4 barriers with equal passing rates, 11 barriers with higher rates for the wild salmon and the same amount with a higher passage rate by escaped salmon (Table 2). Barrier number 5 in Uskedalselva (60 % success in wild and 2 % success in escaped) and barrier number 1 in Sørelva (87 % success of wild and 10 % success in escaped) displayed highest difference in proportion of salmons passed in each of the groups (Figure 3, table 2). Both barriers being above 3 m. in height and consisting of a waterfall with high flow areas upstream.
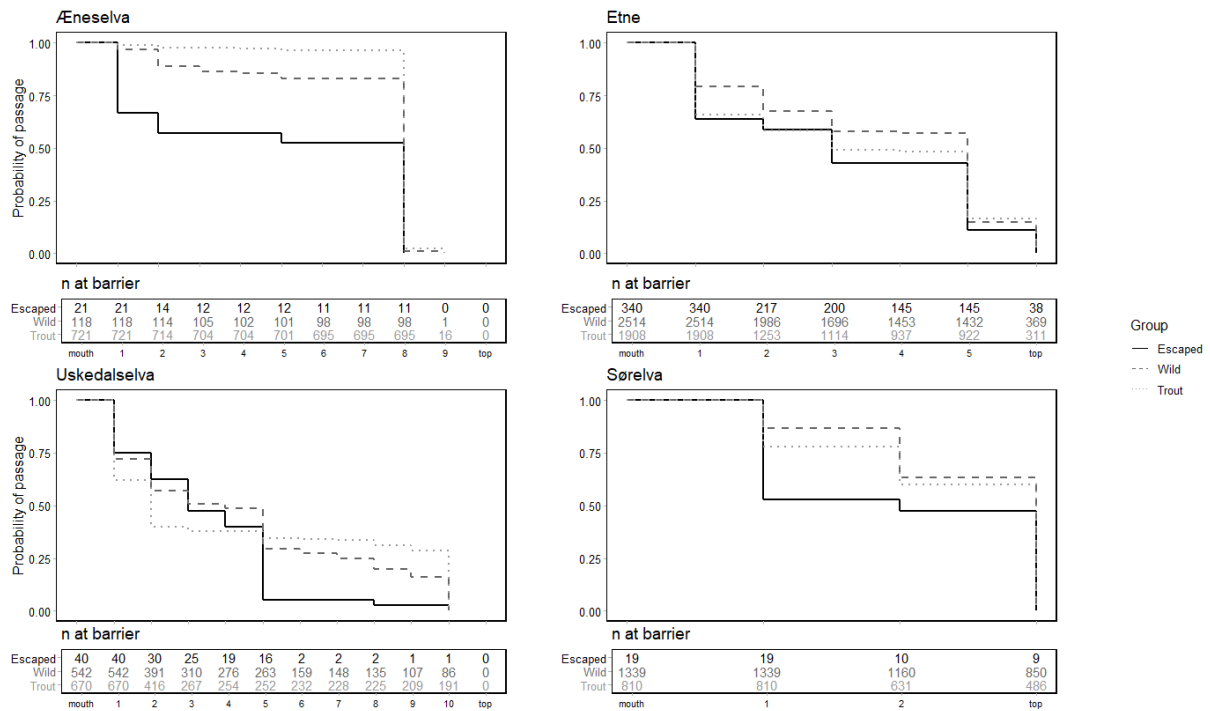
Figure 3: *Survival curves for brown trout and salmon groups in rivers where there were significant differences between wild and escaped salmon probability of passage. The Y-axis show cumulative probability of passage and the x-axis show barriers from river mouth to top of the anadromous reach. The number below the graphs indicate individuals of brown trout and each salmon group able to migrate at least to the barrier.*

River	Barrier number	Wild salmon				Escaped salmon				Brown trout			
		# Reaching barrier	# Stopped at barrier	Passability	Cumulative passability	# Reaching barrier	# Stopped at barrier	Passability	Cumulative passability	# Reaching barrier	# Stopped at barrier	Passability	Cumulative passability
Aeneselva	1	118	4	0.97	0.97	21	7	0.67	0.67	721	7	0.99	0.99
Aeneselva	2	114	9	0.92	0.92	14	2	0.86	0.86	714	10	0.99	0.99
Aeneselva	3	105	3	0.97	0.97	12	0	1.00	1.00	704	0	1.00	1.00
Aeneselva	4	102	1	0.99	0.99	12	0	1.00	1.00	704	3	1.00	1.00
Aeneselva	5	101	3	0.97	0.97	12	1	0.92	0.92	701	6	0.99	0.99
Aeneselva	6	98	0	1.00	1.00	11	0	1.00	1.00	695	0	1.00	1.00
Aeneselva	7	98	0	1.00	1.00	11	0	1.00	1.00	695	0	1.00	1.00
Aeneselva	8	98	97	0.01	0.01	11	11	0.00	0.00	695	679	0.02	0.02
Aeneselva	9	1	1	0.00	0.00	0	0	0.00	0.00	16	16	0.00	0.00
Uskedalselva	1	542	151	0.72	0.72	40	10	0.75	0.75	670	254	0.62	0.62
Uskedalselva	2	391	81	0.79	0.79	30	5	0.83	0.83	416	149	0.64	0.64
Uskedalselva	3	310	34	0.89	0.89	25	6	0.76	0.76	267	13	0.95	0.95
Uskedalselva	4	276	13	0.95	0.95	19	3	0.84	0.84	254	2	0.99	0.99
Uskedalselva	5	263	104	0.60	0.60	16	14	0.13	0.13	252	20	0.92	0.92
Uskedalselva	6	159	11	0.93	0.93	2	0	1.00	1.00	232	4	0.98	0.98
Uskedalselva	7	148	13	0.91	0.91	2	0	1.00	1.00	228	3	0.99	0.99
Uskedalselva	8	135	28	0.79	0.79	2	1	0.50	0.50	225	16	0.93	0.93
Uskedalselva	9	107	21	0.80	0.80	1	0	1.00	1.00	209	18	0.91	0.91
Uskedalselva	10	86	86	0.00	0.00	1	1	0.00	0.00	191	191	0.00	0.00
Etne	1	2514	528	0.79	0.79	340	123	0.64	0.64	1908	655	0.66	0.66
Etne	2	1986	290	0.85	0.85	217	17	0.92	0.92	1253	139	0.89	0.89
Etne	3	1696	243	0.86	0.86	200	55	0.73	0.73	1114	177	0.84	0.84
Etne	4	1453	21	0.99	0.99	145	0	1.00	1.00	937	15	0.98	0.98
Etne	5	1432	1063	0.26	0.26	145	107	0.26	0.26	922	611	0.34	0.34
Sørelva	1	1339	179	0.87	0.87	19	9	0.53	0.53	810	179	0.78	0.78
Sørelva	2	1160	310	0.73	0.73	10	1	0.90	0.90	631	145	0.77	0.77

