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# Marine Migration Behaviour of Brown Trout from Five Watercourses Flowing into a Common Fjord System in Northern Norway

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## **Abstract**

Brown trout is a freshwater fish which exhibits a wide array of life history and migration strategies. These different strategies result in great morphological variation both among and within populations. The aim of the study has been to describe the marine migratory behaviour of five populations of brown trout that all have access to the same fjord system and compare these findings with current theory in the field, with focus on the migration continuum theory of brown trout migration. The marine migration behaviour was studied with acoustic telemetry, and the life histories of the fish through fish scale analysis. In total 137 veteran fish with an assumed or confirmed marine migration were followed for up to two seasons during 2016 and 2017. Difference was seen between the populations, with variation in length-at-age and different ages and sizes of smoltification. Of the fjord migrating fish 65% performed long distance (>19 or >26 km, dependent on watercourses due to difference in receiver locations) migrations and 19% short distance (<15 km) migrations. The different populations varied in the time used to perform a long-distance migration, with a median time of 1.0-5.6 days in 2016 and 2.3-8.5 days in 2017. In 2016, females had a faster outward migration, and Julian day of watercourse exit had a negative correlation with the number of days used to migrate the minimum distance for long-distance migration. In 2017 the total length of the fish that had a negative correlation with time used to migrate the minimum distance for long-distance migration. Duration of marine migration was negatively correlated with the Julian day of river exit, and fish from Saltdalselva had a shorter migration duration than other fish. The different populations utilized the fjord in varying amounts, with fish from Botnvassdraget and Saltdalselva utilizing the whole fjord system while fish from Misvær and Valnesfjord remained within the watercourse or estuary. In Sulitjelma the tagged fish were split between residing in the watercourse and in the fjord system, with males dominating the former group and females the latter. Difference between migration strategies was attributed to the availability or not of high-quality marine areas in the vicinity of the watercourse. The results of this study further support the view of migration strategies in brown trout as a continuum, rather than a dichotomy between residents and fjord migrants. The different strategies have been shaped by the selective pressure each population faces and therefore reflections of the challenges the populations face in the watercourse, the estuary and in the fjord system.



## Oppsummering

Brunørreten er en ferskvannsfisk med stor variasjon innen livshistorie og migrasjonsstrategi. Den starter sitt liv i elven, men etter et varierende antall år som ungfisk vil noen vandre til sjøen, mens andre holder seg til elven resten av livet. De ulike strategiene fører til stor morfologisk variasjon både innad og mellom populasjoner. Blant de sjømigrerende fiskene er det også stor variasjon, hvoriblant dagen fisken forlater elven, lengde på sjøoppholdet og distansen de migrerer kan variere mye. Fokuset i denne studien har vært å beskrive og undersøke denne variasjonen i adferd til de fiskene som vandrer til sjøen. Dette er blitt gjort gjennom å studere fisk fra fem ulike vassdrag som alle har tilgang til det samme fjordsystemet. Den observerte adferden og forskjellene mellom populasjonene har deretter blitt sammenlignet opp mot rådende hypoteser på feltet, med fokus på teorien om migrasjon hos brunørret som et kontinuum av strategier, heller enn en dikotomi. Fiskenes bevegelser ble studert ved hjelp av akustisk telemetri – en sporingsmetode hvor fisken fikk operert inn et merke som ga fra seg et lydsignal, som så kunne oppfattes av lyttestasjoner plassert i fjorden og i vassdragene. For å vite mer om fiskene ble også skjellanalyser gjennomført, hvor skjell samlet fra fiskene ble undersøkt under mikroskop for å regne ut fiskens alder, samt finne ut ved hvilken alder og lengde brunørreten forlot elva første gang som smolt.

Totalt 137 ørretveteraner med antatt eller bekreftet marin vandring ble fulgt gjennom sesongen, i opptil to sesonger i 2016 og 2017. Populasjonene skilte seg fra hverandre, med variasjoner i lengde-ved-alder, og i lengde og alder ved første sjøvandring som smolt. Av fiskene som ble registrert i fjorden gjennomførte 65% langdistansemigrasjoner (>19 or >26 km, avhengig av vassdrag grunnet ulik avstand til lyttestasjoner), mens 19% ikke migrerte lengre enn maks 15 km. Fiskene brukte i 2016 en mediantid på 1.0-5.6 dager på å migrere minimumsavstanden for en langdistanse migrasjon mens mediantiden i 2017 var på 2.3-8.5 dager. I 2016 var denne tiden korrelert med dato for utvandring, hvor fisk som migrerte ut senere var raskere. I 2016 ble det også sett at blant langdistansemigrantene var hunnene raskere enn hannene. I 2017 var tiden det tok å migrere minimumsavstanden for en langdistansemigrasjon negativt korrelert med fiskens totale lengde. Lengden på sjøoppholdet var negativt korrelert med dato for utvandring, og det ble også sett at fisk fra Saltdalselva hadde kortere opphold i sjøen enn fisk fra de andre vassdragene. Fjordsystemet ble brukt i varierende grad, hvor de sjømigrerende fiskene fra Botnvassdraget, Saltdalselva og Sulitjelma oppholdt seg over 70% av tiden i den ytre delen av fjorden, mens all merket fisk fra Misvær, samt 88% av fisken i Valnesfjord og 47% av fisken i Sulitjelma oppholdt seg innad i vassdraget eller i estuariet. I Sulitjelma var merkegruppen

splittet mellom fjordmigranter og individer som holdt seg innad i vassdraget. Mens det var flest hunfisk i den første gruppen, var den siste gruppen dominert av hanfisk.

Resultatene i denne studien støtter synet på at migrasjonen til brunørret best sees på som et kontinuum av strategier, hvor det er stor variasjon, og hvor fordeler og ulemper ved de ulike strategiene over tid har formet de ulike populasjonene og ført til strategier tilpasset de utfordringene hver enkelt populasjon møter i vassdraget, i estuariet og i fjordsystemet.

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# 1 Introduction

Migration is a widespread phenomenon in the animal kingdom (Shaw, 2016), and is characterised by a population's predictable shifting between two or more habitats. If the shifting leads to increased growth, survival or reproduction it can be adaptive (Shaw, 2016) and hence be selected for. Because migration enables individuals to take advantage of several complimentary habitats, instead of being confined to just one throughout the year, it is associated with several benefits, such as the ability to find better feeding opportunities, more suitable areas or partners for reproduction or refuge from predators or adverse conditions (Shaw, 2016).