Table 2: *Number of salmon able to migrate at least to a barrier, numbers of salmon successfully passing a barrier and passage rates (Individual passed a barrier /Individuals reaching a barrier) for each barrier in Æneselva, Uskedalselva, Etne and Sørelva.*

3.3   Influence of fish size and year

Size classes within escaped Atlantic salmon differed in the number of passed barriers in all of the tested rivers except Sørelva (p = 0.2), as predicted by the Cox proportional hazards model. Size classes within wild Atlantic salmon group only differed in Etne (p < 0.001). Escaped small Atlantic salmon had a lower probability of passing barriers compared to large escaped salmon in the river Æneselva (P = 0.013) and Etne (P = 0.003). Escaped small salmon also had a lower probability of passing barriers compared to medium sized escaped Atlantic salmon in Æneselva (P = 0.012) and Uskedalselva (P = 0.007).   No differences were found between medium- and large sized escapees. Wild salmon of medium size show higher probability of passing a barrier than large sized individuals in Etne (P = 0.016) (Figure 4).

Year of observation was found to influence probabilities of stopping at barriers in all rivers but Sørelva for escaped salmon and all rivers but Æneselva for wild salmon. Wild salmon passed more barriers in 2011 (Cox PH, p = 0.015) and 2012 (Cox PH, p = 0.037) when comparing to 2007 in Uskedalselva. Wild salmon also pass more barriers in 2007 compared to 2006 (Cox PH, p < 0.01) and 2012 (Cox PH, p < 0.01) in Etne and more barriers in 2013 compared to 2006 (Cox PH, p = 0.047) in Sørelva. Escaped salmon pass more barriers in 2011 compared to 2014 (Cox PH, p = 0.012) in Æneselva and more in 2011 (Cox PH, p = 0.006), 2012 (Cox PH, p < 0.001) and 2013 (Cox PH, p < 0.001) compared to 2007 in Uskedalselva. Escaped salmon in Etne passed more barriers in 2007 compared to 2006 (Cox PH, p < 0.001) and 2012 (Cox PH, p < 0.01) and in 2006 compared to 2012 (Cox PH, p = 0.01). Final models of escaped group included factors, size and year for rivers Æneselva, Uskedalselva and Etne. Null model had best fit in Sørelva and neither size nor year was included. Final models for Wild populations included both factor year and size in Etne, only year in Sørelva and Uskedalselva and only size in Æneselva. All final models displayed proportional hazards.
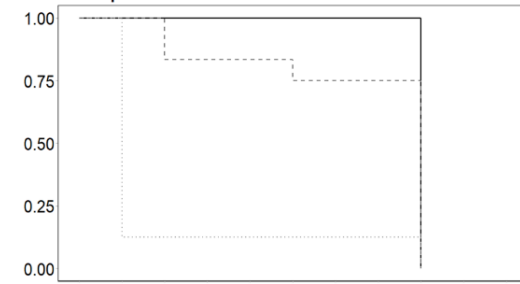
Æneselva

Wild
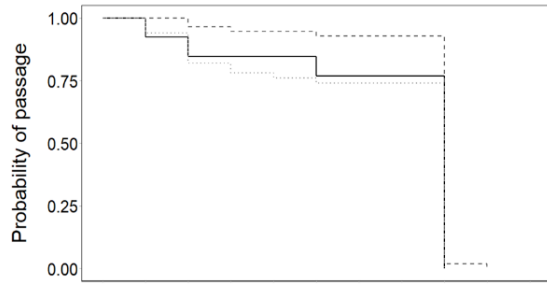
n at barrier	mouth	1	2	3	4	5	6	7	8	9	top
Large	13	13	12	11	11	11	10	10	10	0	0
Medium	55	55	55	53	52	52	51	51	51	1	0
Small	50	50	47	41	39	38	37	37	37	0	0

Escaped

n at barrier	mouth	1	2	3	4	5	6	7	8	9	top
Large	1	1	1	1	1	1	1	1	1	0	0
Medium	12	12	12	10	10	10	9	9	9	0	0
Small	8	8	1	1	1	1	1	1	1	0	0

Uskedalselva

Wild

n at barrier	mouth	1	2	3	4	5	6	7	8	9	10	top
Large	36	36	28	26	25	25	8	8	7	6	6	0
Medium	335	335	251	202	181	170	97	86	79	65	49	0
Small	171	171	112	82	70	68	54	54	49	36	31	0

Escaped
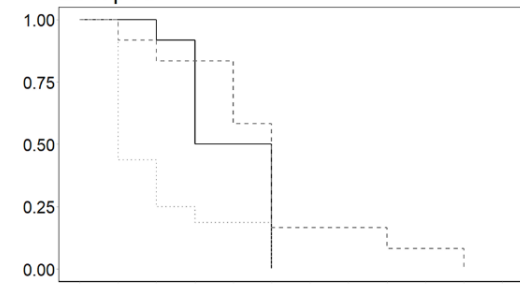
n at barrier	mouth	1	2	3	4	5	6	7	8	9	10	top
Large	12	12	12	11	6	6	0	0	0	0	0	0
Medium	12	12	11	10	10	7	2	2	2	1	1	0
Small	16	16	7	4	3	3	0	0	0	0	0	0

Size
— Large
-- Medium
⋯ Small

Figure 4: *Survival curves for each size class of Atlantic salmon. The Y-axis show cumulative probability of passage and the x-axis show barriers from river mouth to top of the anadromous reach. The number below the graphs indicate individuals in each size class able to migrate at least to the barrier.*