Fish that migrate are separated into three different categories based on the nature of their migration: if it takes place in freshwater (potamodromous), in seawater (oceanodromous) or between freshwater and seawater (diadromous) (Gross, 1987). Diadromous migrations are again separated into two categories: anadromy, in which the animal migrate to seawater to feed and to freshwater to reproduce, and catadromy, where individuals do the opposite. The underlying factor behind diadromy is the productivity gradient between sea and freshwater (Gross *et al.*, 1988). Around equator freshwater has the highest productivity, and catadromy is common. In the temperate and Arctic regions the ocean is more productive than freshwater, and anadromy is prevalent (Gross *et al.*, 1988).

Brown trout (*Salmo trutta*, L, 1758) is a freshwater fish in the salmonid family (*Salmonidae*). Populations found in watercourses with a connection to the ocean display a wide variety of migration behaviour, often termed the *brown trout migration continuum* (Cucherousset *et al.*, 2005; Boel *et al.*, 2014). Some fish reside in their home river their entire life, others migrate to connected lakes or side-rivers, while others again will migrate to seawater (Jonsson, 1985). Non-migrating individuals are often referred to as “residents” while the individuals that migrate to sea often are called “sea trouts”. Inside the marine migration strategy there is also individual variation, where the duration of the sea migration for can vary from lasting only a couple of weeks before returning, to being a permanent residency in seawater, with only a short trip to the river for spawning (Jensen & Rikardsen, 2012; Thorstad *et al.*, 2016; Aldvén, 2017). In addition to variation in the time spent at sea, there has also been observed large variation in the marine distance travelled during migration. (Eldøy *et al.*, 2015; Thorstad *et al.*, 2016; Bordeleau *et al.*, in press).

This phenomenon, that some individuals in a population migrate while the others do not is called *partial migration* and is displayed by many of the species that migrate (Chapman *et al.*, 2012). This has been studied in a range of animals, especially birds (Chapman *et al.*, 2012). The current overarching hypothesis is that migration is *one* possible response to an environment with predictable fluctuations (e.g. fluctuating temperatures, food availability or predator pressure; Chapman *et al.*, 2012), but not necessarily the best for all individuals. As migration is also associated with costs for the individual, the strategy that will maximize an animal's fitness will depend on the cost-benefit trade-off between the two strategies. When two life-history strategies coexists it tells us that they are either in fitness equilibrium (an evolutionary stable strategy (ESS)) or that the best strategy is condition dependent, and will differ between individuals and between years (Chapman *et al.*, 2012).

For brown trout, one of the benefits of marine migration is the better feeding conditions (Jonsson & Jonsson, 2006b; Solomon, 2006), as the sea is more productive than freshwater within their natural distribution range (Gross *et al.*, 1988), and sea trout therefore tend to be larger than resident fish (Klemetsen *et al.*, 2003; Jonsson & Jonsson, 2006b). Because reproduction in fish is resource restrained, (and especially for females (Ferguson, 2006)), migrant fish will tend to have higher fecundity (Solomon, 1997; Ferguson, 2006) and therefore higher fitness. Migratory individuals may also have higher rates of survival, as migration can be a way to escape adverse conditions in the watercourse, such as unstable waterflow, high water temperatures or a drying up of the river (Thorstad *et al.*, 2016). The costs of migration for brown trout are among others the energy and stress associated with the smoltification process (Ferguson, 2006), the energy required for locomotion (Jonsson & Jonsson, 2006b) and the potential for increased mortality (Solomon, 2006; Thorstad *et al.*, 2016), stemming from e.g. increased predation or from increased risk of disease and of parasites (Ferguson, 2006), such as salmon lice (*Lepeophtheirus salmonis*, Krøyer, 1838).

The brown trout migration continuum (Cucherousset *et al.*, 2005; Boel *et al.*, 2014) therefore represent the different strategies brown trout have evolved in order to maximize fitness. Solomon (2006) lists different factors that are thought to promote marine migration in brown trout, among them poor growth conditions in the river (because of food limitations or low temperatures) or being from river that is vulnerable to draught or has a high predation pressure. Good conditions for migration (e.g. safe passage to sea or abundant food in the marine environment) is also a pull factor for migration. The opposite conditions will favour residency (good conditions in the river which enables growth, and poor or dangerous conditions in the

marine environment). Differences within the marine migration strategy are thought to depend on the same cost-benefit trade-off, with animals migrating just as far, or residing in the fjord for just as long, as is needed to maximize the benefits, compared to the costs (Solomon, 2006).

There has been observed a decline in brown trout populations in many countries in Europe, including Norway (ICES, 2013), and this has led to an increased focus on brown trout, and especially on the marine part of their life. It is hard to quantify the populations exactly (Höjesjö *et al.*, 2017), as fish caught by recreational fisheries outside the rivers are not reported and the quality of many river catchments reports are unknown (Anon., 2015), but the data that exists shows an 23-66% reduction in river catches during the last twenty years (ICES, 2013). As individuals that migrate tend to have higher fecundity (Solomon, 1997; Ferguson, 2006; Thorstad *et al.*, 2016), the migratory individuals can therefore be especially important for the recruitment of the populations. Understanding the risk factors that the sea trouts face at sea, including both natural and human impacts, will therefore help us create the best solutions for the preservation of the populations.

The objective of this study was to investigate the marine migration continuum in brown trout by describing and comparing the marine migration behaviour of brown trout from five different watercourses, hereafter termed “populations”, that all had access to the same fjord system. This was done by acoustic telemetry, and the fish was followed throughout the year, for up to two seasons. The basis of the comparisons was the duration of the marine migration, the first and last day of migration, the distance travelled during the marine migration and the geographic use of the fjord, as well as the data collected from the study populations and from the watercourses.

The hypothesis tested was that marine migratory behaviour differed between the populations, and that the observed variation could be explained by difference in the populations freshwater- and estuarine habitats, in accordance with current theory in the field.



## 2 Materials and methods

### 2.1 Study area

This study took place in a fjord system located within the three municipalities Fauske, Bodø and Saltdal in Nordland county (Norway; figure 1). This fjord system consists of the Skjerstad, Saltdal, Misvær and Valnes fjords. It is located at  $67^{\circ} N 15^{\circ} E$ , and the entire fjord system is 51 km long from the innermost parts at the mouth of the river Saltdalselva to where the fjord exits into the Salt fjord. Saltstraumen, the strongest tidal current in the world (Plassen *et al.*, 2015), is located in the connection between the fjord system and the Salt fjord. During one tidal period (duration 6 hours), up to 370 million  $m^3$  of water can enter or exit the system. Five fish farms (figure 1) are located in the fjord system.

Because of the freshwater input from the connected rivers, the uppermost layer of water in the fjord has a lower salinity than the deeper water masses and a temperature that varies with the seasons (T. Busch *et al.*, 2014). The deeper water masses (below 25-30 metres) have a stable temperature and salinity. The fjord system is therefore a mix between euhaline (salinity  $> 30$  ppt) and polyhaline (salinity between 18-30 ppt; T. Busch *et al.*, 2014).

In addition to the fjord system the study area includes the watercourses of Misvær (River Lakselva), Botnvassdraget (River Botnelva), River Saltdalselva, Valnesfjord (including lake Valnesfjordvatnet) and Sulitjelma (River Laksåga; table 1, figure 1).

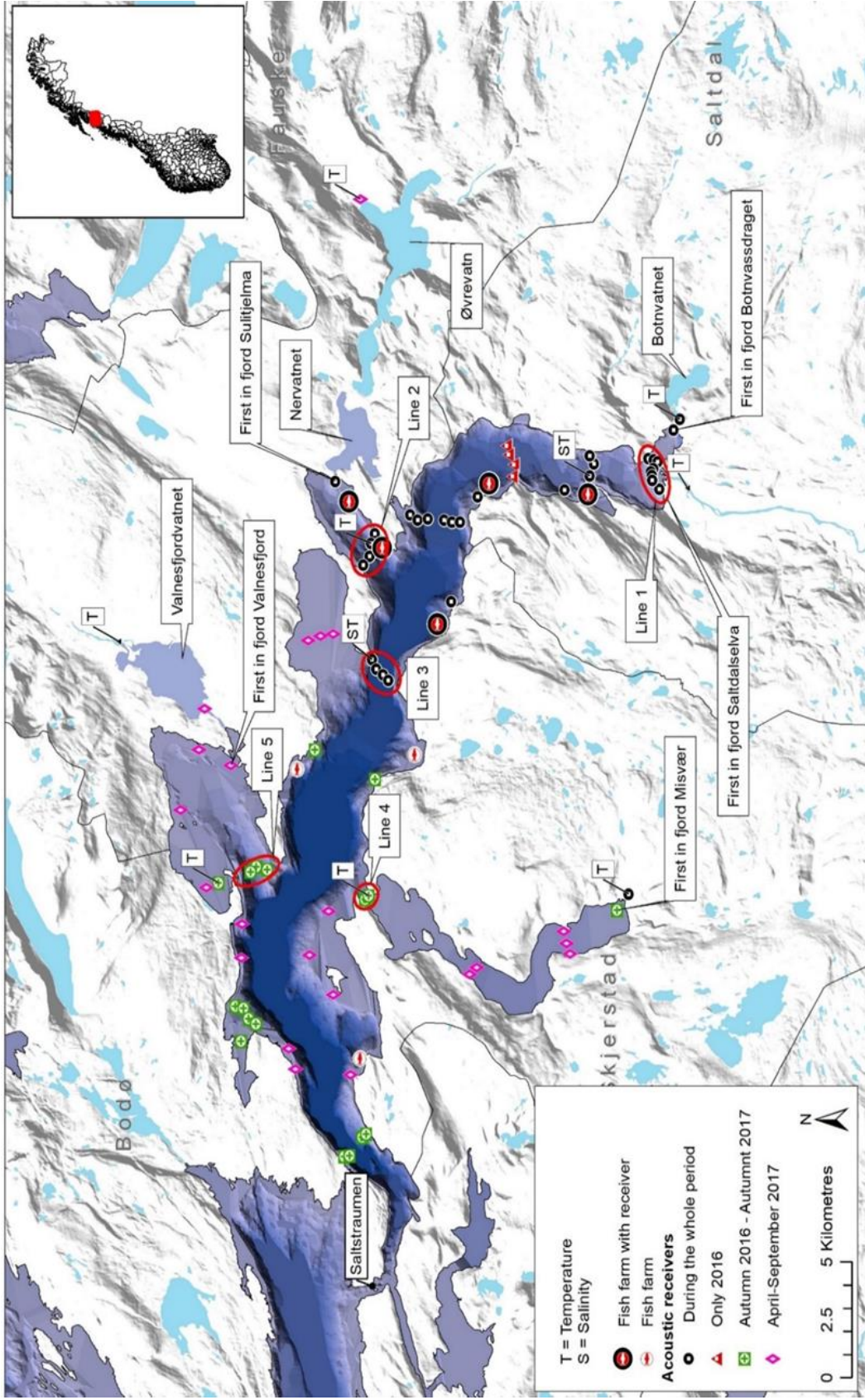


Figure 1: Map of the study area (Skjerstadfjorden, Nordland) showing the position of the acoustic receivers used in the study, as well as the time period each receiver was operational. Red circles indicate lines of receivers used in the analyses, and receivers used for determining first and last day of migration are labelled as “First in fjord”-receivers. The location of temperature and salinity loggers is also labelled.



### 2.1.1 The five watercourses

Botnvassdraget (table 1; Miljødirektoratet, 2018a) is a watercourse consisting of two rivers (Ingeborgelva and Knallerdalselva) flowing into the water Botnvatnet, which is 2.0 km<sup>2</sup>, and located at 12 m a.s.l (NVE, 1991b). This lake was created when the glaciers melted, and the moraines separated the waterbody from the ocean it had been a part of (a meromictic lake as described in Økland (1983)). There is still a layer of seawater at the bottom of the lake. Both Arctic charr (*Salvelinus alpinus*, L, 1758) and brown trout utilize this watercourse (NVE, 1991b).

The Misvær watercourse (table 1; Miljødirektoratet, 2018a) is located in the end of the side fjord to Skjerstadvjorden, Misvær fjorden. The river, Lakselva, is 4 km long and 2-6 metres wide (Olsen, 2005). The annual mean water level in the river, measured at the entrance to the fjord, has been measured to 6.7 m s<sup>-3</sup> (Pettersson, 2003). The river is not regulated and has yearly variation in flow, with maximum waterflows during snow melting in May-June, and a secondary, smaller, peak in autumn (Pettersson, 2003). The elevation of the drainage area is relatively low compared to other watercourses in the area, and the river therefore has higher water temperatures than other rivers (Jensen, 1987). Both brown trout and Atlantic salmon (*Salmo salar*, L, 1758) is found in the river, and the river has been classified as “very good” with regards to spawning and the conditions for juvenile fish (Olsen, 2005). The river has been characterised as nutrient rich watercourse (NVE, 2002), with both high natural content of nutrient and additional nutrients added through run-off from surrounding farms. The estuary has been classified as a brackish-water delta (Miljødirektoratet, 2018b), a land type characterised as being highly productive.