3.4   Passability of barriers

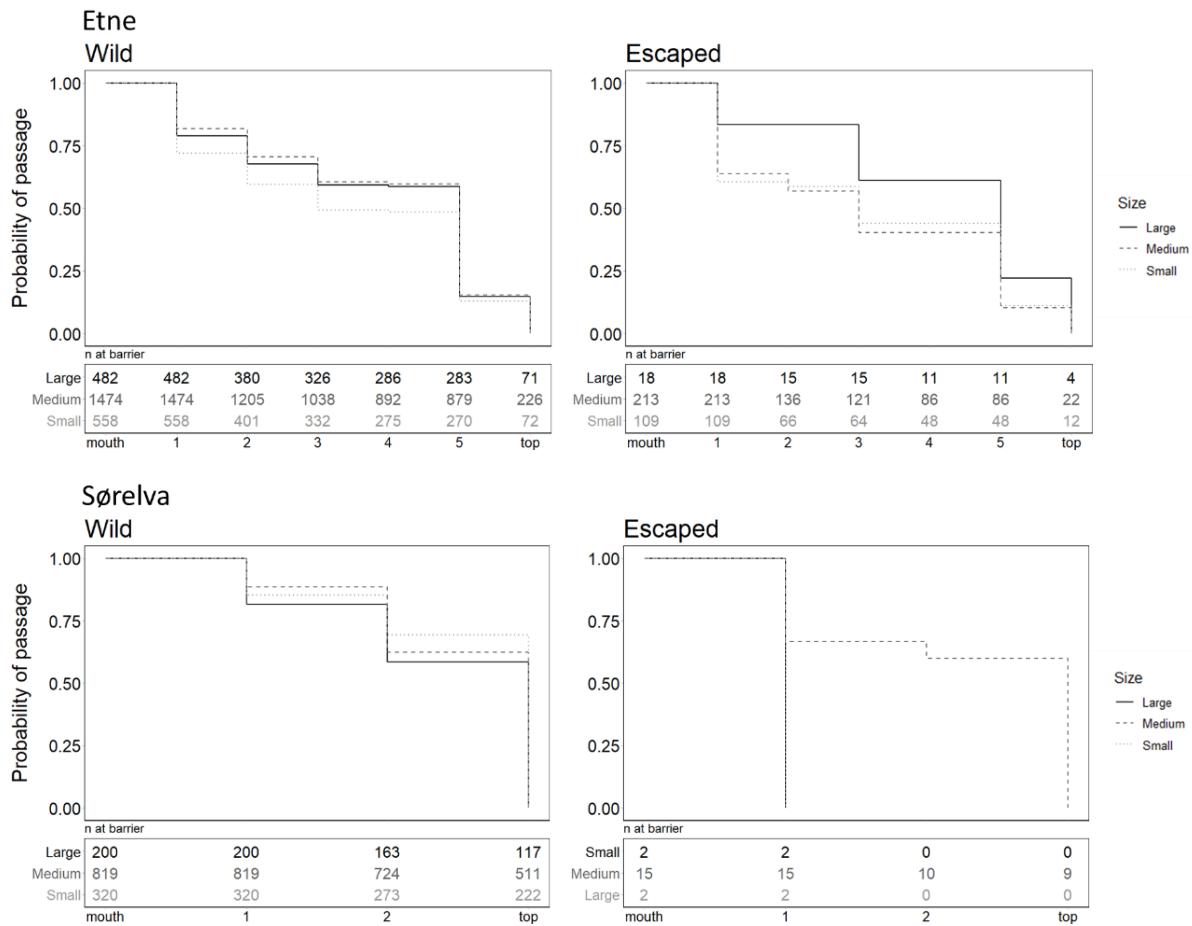The number of fish above barriers was significantly influenced by barrier height (Poisson regression, p = 0.077), barrier length (Poisson regression, p = 0.005) and by previous barriers passed (Poisson regression, P < 0.001). All variables were found to increase model fit.

Passability scores and cumulative passability of all barriers found in study rivers show that barriers 1 and 2 in Steinsdalselva, barrier 5 in Veig, barrier 3 in Granvinselva, barrier 9 and 8 in Æneselva and barrier 10 in Uskedalselva has passage rates of less than 15 % of brown trout, wild and escaped salmon, indicating possible strong migration barriers (Table.3) Barrier 10 in Uskedalselva and barrier 2 in Steinsdalselva are situated at top of anadromous reach and no counts have been made above the barrier. All other barriers sits close to top of anadromous reach and all except number 8 in Æneselva are higher than 1.8 m and characterized by rapids or waterfalls (Table 3). In addition, it was detected that all barriers of lower height than 1.5 m had a passability of > 66 % and that wild salmon hade higher passability in all barriers with slope > 50 %.

Testing passability for correlation to barrier characteristics height, length, distance from river mouth and previous barriers passed show that height (p = 0.002) and distance from river mouth (p < 0.001) had a significant negative effect on passability for brown trout, wild and escaped salmon combined. Cumulative passability was only affected by distance to river mouth (Figure 5). Testing passability for each group individually showed only an effect of distance from river mouth in escaped (p = 0.03) and wild salmon (p = 0.03) but not trout (p = 0.09). Testing cumulative passability for each group individually showed an effect of distance to river mouth for wild salmon (p=0.02) and brown trout (p=0.02).

River	Barrier number	Distance (km)	Height (m)	Type	Detection type	Passability Wild salmon	Passability escaped salmon	Passability brown trout
Steinsdalselva	1	4.1	1.8	Rapid	Expert	0.07	0.04	0.01
Steinsdalselva	2	4.2	4	Waterfall	Expert + Remote	0.00	0.00	0.00
Granvinselva	3	12.6	4.5	Waterfall	Expert + Remote	0.01	0.11	0.03
Veig	5	3	7	Rapid	Remote	0.14	0.00	0.13
Aeneselva	8	5.7	0.5	Riffle area	Expert	0.01	0.00	0.02
Aeneselva	9	6.1	3	Rapid	Expert + Remote	0.00	0.00	0.00
Uskedalselva	10	10.2	3.4	Rapid	Expert + Remote	0.00	0.00	0.00