Saltdalselva (table 1; Miljødirektoratet, 2018a) is located in the innermost parts of the fjord. The length of the river is 80 km (Kanstad-Hanssen *et al.*, 2017). The temperature in the river is low because of glacier water inflow from Saltfjellet (Brettum *et al.*, 1980). It is not a regulated river, but the lower parts of the river has been heavily modified for flood-protection (NVE, 2005). Atlantic salmon, brown trout and Arctic charr are recorded in the river (NVE, 1991a), and this has historically been an important salmon river. The lower four km of the river are influenced by the ocean at high tide, and the lower stretches of the river are also surrounded by farmland (NVE, 1991a). Productivity in the river is low because of low water temperatures and low nutrient levels (Brettum *et al.*, 1980).

Sulitjelma (table 1; Miljødirektoratet, 2018a) is a large watershed consisting of several lakes. Contained in the watershed is two glaciers (Aanes *et al.*, 1987). The area has lower temperatures

than surrounding areas, because of drainage from the glaciers as well as cold winds coming from the mountains (Aanes *et al.*, 1987). In Laksåga, the river the fish was caught in, the river is regulated (Aanes *et al.*, 1987). This river flows into lake Øvervatn, which is downstream from Langvatn. This lake is located next to the town Sulitjelma, which had an active mining industry for over 100 years, mining copper. The mines were closed down in 1991, and environmental surveys have later been performed. This survey found that Lake Øvervatn is influenced by the tide, and salinity markedly increases around 15 meters depth, and oxygen level drops around 25 meters, and is depleted at 40 meters (Iversen *et al.*, 2009). These results are unchanged from last survey of the lake, which was in 1993, and the lake still contains approximately the same levels of cobber and zink as in 1993 (19.1 µg/l Cu and 23.9 µg/l Zn at 1 m; Iversen *et al.*, 2009). From this lake the water flows onwards into the lake Nervatnet, which is connected to the fjord through a tidal current (Finneidstraumen).

Valnesfjordvassdraget (table 1; Miljødirektoratet, 2018a) contains the lake Valnesfjordvannet (8.3 km<sup>2</sup>). This lake is only 1 m a.s.l, and at high tide seawater enters the lake through the stream called Laukåsstrømmen (NVE, 2018). This stream will later be referred to as the estuary in Valnesfjord. The river (Lakselva) has Atlantic salmon and brown trout (both resident and sea trout ) and cod (*Gadus morhua*, L, 1758) has been registered in the lake (NVE, 2018), as well as Arctic charr. Located where the river Lakselva flows into the lake is a freshwater estuary, an important area for many bird species (NVE, 2018). Minks (*Mustela lutreola*, L, 1761) and otter (*Lutra lutra*, L, 1758) also reside in the area (NVE, 2018).

Table 1: Information about the five watercourses where fish were tagged for this study. If the watercourse consisted of several rivers it is the river that fish were captured in that is stated. The conductivity was measured once and the calcium content twice (except from in Saltdalselva).

Watercourse	Botnassdraget	Misvær	Saltdalselva	Sultjelma	Valnesfjord
River name	Botnelva	Lakselva	Saltdalselva	Laksåga	Lakselva
Coordinates	67°4'59"N 15°31'38"E	67°7'10"N 15°0'26"E	67°6'2"N 15°25'14"E	67°14'11"N 15°42'14"E	67°20'35"N 15°15'28"E
Conductivity	35.5 microsiemens	56 microsiemens	52.7 microsiemens	30 microsiemens	42.3 microsiemens
Date measured	03.05.2017	05.05.2017	03.05.2017	30.05.2017	11.05.2017
Calcium (Ca)	8 and 2-3 mg L <sup>-1</sup>	20 and 18 mg L <sup>-1</sup>	16 mg L <sup>-1</sup>	≤ 8 mg L <sup>-1</sup> x2	≤ 8 mg L <sup>-1</sup> x2
Date measured	03.05.17, 23.08.17	05.05.17, 23.08.17	03.05.2017	30.05.17, 23.08.17	11.05.17, 23.08.17
Highest point in watershed	1187 m a.s.l	836 m a.s.l	1751 m a.s.l	1900 m a.s.l	1135 m a.s.l
Catchment area	99 km <sup>2</sup>	146 km <sup>2</sup>	1537 km <sup>2</sup>	774 km <sup>2</sup>	194 km <sup>2</sup>
Salmon-producing stretch	10 km	6.5 km	65 km	26.9 km	34 km
Watercourse characteristics	Contains lake		High modification of lower stretches for flood protection	Contains several lakes, one which is influenced by tide. Past mining activity.	Contains lake influenced by tide.

## 2.2 Telemetry

### 2.2.1 Fish capture and tagging

#### 2.2.1.1 Fish capture method

Fish was caught using fishing rods (single or triple hooks), gill nets (35-45 mm mesh size) or dip nets. The fishing hooks were removed with the use of pliers to ensure minimal damage. Gill nets were checked regularly, and to avoid damage, fish were removed from net by cutting them free with scissors. After capture the fish were stored in holding nets until tagging (< 4 hours).

#### 2.2.1.2 Study populations

Fish was tagged in eight rounds during a period of two years (table 2). In Botnvassdraget fish was caught in two different parts of the system, in the lake Litlevatnet (a constricted part of the lake Botnvatnet) and in the inlet river to the lake (River Knallerdalselva). In Misvær fish was caught in the river and in the estuary. All fish from Saltdalselva was caught in the river. In Sulitjelma all fish were caught by the river outlet of the river Laksåga, in the lake Øvervatnet. In Valnesfjord the fish was caught in two different locations, in the lake Valnesfjordvatnet and in the estuary Laukåsstraumen.

Of the total number of 175 fish, 35% was tagged in Botnvassdraget ( $n=61$ ), 10% in Misvær ( $n=17$ ), 23% in Saltdalselva ( $n=40$ ), 19% in Sulitjelma ( $n=34$ ) and 13% in Valnesfjord ( $n=23$ ).