Table 3: *Barriers with low passabilities of brown trout and both salmon groups. Barrier number represent the order of the barrier in river, counted from mouth to top, Distance represent distance from river mouth, height represent height difference between water surfaces directly below and above the barrier, type represent the dominating characteristic of the barrier and detection type represent if the barrier was detected by expert, remote sensing or both*
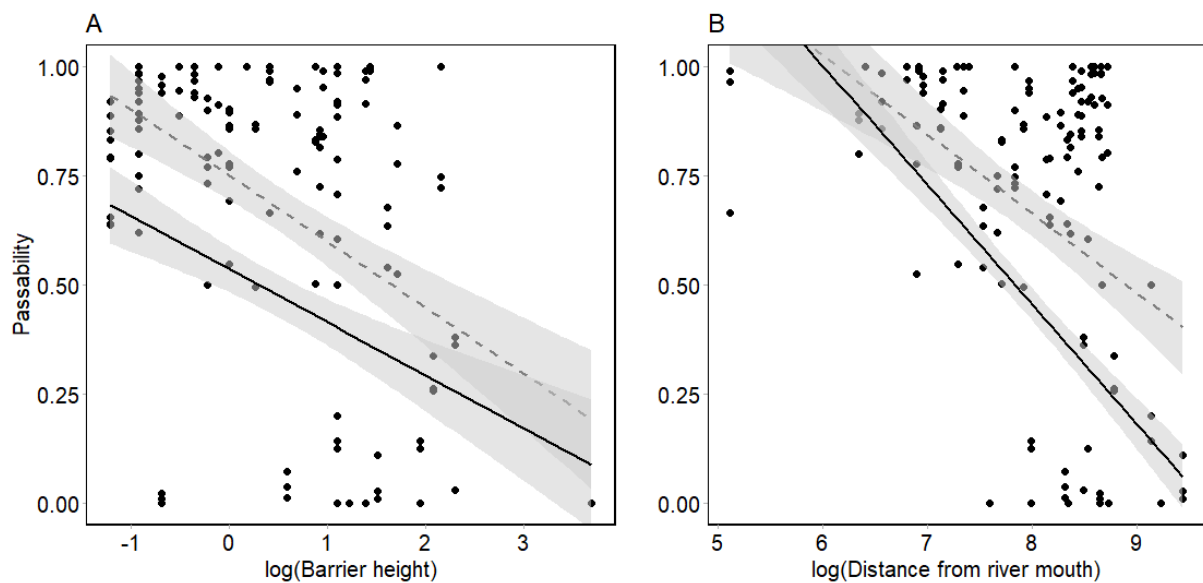

Figure 5: *Passability (solid line) and cumulative passability (dashed line) versus barrier height (plot A) and distance from river mouth (plot B). The y-axis show passability of individual barriers and the x-axis show log values of barrier height in meters and distance from river mouth in meters. Dots show observed values and line show predicted values with standard error.*

A total of 48 possible barriers were detected by remote detection via digital terrain models and expert knowledge. 34 barriers were identified by expert knowledge only, two barriers were identified exclusively via remote detection and 12 were identified by both methods (Appendix 3). Out of the seven barriers with lowest passability by brown trout, wild salmon and escaped salmon two were detected by expert knowledge and one by remote sensing only, the rest were identified in both methods (Table 3).

26 of the possible barriers were located in rivers displaying differences in barriers passed between wild and escaped salmon (Æneselva, Uskedalselva, Etne and Sørelva). 19 of these were exclusively identified by expert knowledge and the rest by both expert knowledge and remote sensing.

Only barrier number 10 in Uskedalselva was measured using differential GPS due to high water discharge during the field work. 22 of the detected barriers were visited in the field, and characteristics of 19 were measured manually using measuring tape. Three of the barriers were too high or located in too dangerous areas to be measured.

Drop height- and length of all barriers, including barriers not visited during the field work, were measured using elevation data in ArcMap. A comparison of average length acquired in ArcMap and measured manually in field indicated that the lengths were 0.5 m longer in ArcMap. Comparison of barrier height showed an average of 0.98 m higher using ArcMap. Comparing manually measurements to measurement by differential GPS made at Uskedal barrier 10, show that manual measurements overestimate barrier length by approximately 13 m. and barrier height by 0.3 m. (Appendix 4)

4 Discussion

The present study has presented variations in the passage of natural barriers among brown trout, wild and escaped Atlantics salmon. The potential natural barriers were detected through analysis of elevation changes along river stretches using ArcMAP and by consulting an expert with much experience from the rivers. Results have shown that the method constitutes a quick and easy way to detect potential natural barriers in rivers without the need of extensive field work or full river investigation.

4.1 Group dependent passage of barriers

Wild salmon was found to pass more natural barriers on average than escaped salmon when comparing all study rivers combined. Passability scores of barriers were also found which show higher passability by wild than escaped salmon. This could be explained by differences in ability to ascend a barrier, as found at a waterfall by Gausen and Moen (1990) and in Heggberget et al. (1996) at a fish

ladder. Brown trout was found to pass more barriers than escaped salmon but less than wild. This can be explained by the barrier passability being dependent on swimming and jumping capabilities (Glover et al. 2008, Baudoin et al. 2015) which are greater than brown trout in Wild Atlantic salmon (Booth et al. 1997, Baudoin et al. 2015, Hvas et al. 2017, Hvas & Oppedal 2017, Taugbøl et al. 2019). Testing of individual rivers revealed differences in the probability of passing barriers by wild and escaped salmon in four of the study-rivers, where wild salmon passed more barriers than escaped salmon. Adding brown trout as a response group show that it pass less barriers than wild but more than escaped in all of the four rivers except for Sørelva, where no difference is found. Barriers were found that indicate higher passability by escaped salmon compared to wild. These results can be explained by escaped salmons swimming far upstream without goal while wild salmons stop at spawning areas (Heggberget et al. 1996, Thorstad et al. 1998, Moe et al. 2016). As such, barriers where escaped salmon pass at a higher rate than wild would presumably have no real effect on either population.

Jensen et al. (1998) concluded that factors stimulating upstream migration and passage of barriers could be specific for rivers. It was found similar temperature and discharge had higher effects on wild Atlantic salmon migration in the river Vefsna compared to Austefjord (Jensen et al. 1998). Other research have concluded that escaped salmon is less apt to migrate pass natural barriers (Gausen & Moen 1990, Moe et al. 2016) but also that escaped salmon migrate back downstream after passing a barrier (Kennedy et al. 2013), as well as distributing themselves far upstream a river when possible (Økland et al. 1995). Farmed salmon may also stop migration without reaching barriers (Thorstad et al. 2003). Uncertainties of escaped salmon migration behaviour also indicate the barrier passage is river- specific which would make it possible that natural barriers do not affect populations in different rivers equal.

Wild Atlantic salmon and brown trout migrate to a specific spawning area imprinted at pre-smolt stage and will stop when this area is reached (Økland et al. 2001, Finstad et al. 2005). In this study stoppage was considered to be a consequence of reaching a barrier, which would be incorrect in more cases than not for wild salmon and trout. However, the same stop signal is lacking in escaped salmon, which could make them more prone to migrate far upstream, only to stop when they lack the ability to continue (Heggberget et al. 1996, Thorstad et al. 1998, Moe et al. 2016) making them more suitable in this analysis. Lack of imprint and previous experience of the river might reduce motivation to migrate upstream (Økland et al. 1995), but as several papers have documented extensive upstream movement by escaped salmon without previous knowledge of the rivers, a lack of imprint is not assumed cause stoppage of escaped salmon in this study (Heggberget et al. 1996, Thorstad et al. 1998, Moe et al. 2016). Comparing passage of wild and escaped salmon allow us to detect barriers that have

high effect on escaped salmon but low on wild. As salmon and trout is sympatric in many Norwegian rivers (Finstad et al. 2005), it is also important to consider trout ability to pass barriers.