### 2.2.1.3 Fish tagging procedure

The following procedure was used to tag all the fish in the study, as also described in Eldøy *et al.* (2015). A solution with 2-phenoxy-ethanol (EEC No 204 589-7, 0.5 ml per L water) was prepared and the fish was transferred from the holding net into a container with the solution. The container was covered to keep it dark, and the fish was held in the solution for 4 minutes. If not anaesthetised by that point, it was kept in the solution for an additional 15-30 seconds until fully anaesthetised. Then the fish was transferred to a plastic tube. An incision was made on the side of the linear alba approximately 1,5 cm long, and a disinfected acoustic transmitter was placed in the body cavity. Size of transmitter was chosen based on size of fish (see 2.2.2). The incision was closed with two or three sutures (Resolon 3/0). A modified carlin tag was attached in the back, just below the dorsal fin of the fish using two cannulas. Water was continuously pored over the gills during the procedure. The total length ( $L_T$ ) of the fish was recorded (length from tip of snout to tip of longest caudal fin), and after collecting scales (described in 2.4) and a DNA-sample from the adipose fin, the fish was weighted before being placed in a holding tank. There the fish was left under cover until normal behaviour had been regained. The fish was then released into a calm area of the water nearby the tagging site.

### 2.2.2 Acoustic transmitters

The fish were, depending on  $L_T$ , tagged with one of two sizes of 69 kHz acoustic transmitters from Thelma Biotel AS. Modell MP-9 (5.2 g in air, 0.1 – 3.7% of fish total body mass; estimated battery life of ~15 months; output 146 dB re 1uPa @ 1m) was used for fish  $L_T > 260$  mm while model MP-13 (11.8 g in air, 0.2 – 5.3% of fish total body mass; estimated battery life of ~24 months; output 153 dB re 1uPa @ 1m) was used for fish with  $L_T > 340$  mm. The tags transmitted the acoustic signal with a random delay between 30 – 90 seconds. Some tags had a build-in temperature sensor (data not used in this study) which slightly decreased the battery life (see table 3 for actual battery life for each tagging group).

Table 3: Several different types of acoustic transmitters were used in the study, which varied in battery time. The number of fish tagged with the different tags in the different watercourses and the different years are detailed below. 19 fish from Botnvassdraget (2016) were excluded from the table because of lacking data.

<b>Tag battery life time (months)</b>	<b>%</b>	<b><i>n</i></b>	<b>Watercourse</b>
13.5	14%	22	Misvær (2017), Sulitjelma (2017), Valnesfjord (2017)
15	7%	11	Saltdalselva (2016), Botnvassdraget (2016)
19	27%	42	Misvær (2017), Sulitjelma (2017), Valnesfjord (2017)
24	52%	81	Saltdalselva (2016), Botnvassdraget (2016), Misvær (2016), Sulitjelma (2017)

### 2.2.3 Tracking of tagged fish

Overall, 85 acoustic receivers (Vemco Inc., Canada, models VR2, VR2W and VR2W-AR) were used to track the study populations. Of these, 82 were located in the fjord and three in the watercourses of Botnvassdraget, Misvær and Sulitjelma. The number of operational receivers varied during the course of the study, and the different time periods are shown in figure 1. Receivers were deployed with different methods: in the lake in Botnvassdraget and in the river in Misvær they were fitted to a 20 kg tile and attached to land with wire. In the lake in Sulitjelma (Øvervatnet) a 20 kg tile was moored to a surface buoy and the receiver attached on the connecting rope. The receivers in the fjord were either chained to existing infrastructure at the fish farm facilities, moored to buoys or immersed on the seabed with an on-board acoustic release system (Vemco model VRW-2 AR) or an external acoustic release (Subseasonic modell AR-60- E). In freshwater, receivers were placed at 0.5 – 3.0 m depth, while most receivers at sea were moored at 5 m depth, however few receivers were moored at 50 – 150 m depth.

Since the study system is a long and complex fjord system with large spatial and temporal variation in environmental conditions such as wind, salinity, currents and haloclines, detection range may vary between different parts of the fjord and during the year. In order to evaluate if the receiver lines were reliable for the analyses performed in this study, two methods were used.

1. The ID of tagged brown trout from Lake Botnvassdraget registered at the outermost line of receivers (east of Saltstraumen, n=9), were compared to the ID of fish recorded at the first line north of line 1 (figure 1). All nine fish were also detected at the inner line given a detection efficiency of the latter of 100%

2. In 2017, 22 acoustic receivers with built-in pinger tags (Vemco model VR2-W-AR) were deployed in the system. The pinger tags were programmed to transmit a signal similar to those from the tagged fish once every ten minutes. When analysing data from these signals, detection range was found to be similar to other comparable studies (200-400 m; see e.g. Eldøy *et al.*, (2016); Bordeleau *et al.*, (in press)).

Hence it was concluded that the receiver lines had an acceptable performance and were suitable to answer the research questions in the study.

### 2.3 Genetic sex determination

Samples taken from the adipose fin of each fish was genetically analysed at the NTNU University Museum to determine the sex of each tagged fish. DNA was extracted from ethanol preserved fin clips with the QuickExtract kit (Epigen), according to manufactures protocol with the exception for the extraction volume, which was reduced to 150 µl.

Sex was hence determined by PCR amplification of a ca 200 bp fragment situated in the first intron of the male specific SDY gene, using the *Salmo*-sdY-F and *Salmo* sDY-R primers (Quéméré *et al.*, 2014).

The PCR was performed in 10 µl reactions using the Qiagen Multiplex PCR kit. The following PCR profile was used: 95°C for 15 min, 11 cycles of touchdown PCR, 94°C for 30 sec, 63–52°C for 30 sec, 72°C for 1 min, followed by 25 cycles of 94°C for 30 sec, 52°C for 30 sec, 72°C for 1 min, with a final extension at 72°C for 10 min. Sex was scored by running the PCR products on 1% Agarose gels. A number of blind samples with known sex was included to check the quality of the method and indicated a positive identification of the sex by 95%.

### 2.4 Scale sample analysis

Scales were sampled from all fish during the tagging procedure. Five to ten scales were collected from the area past the dorsal fin and above the lateral line using a pair of forceps. The samples were stored in paper envelopes before analysis. At the NTNU University museum, each sample was investigated using a light microscope. Scales suitable for age analysis were copied onto 1 mm Lexan plates using a pressing iron. The criteria used for sorting the scales were to avoid replacement scales and scales with damages that made them hard to read. The pressed replicates were then analysed with a computer-controlled stereoscope (Leica M165C with camera Leica MC170 HD) and its connected software, LAS V4.5 (Leica, 2014)



Using the method developed by Lea and Dahl (Dahl, 1910; Lea, 1910), which says that the ratio between total body length ( $L_T$ ) and scale length remains the same through the life of the fish,  $L_T$  at the end of each winter could be back calculated. These calculations involved the length of the fish at capture, the length of the fish scale (measured from the centre and out to the perimeter) and the lengths from the end of one winter zone until the next. During this analysis the age of the fish and the age at smoltification was also recorded. Measurements were taken on one scale per sample, but all pressed scales were examined before measuring was done, to be more confident in the year identification process.

During the scale reading process, three different sources of uncertainty in the data was identified:

1. Uncertain of number of years since smoltification, caused by the annuli being tightly packed
2. Uncertain age at smoltification, because of missing circuli.
3. Uncertain age at smoltification, because of “untypical” growth patten (no large shifts in growth between slow freshwater growth in river and fast marine growth).

The consequence of these three cases of uncertainty was in the case of nr 1 and 2 that the age at capture estimate was unsure, but the length at smoltification was sure in both, and in nr 1 the age of smoltification was also sure. In nr 3 we had a sure estimate of the age at capture, but not of the other two variables. During the analysis process of the data, these three different uncertainties were handled the following way:

In the case of uncertainty in the estimate, the numbers produced though both readings were included, and the sample marked with the cause of the uncertainty. Whenever age at capture was included in the analysis, the lowest age estimate was used. For uncertain estimates of smolt age when the variation was one year between estimates, the primary reading was used. For uncertain smolt age estimates where more than one year was separating the estimates, these were excluded from analysis. In these cases smolt length was also excluded. Seven samples were excluded based on this criterion.

The age of the fish during the first spring they were tracked was calculated by adding one year to all age estimates from fish tagged during the autumn, reflecting the age they would be the next season.

In order to avoid among-observer effects the majority of the scales (95%) were read by the same person. Results were later discussed, and quality checked with a person with long experience in brown trout scale reading, which also read the remaining scales.

## 2.5 Data analysis

### 2.5.1 Condition factor

Individual condition factor ( $K$ ) (Ricker, 1975) was calculated by applying the formula

$$K = 100 * W * LT - 3.$$

### 2.5.2 Filtration of telemetry data

Registrations used in this study were collected during the time period 30.04.2016-31.01.2018. Data was stored and managed in the program VUE [version 2.3.0, VEMCO, 09.2016].

The stations located in or close to the watercourses (first in fjord-stations, figure 1) were last downloaded on the 24.10.17 and 23.8.17 in Botnvassdraget, the 20.9.17 for Misvær, the 3.5.17, 22.8.17, 24.10.17 and 31.01.18 for Saltdalselva, the 23.10.17 and 31.01.18 for Sulitjelma and the 10.08.17 and 23.10.17 for Valnesfjord.

Acoustic telemetry is based on sound, and this introduces two main sources of error: sound pollution and tag collision. The first, sound pollution, occurs when sound from other sources than the acoustic tags (waves, wind, boat traffic etc) is interpreted as a tag signal by the receiver. The second, tag collision, occurs when signals from different acoustic transmitters co-occur, and the receiver interpret the combination of these signals as an own, separate signal.

Because of their different nature, these two results in two different types of errors. Sound pollution is assumed to result in mostly random registrations, and the problem is therefore assumed to be negligible when tag IDs that have not been used in the study have been removed. Tag collisions on the other hand have a much higher chance of producing signals that match existing IDs used, as these registrations stems from tags with similar codes. This is then what is called “false registrations”: when a tag signal is registered without this being a true reflection of where the tagged individual has been (Pincock, 2012).

The problem with false registrations can never be completely eliminated (Pincock, 2012), but though careful filtration it can be reduced. Four receivers in this study, nr 1, 46, 81 and 82, were selected for filtration because they were situated in areas where fish were residing in numbers (in the lake of Botnvassdraget, the estuary of Lakselva Misvær, the river Laksåga in Sulitjelma

and the lake in Valnesfjordvassdraget, respectively). As tag collision happens when several tag signals are received at the same time, it was likely that these stations could have a problem with this.

The registrations from these four receivers were filtered, meaning that all registrations that were not followed by a second registration of the same ID on the same receiver within ten minutes were excluded from the study. The idea behind this process is that false registrations differs temporally from real registrations (Pincock, 2012): if a registration is randomly produced by sound pollution or tag collision it is not likely that the same error would occur many times in a short time. While this is exactly the pattern we would expect from real registrations: as a tag sends out a signal with a random delay every 30-90 seconds it is likely that each signal would be heard many times if the fish truly was in the area.

#### 2.5.2.1 Removal of registrations

The first processing that was done with the data was to remove all tag-IDs that had not been used in the study. After this step there was 1 237 322 registrations in the database. During a visual inspection of the data four of the transmitters were classified as “stationary”, meaning that the tags detection pattern indicated that the tag had stayed in the same place for at least a week. Since this is not likely behaviour for a living fish, all registrations past the first day of the stationary period was excluded from further analysis. This removed 333 209 registrations from the database (27%).

The next step was to filtrate station 1, 46, 82 and 81 because of possible tag collisions (all these are stations located in rivers or lakes, or close to the rivers). The ten minutes filter removed 12 334 registrations.

The final set of that that was used in the analysis contained 891 779 registrations.

#### 2.5.3 Marine migration distance in fjord

In order to analyse potential differences between the populations in distance migrated in the fjord, each individual was classified as either a short, medium or long-distance migrant. The classification was done based on a set of rules for what would constitute a short, a medium and a long-distance migration. The distances each fish was measured to travel should be considered a minimum estimate of the true marine migration distance, as distance was measured as aerial distance, and not the true path the fish took in the fjord.

- Fish that were not recorded past the closest line to their watercourse (line 1-2 and 4-5, figure 1) were classified as short distance migrants.
- Fish that were recorded on line 3 (figure 1) in 2016, and on a receiver past line 3 in 2017 were classified as long-distance migrants. This line was selected as it was the outmost line in 2016 (figure 1). In 2017 this line was not operational, so in 2017 the criteria used for “long” migration was a registration of the fish of any of the stations past this line.
- Fish that were recorded past the closest line to their watercourse, but that did not fulfil the criteria for long migration, were classified as medium distance migrants.
- Fish that classified as short- or medium distance migrants and who did not return from migration were excluded from analysis if the number of days they had been followed in the fjord did not exceed a minimum threshold set for each population. The cut-off time for each watercourse was defined as the average time long distance migrating fish from that watercourse spent from first day of migration until they had fulfilled the criteria for long-distance migration, added with this measurement’s standard deviation. This was done to exclude fish that only had a short or medium migration because they disappeared from the study before they had the time to perform a long-distance migration.