4.2 Passage of barriers by different sized salmons

Differences among size classes of wild and escaped salmon in all study rivers regarding probability of passing a barrier suggest that fish size is an important factor to passing barriers for escaped Atlantic salmon but not for wild conspecifics. Testing for size dependence in individual rivers with differences between wild and escaped salmon showed the same result. The effect of size class in escaped salmon can likely be explained by increased swimming and jumping capabilities in larger individuals (Peake et al. 1997).

Passage of anthropogenic barriers by Atlantic salmon is positively correlated to swimming speeds and jumping capabilities, which in turn is positively correlated to fish size (Peake et al. 1997, Baudoin et al. 2015). As natural migration barriers would subject fish to challenges similar to that of anthropogenic barriers (Kemp et al. 2008), it is safe to assume that passage of natural barriers also can be positively correlated to fish size. These result are in line with what have been found in this study in regards to escaped salmon. Unexpectedly, the same size dependent passage of barriers in not found for wild salmon. This could be explained by differences in migration patterns. Wild Atlantic salmon have been shown to enter rivers earlier and have longer migration period than its farmed conspecific (Laine et al. 2002). If smaller sizes of salmon is less apt to swim against high flow and need low flow conditions to pass a barrier as stated by Baudoin et al. (2015) and Peake et al. (1997), a longer migration period would result in a higher chance of experiencing optimal migration conditions (Laine et al. 2002, Reiser et al. 2006). The earlier start of migration would then give wild salmon a higher probability of experiencing size specific requirements for barrier passage in a river where flow and temperature varies within the migration period.

4.3 Barriers characteristics

Barriers displaying higher passability by wild than escaped salmon were found as well as the opposite. At barriers where the gradient was higher than 50 % wild salmon always passed at a higher rate than escaped salmon. This value is above the value of 10 % gradient over six consecutive meters used by Glover et al. (2008). As this value was set with potadromous brown trout as target species, results are expected. At barriers lower than 1.5 m in height, all salmonids had a passage rate of at least 66 % excluding barrier 8 in Æneselva. A height of 1.5 is considered a low impact barrier when water depth is one meter or lower (depending on slope) by Baudoin et al. (2015) and findings are thus as expected. Findings stating that shallow areas can constitute barriers have been done (Økland et al. 2001, Baudoin et al. 2015) and this can explain the low passability of barrier 8 in Æneselva. Another explanation can be the effect of multiple downstream barriers which also has been found by Thorstad et al. (2003). The

highest difference between wild and escaped salmon passage rates was found at Barriers 5 in Uskedalselva (60 % success in wild and 2 % success in escaped) and 1 in Sørelva (87 % success of wild and 10 % success in escaped). Both of these barriers have heights above 3 m and are characterised by a water fall with metrics similar to definition of a full barrier with >3 m vertical drop (Baudoin et al. 2015). In addition, low or zero probability of passage were found at barriers 8 and 9 in Æneselva, indicating a potential full barrier for both wild and escaped salmon. Barrier number 8 has a height of 0.5 m and is characterised by a shallow area, while barrier 9 is situated in a strong rapid and is 3 m high both corresponding to previously found barriers (Økland et al. 2001, Baudoin et al. 2015)

Characteristics of natural barriers are poorly defined and what metrics to be used when assessing their impact are not standardized (Thorstad et al. 2008). By adopting metrics set for anthropogenic barriers (SNIFFER 2010, Baudoin et al. 2015), an estimation of impact can be made. However, the estimation of impact may not be accurate when used on natural structures. Estimations may be unreliable because of bottom roughness that offer resting spots and varying water velocities within the barrier (Castro-Santos 2005, Baudoin et al. 2015). In addition, impassable falls have been defined as 3 m drops (Glover et al. 2008, Baudoin et al. 2015) but observations have been made of salmon passing waterfalls of 5 m (Kennedy et al. 2013) and 4 m height (Rivinoja et al. 2001).

4.4   Passage of barriers and passability scores

An anthropogenic barrier is commonly measured using the characteristics height, length and slope to assess its impact on river connectivity (Glover et al. 2008, Meixler et al. 2009, SNIFFER 2010, Baudoin et al. 2015). These characteristics, as well as distance from river mouth and number of previous barriers passed, were found to have an effect on the number of salmon and trout able to pass a barrier in this study. As a natural barrier would create similar challenges for passage (i.e., high water flow and steep elevation changes) as anthropogenic barriers (Castro-Santos 2006), and as passage of multiple barriers can have a negative effect on upstream migration (Thorstad et al. 2003), these results were as expected. Passability and cumulative passability for brown trout, wild salmon and escaped salmon were not found to be affected by height, length or slope which was unexpected. According to protocols, barriers should be assessed based on height, length and slope of a barrier (Glover et al. 2008, SNIFFER 2010, Baudoin et al. 2015). This can possibly be a result of inaccurate calculations of passability.

The passability and cumulative passability of a barrier can be used to estimate the barrier impact and the effect of passing multiple barriers (O'Hanley & Tomberlin 2005, Kemp & O'Hanley 2010, Baudoin et al. 2015). In this study, it was assumed migration of all individuals in a population is blocked due to inability to pass a potential barrier. This definition is most possibly incorrect since wild salmon home to a spawning site in river and escaped salmon can lose motivation and stop migrating without

the presence of a barrier (Heggberget et al. 1993, Thorstad et al. 2003, Moe et al. 2016). Escaped and wild salmon might therefore stop migration by other reasons than the assumed incapability of passing the next barrier, which would lead to an underestimation of passability. On the other hand, escaped salmon may undertake extensive up- and downstream movement during the spawning season (Økland et al. 1995, Kennedy et al. 2013) and successfully pass barriers only to return downstream (Kennedy et al. 2013), which would lead to an overestimation of passability.

Passability scores and cumulative passabilities were calculated based on fish positions in river relative to the barrier. A more fine scale validation would be beneficial when calculating passability since passability ideally should reflect both the proportion of a population attempting to pass, the number of passage successes, and the time taken to succeed (Kemp & O'Hanley 2010). Experiments tracking individual fish could, for example, be used to more accurately estimate the numbers of salmon actually failing to pass a barrier (Kemp et al. 2008, Kemp & O'Hanley 2010). Using observations of all salmonids trying and succeeding to pass a barrier, the correct number of attempts and passages can be used to more precisely calculate passability.

4.5   Barrier detection and verification

The method of detecting barriers remotely using terrain models show great promise. Several sites with high gradients could be identified and only a few detections of clear non-barriers were made.

Most barriers were easily detectable in the field but start and stop of a barrier were sometimes hard to identify. When classifying anthropogenic barriers, the entire structure is included in measurements and combined features of vertical falls and inclined faces are considered (Ovidio et al. 2007, Baudoin et al. 2015). When measuring natural migration barriers, these features become more diffuse and measurements become less accurate. Bottom structures can cause turbulent flow, and also create small resting places and small pools within a barrier that can affect passage in any direction (Haro et al. 2004, Baudoin et al. 2015).

Remote barrier detection using digital terrain models present a much needed way to quickly identify potential barriers in a river that limits time-demanding work in field. This study used a barrier detection level of 0.5 m abrupt change in elevation and 10 % gradient over six consecutive meters as defined by Glover et al. (2008). Examination of passabilities suggested that when using Atlantic salmon or brown trout as study species, detection levels should not be higher than 50 % gradient and 1.5 m of abrupt elevation change to fully cover potential natural barriers.

4.6   Year dependent passage of barriers

The passing of barriers varies among years for both wild and escaped Atlantic salmon in Æneselva, Uskedalselva, Etne and Sørelva. No individual year had positive or negative effect on barriers passed

by any salmon population across all tested rivers and no trend could be seen over time. These differences between years could likely be explained by variations of flow and temperature from year to year. Previous research have shown that discharge and temperature affect the motivation to migrate in salmonids (Jensen et al. 1998, Laine et al. 2002, Reiser et al. 2006, Kennedy et al. 2013). No measurements of water discharges or temperature were considered in this study but it is likely that these factors were not equal among years.

5 Conclusion

This project has presented a method to remotely detect possible natural barriers to Atlantic salmon and brown trout migration. Natural barriers have been found that display a higher passage rate by wild than escaped salmon. These barriers have been used to examine the defining characteristics of natural barriers and compared to known natural barriers in previous studies.

This study contributes much needed knowledge about salmonid migration in natural systems that can be of aid in future efforts to increase river connectivity. River restoration and dam removal can be focused on sections of a river where natural connectivity is high to maximize the chance of opening previously closed habitats for salmonids. In addition, natural barriers affect escaped salmon more than wild. This means that they also can be considered as a mean to restrict movement by escaped salmon and reduce gene flow between wild and farmed populations of salmon. This will be of aid to conserve the wild population by reducing gene flow and competition between the two conspecifics.

Natural barriers can have an impact on river connectivity by stopping escaped salmon and possibly delaying or stopping wild salmon and brown trout. These barriers also have a variety of appearances, from riffle areas to waterfalls, and their effect on salmonid migration varies. Future efforts to increase river connectivity thus need to address the presence of natural barriers to fully increased habitat for migrating fish species. As natural barriers are a part of the natural river system and therefore a desired limitation to salmonid migration, they should not be removed. Instead, efforts need to be located where risk of negation by natural barriers can be minimum.

6   References

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7 Appendices

Appendix 1: *Table of all detected potential natural barriers and their passability and cumulative passability for each of the study groups. Barrier number is number of the barrier counted from river mouth, distance is distance from river mouth, height is barrier height, length is length between downstream- and upstream pool, detection type is the method used for detecting the barrier. # Reaching barrier = All individuals migrating passed all downstream barriers, # Stopped at barrier = n individuals stopping between closest downstream barrier and the barrier in question.*

River	Wild salmon				Escaped salmon				Brown trout			
	# Reaching barrier	# Stopped at barrier	Passability	Cumulative passability	# Reaching barrier	# Stopped at barrier	Passability	Cumulative passability	# Reaching barrier	# Stopped at barrier	Passability	Cumulative passability
Steinsdalselva	373	346	0.07	0.07	77	74	0.04	0.04	1363	1345	0.01	0.01
Steinsdalselva	27	27	0.00	0.00	3	3	0.00	0.00	18	18	0.00	0.00
Granvinselva	497	21	0.96	0.96	67	4	0.94	0.94	5256	112	0.98	0.98
Granvinselva	476	381	0.20	0.20	63	54	0.14	0.14	5144	2567	0.50	0.50
Granvinselva	95	94	0.01	0.01	9	8	0.11	0.11	2577	2504	0.03	0.03
Eio	150	0	1.00	1.00	4	0	1.00	1.00	904	94	0.90	0.90
Veig	43	6	0.86	0.86	7	1	0.86	0.86	314	30	0.90	0.90
Veig	37	2	0.95	0.95	6	0	1.00	1.00	284	32	0.89	0.89
Veig	35	6	0.83	0.83	6	1	0.83	0.83	252	125	0.50	0.50
Veig	29	8	0.72	0.72	5	0	1.00	1.00	127	32	0.75	0.75
Veig	21	18	0.14	0.14	5	5	0.00	0.00	95	83	0.13	0.13
Bjoreio	357	51	0.86	0.86	23	3	0.87	0.87	2382	1202	0.50	0.50
Bjoreio	306	10	0.97	0.97	20	1	0.95	0.95	1180	70	0.94	0.94
Bjoreio	296	34	0.89	0.89	19	4	0.79	0.79	1110	324	0.71	0.71
Bjoreio	262	27	0.90	0.90	15	2	0.87	0.87	786	241	0.69	0.69
Bjoreio	235	43	0.82	0.82	13	2	0.85	0.85	545	208	0.62	0.62
Bjoreio	192	6	0.97	0.97	11	0	1.00	1.00	337	20	0.94	0.94
Bjoreio	186	115	0.38	0.38	11	7	0.36	0.36	317	307	0.03	0.03
Aeneselva	118	4	0.97	0.97	21	7	0.67	0.67	721	7	0.99	0.99
Aeneselva	114	9	0.92	0.92	14	2	0.86	0.86	714	10	0.99	0.99
Aeneselva	105	3	0.97	0.97	12	0	1.00	1.00	704	0	1.00	1.00
Aeneselva	102	1	0.99	0.99	12	0	1.00	1.00	704	3	1.00	1.00
Aeneselva	101	3	0.97	0.97	12	1	0.92	0.92	701	6	0.99	0.99
Aeneselva	98	0	1.00	1.00	11	0	1.00	1.00	695	0	1.00	1.00
Aeneselva	98	0	1.00	1.00	11	0	1.00	1.00	695	0	1.00	1.00
Aeneselva	98	97	0.01	0.01	11	11	0.00	0.00	695	679	0.02	0.02
Aeneselva	1	1	0.00	0.00	0	0	0.00	0.00	16	16	0.00	0.00
Hattebergselva	199	21	0.89	0.89	45	9	0.80	0.80	131	16	0.88	0.88
Hattebergselva	178	41	0.77	0.77	36	8	0.78	0.78	115	52	0.55	0.55
Hattebergselva	137	50	0.64	0.64	28	9	0.68	0.68	63	29	0.54	0.54
Hattebergselva	87	54	0.38	0.38	19	10	0.47	0.47	34	21	0.38	0.38
Uskedalselva	542	151	0.72	0.72	40	10	0.75	0.75	670	254	0.62	0.62
Uskedalselva	391	81	0.79	0.79	30	5	0.83	0.83	416	149	0.64	0.64
Uskedalselva	310	34	0.89	0.89	25	6	0.76	0.76	267	13	0.95	0.95
Uskedalselva	276	13	0.95	0.95	19	3	0.84	0.84	254	2	0.99	0.99
Uskedalselva	263	104	0.60	0.60	16	14	0.13	0.13	252	20	0.92	0.92
Uskedalselva	159	11	0.93	0.93	2	0	1.00	1.00	232	4	0.98	0.98
Uskedalselva	148	13	0.91	0.91	2	0	1.00	1.00	228	3	0.99	0.99
Uskedalselva	135	28	0.79	0.79	2	1	0.50	0.50	225	16	0.93	0.93
Uskedalselva	107	21	0.80	0.80	1	0	1.00	1.00	209	18	0.91	0.91
Uskedalselva	86	86	0.00	0.00	1	1	0.00	0.00	191	191	0.00	0.00
Etne	2514	528	0.79	0.79	340	123	0.64	0.64	1908	655	0.66	0.66
Etne	1986	290	0.85	0.85	217	17	0.92	0.92	1253	139	0.89	0.89
Etne	1696	243	0.86	0.86	200	55	0.73	0.73	1114	177	0.84	0.84
Etne	1453	21	0.99	0.99	145	0	1.00	1.00	937	15	0.98	0.98
Etne	1432	1063	0.26	0.26	145	107	0.26	0.26	922	611	0.34	0.34
Sørelva	1339	179	0.87	0.87	19	9	0.53	0.53	810	179	0.78	0.78
Sørelva	1160	310	0.73	0.73	10	1	0.90	0.90	631	145	0.77	0.77