For Botnvassdraget the cut-off time was 4.7 days in 2016 (mean=2.3 days, SD=2.4 days) and 13.7 days (mean=5.8 days, 7.9 days SD) in 2017. For Saltdalselva the cut-off time was set at 22.9 days (mean=10.8 days, SD=12.1 days) in 2016, and in Sulitjelma in 2017 the cut-off was set at 22.2 days (mean=11.7 days, SD=10.5 days).

The distance for short, median and long migration:

- Short = <3 km for Botnvassdraget, <2 km for Saltdalselva, <5 km for Sulitjelma, <15 km for Misvær and <3 km for Valnesfjord
- Long = 26 km from the river Laksåga in Sulitjelma and to line 3, 19 km from the first point in the fjord and to line 3 for fish from Botnvassdraget and Saltdalselva. As fish from Misvær and Valnesfjord only were observed close to their watercourses, it was not necessary to define long migration criteria for these populations.
- Medium distance migrants therefore have a migration longer than the short distance migrations, but shorter than the long-distance migrations.

For fish that were classified as long-distance migrants, the time used to migrate the minimum distance for long-distance migration was also recorded, measured from the first registration at

sea for fish from Saltdalselva and Botnvassdraget, and the last registration on the receiver in Lake Øvrevatn for fish from Sulitjelma.

#### 2.5.4 Duration of marine migration

The following rules were used to calculate the duration of the marine migrations of the fish.

- Start of the fjord residency was defined as the first registration of the fish in the fjord. If this registration did not happen on the first acoustic receiver the fish would encounter in the fjord (receivers marked as “first in fjord”, figure 1), two different courses of action were undertaken, depending on the watercourse of origin, and the placement of the acoustic receiver it was first registered on.
  1. If it was from Botnvassdraget or Valnesfjord the day of first fjord entry would be changed to the last registration of the fish in the watercourse, because the distance from the acoustic receiver in the lake to the fjord was short. This was done with four of the fish.
  2. If the fish was from any other watercourse the date of fjord entry was excluded from analysis, *if* the acoustic receiver it was first detected on was not in close proximity of the original first receiver. If it was, the delay in registration of the fish was assumed to be minimal and the registration kept as the first registration in the fjord. As this was the case for all four of the fish that this happened to, none needed to be excluded.
- Note that for the fish tagged in Misvær in the spring of 2017, all estimates were minimum estimates, as these fish were caught in the estuary and therefore were residing in the fjord already at time of capture.
- A fish was assumed to have returned to fresh water if the last registration of the fish in the fjord was on the receiver that was closest to its watercourse (“first in fjord”-receivers, figure 1). If a fish was not detected at the closest receiver to the watercourse, but instead was detected on the receiver *in* the watercourse, two different strategies were used:
  1. For fish from Botnvassdraget, the first registration in the watercourse was substituted for the last date of the fjord residency, as time spent travelling from the fjord to the lake had been observed to be short ( $n=8$ , mean time from last

registration on the “first in fjord”-receiver until it was registered in the lake=7.1 hours, SD=4.2 hours). This was done with two of the fish.

2. For fish from Sulitjelma, the last registration in the fjord overall was used as the last date of the fjord residency, as the time it took to travel from the fjord to the receiver was unsure. In these instances, the calculated duration of the marine migration was a minimum estimate. This was the case for one of the fish.
- If a fish returned to the watercourse several times during the migration period, the process was repeated, and the measurements summed up to the total time spent in the fjord.

### 2.5.5 Geographic use of the fjord

In order to see where in the fjord the fish spent the time during the marine migration the fjord was divided into five zones. Each of the acoustic receivers located in the fjord was assigned to one of these. Four lines of receivers were used to define the different zones (line 1-2 and 4-5, figure 1). The five zones were the inner-fjord zone, the Fauske zone, the Misvær zone, the Valnesfjord zone and the fjord zone.

The following rules were used to determine when residency in a zone started and ended:

- Each of these zones, except for the fjord zone, was defined by a line of receivers. The inner-fjord zone by line 1, the Fauske zone by line 2, the Misvær zone by line 4 and the Valnesfjord zone by line 5. Residency in the zone started on the **last** registration on this line *if* the next detection of the fish was on a receiver located inside the zone.
- Residency was considered over at **first** registration on the line that defines the zone *if* the next detection of the fish was on a station outside the zone.
- If the fish was not detected on the line either in or out, the residency was started at the first detection inside the zone and ended at the last detection inside the zone. The same rule was applied to the inner fjord zone as there was no defining line here (the receiver set up was different, with the line in the midst of the zone and not at the perimeter).
- Fjord zone residency was started when the residency in the other zones had ended and ended when residency in another zone started.

To investigate the estuary-use of the fish in Valnesfjord, a post-hoc analysis was done by creating a sixth zone, the Valnesfjord estuary zone. This zone extended from the receiver

located in the lake to the “first in fjord” receiver (figure 1). Residency here could only be calculated for the fish that had been tagged in the estuary (tag group VSE17,  $n=9$ ) and the fish tagged in the lake that was recorded in the fjord ( $n=1$ ), and only for the time period from the time of tagging until the first registration of the fish on the receiver in the lake, or from the time period between registration at the receiver in the lake and the first receiver in the fjord (figure 1). This was because of the setup of the receivers in this watercourse, which could tell when an animal was present around the receiver, but not which direction it was swimming. These estimates are therefore a minimum estimate of the time spent in the Valnesfjord estuary, as some of the fish resided in the estuary also before tagging, and because all registrations past the first registration in the lake will had to be discarded, as it was unsure if the fish was in the lake or in the estuary from that point onwards. Of the same reason, fish tagged in the lake did not get an estimate of the estuary time, as it was impossible to be sure of their location.

The limitations of the estimates produced from this analysis were the same as for telemetry data in general; the data can only tell where the fish were when they were followed, and fish that disappear during the study period will therefore only have minimum estimates, as we cannot know where it was residing after the last detection of the fish. The same applies for fish that have unsure dates of fjord entry or exit (described in 2.5.4).

## 2.5.6 Statistical analyses

The chosen level for statistical significance was set as  $P=0.05$  for all tests performed.

All statistical analysis was done with R Studio (RStudio Team, 2016).