Appendix 2: *Survival curves of escaped Atlantic salmon (solid black), brown trout (dashed dark gray) and wild Atlantic salmon (dotted light gray). P-values for log rank testing of differences in passage between salmon groups are displayed for each river. Eio river failed to produce a p value as no salmons stopped below the only found barrier.*
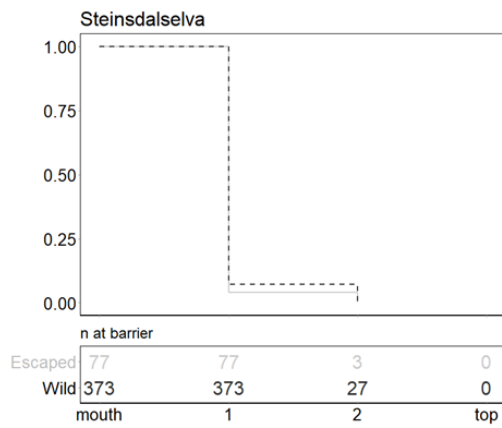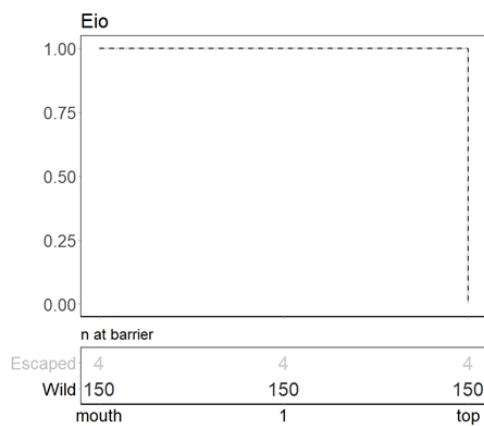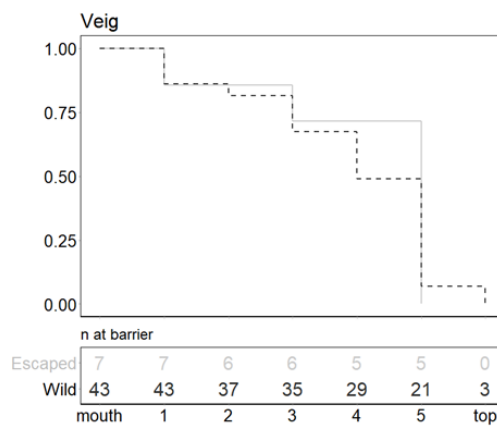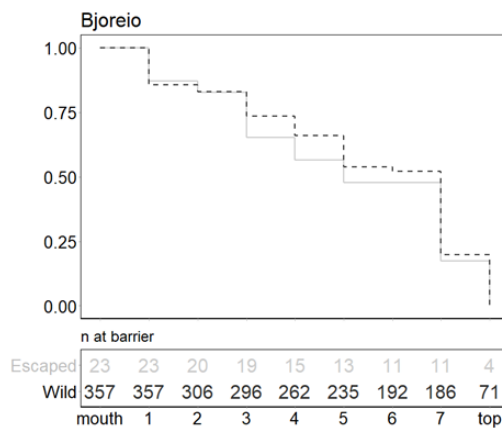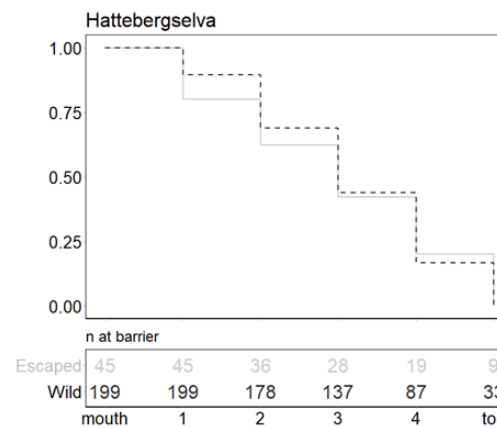

P = 0.28
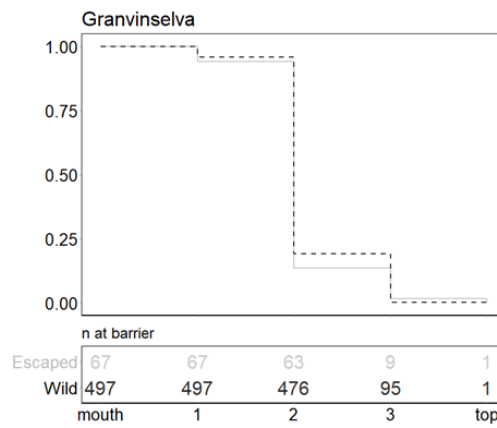
P = 0.32

P = NA

P = 0.61

P = 0.61

P = 0.86

Appendix 3: Table of barrier characteristics of each individual barrier. Type = defining characteristic of the barrier. Height digital and length digital = measurments of barrier height and length performed in ArcMap. Height field and length field = measurments of height and length performed at field visit. NA values are present where no field measurements could be done.

River	Barrier_ID	Type	Distance from mouth (km)	Detection method	Length Digital (m)	Height Digital (m)	Length Field (m)	Height Field (m)
Æneselva	Æn1	Rapid	0.17	Expert	18.7	1.5	15.00	1.50
Æneselva	Æn2	Rapid	0.71	Expert	217.7	11.8	NA	NA
Æneselva	Æn3	Rapid	0.90	Expert	50	4.2	NA	NA
Æneselva	Æn4	Rapid	1.01	Expert	3.9	0.8	NA	NA
Æneselva	Æn5	Rapid	1.26	Expert + Remote	99	8.8	100.00	10.00
Æneselva	Æn6	Rapid	1.44	Expert	20.8	2.7	NA	NA
Æneselva	Æn7	Rapid	1.63	Expert	53.8	5.5	NA	NA
Æneselva	Æn8	Riffle	5.71	Expert	4.9	0.8	2.00	0.50
Æneselva	Æn9	Rapid	6.15	Expert + Remote	55.6	4	50.00	3.00
Bjoreio	Bj1	Rapid	2.74	Expert	4	0.75	NA	NA
Bjoreio	Bj2	Rapid	2.88	Expert	26	1.5	NA	NA
Bjoreio	Bj3	Rapid	3.40	Expert + Remote	117.1	5.2	15.00	3.00
Bjoreio	Bj4	Rapid	3.91	Expert	9.8	1	NA	NA
Bjoreio	Bj5	Rapid	4.27	Expert + Remote	10.8	2.5	NA	NA
Bjoreio	Bj6	Rapid	4.39	Expert	2.8	0.7	NA	NA
Bjoreio	Bj7	Rapid	4.87	Expert + Remote	132	9.8	NA	NA
Eio	Ei1	Threshold	0.60	Expert	4	1	0.30	0.60
Etne	Et1	Threshold	3.52	Expert	3.7	0.4	0.20	0.30
Etne	Et2	Threshold	4.76	Expert	1.5	0.4	0.80	0.30
Etne	Et3	Rapid	5.62	Expert + Remote	17.7	4	15.00	2.50
Etne	Et4	Threshold	5.72	Expert	3	0.4	NA	NA
Etne	Et5	Waterfall	6.53	Expert + Remote	59.7	10	32.00	8.00
Granvinselva	Gr1	Rapid	1.05	Expert	1.9	0.3	10.00	0.50
Granvinselva	Gr2	Rapid	9.27	Expert	15.3	0.5	50.00	3.00
Granvinselva	Gr3	Waterfall	12.60	Expert	9	4.5	NA	NA
Hattebergselva	Ha1	Riffle	0.56	Expert	3.8	0.4	NA	NA
Hattebergselva	Ha2	Rapid	1.47	Expert	10	1	NA	NA
Hattebergselva	Ha3	Rapid	1.85	Expert	41	4.8	30.00	5.00
Hattebergselva	Ha4	Waterfall	1.99	Expert + Remote	98.4	21	100.00	40.00
Sorelva	So1	Rapid	0.98	Expert + Remote	37	5.5	NA	NA
Sorelva	So2	Rapid	2.52	Expert	13.9	0.8	NA	NA
Steinsdalselva	St1	Rapid	4.07	Expert + Remote	21	4.7	15.00	4.00
Steinsdalselva	St2	Waterfall	4.20	Expert + Remote	2	1.7	1.00	1.80
Uskedalselva	Us1	Rapid	2.13	Expert	2.9	0.4	NA	NA
Uskedalselva	Us2	Rapid	4.16	Expert	2	0.3	NA	NA
Uskedalselva	Us3	Rapid	4.62	Expert + Remote	27.8	2.2	30.00	2.00
Uskedalselva	Us4	Rapid	4.74	Expert	36.4	2.6	NA	NA
Uskedalselva	Us5	Waterfall	5.08	Expert + Remote	125.3	4.2	100.00	5.00
Uskedalselva	Us6	Rapid	5.24	Expert	3	0.7	NA	NA
Uskedalselva	Us7	Rapid	5.40	Expert + Remote	43	3.4	50.00	3.00
Uskedalselva	Us8	Rapid	5.79	Expert	2	0.8	NA	NA
Uskedalselva	Us9	Rapid	6.10	Expert	3	0.9	NA	NA
Uskedalselva	Us10	Rapid	10.15	Expert + Remote	42.3	3.4	35.00	2.50
Veig	Ve1	Rapid	1.24	Expert	4	0.6	1.00	1.00
Veig	Ve2	Rapid	1.54	Expert	2.9	0.6	NA	NA
Veig	Ve3	Rapid	2.22	Expert + Remote	23.1	2.4	NA	NA
Veig	Ve4	Rapid	2.53	Remote	104	8.6	NA	NA
Veig	Ve5	Rapid	2.95	Remote	1.5	3.92	10.00	7.00

Appendix 4: *Comparing measurements of barrier 10 in Uskedalselva. Measurements were made by differential GPS, manual measurements using measuring tape and digitally in ArcMap.*

Measurement	Length	Height	Depth downstream pool	Depth upstream pool	Depth in barrier
Differential GPS	20	2.8	0.3	0.7	0.5
Manual	35	2.5	1	0.5	0.3
ArcMap	42.3	3.4	NA	NA	NA