### 2.5.6.1 Comparisons between groups

Comparisons between two groups were done with either Welch two-sample t-test or the Mann-Whitney-Wilcoxon test. To determine if the assumptions of the t-test were met, the groups were examined to see if the results were normally distributed (with the functions `plot()`, `boxplot()`, `hist()`, `qqnorm()`, and `shapiro.test` in R Studio (RStudio Team, 2016)).

Comparisons between several groups were done with ANOVA or the Kruskal–Wallis test. All groups were first examined with ANOVA, and then the residuals of the model were examined, and if these indicated that the assumptions for the ANOVA were not met, the Kruskal-Wallis test was used).

Comparisons between groups were followed up with post-hoc analysis to locate the difference between groups, if the first test showed significant effects. This was done with Tukey test for ANOVA and the Wilcoxon rank sum test for Kruskal–Wallis tests.

#### 2.5.6.2 Statistical models

ANCOVA was done to examine correlations between groups. Model selection was done with the function `step()` in R Studio (RStudio Team, 2016), and with the function `anova()`.



## 3 Results

### 3.1 Study populations

Total length ( $L_T$ ) of the fish in the study varied from 260 mm to 880 mm, body mass from 180 g to 6200 g and condition factor ( $K$ ) from 0.6 to 1.2 (table 2, figure 2). The age of the fish during first spring they were tracked at sea ranged from three to 14 years, and back calculated smolt age from two to six years. The back calculated smolt length varied from 74 mm to 280 mm.

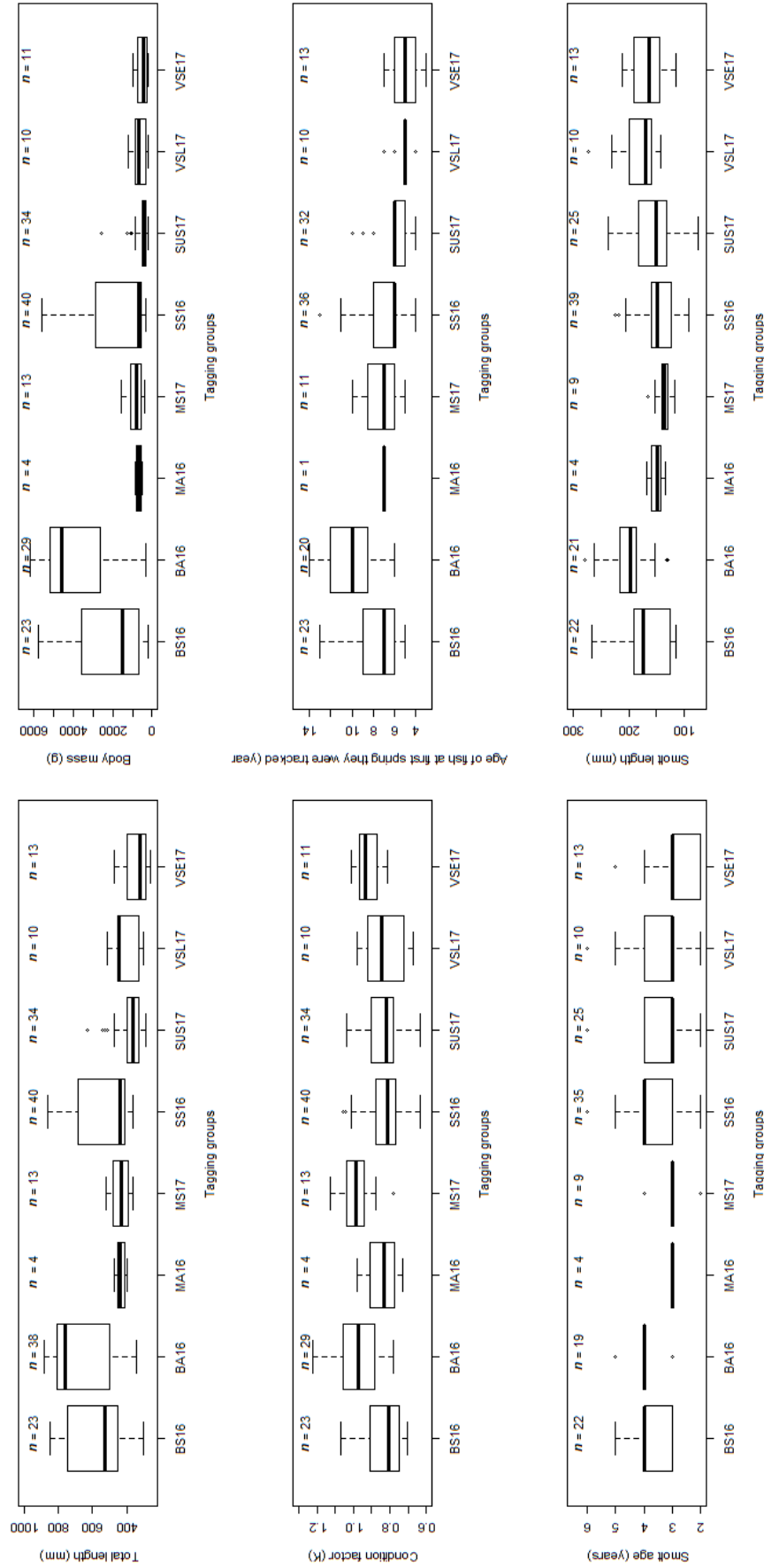


Figure 2: The total length, body mass, condition factor, age during first season of tracking, smolt age and smolt length of all tagged fish. Tagging groups have been named after the watercourse of origin (B=Botnassdraget, M=Misvær, S=Saltlalselva, V=Valnesfjord), the season of tagging (S=spring, A=Autumn) and the year of tagging. And in the case of Valnesfjord, also where in the watercourse the fish was tagged (L=lake, E=estuary). The box-and-whisker plots show median values (bold line), the interquartile ranges (box) and the 5<sup>th</sup> and 95<sup>th</sup> percentiles (whiskers) and outliers (O).

The relationship between  $L_T$  and age of the fish (length-at-age) was examined with an ANCOVA ( $n=146$ , adjusted  $r^2=0.82$ ; figure 3), in which the best model contained three different rates and two different intercepts, and the explanation variables age and four different watercourses (Botnvassdraget, Saltdalselva, Misvær and Sulitjelma and Valnesfjord combined). There were three different growth rates between age and  $L_T$ , where Botnvassdraget and Saltdalselva had the same ( $P=0.20$ ), Misvær was different ( $P=<0.001$ ), and Valnesfjord and Sulitjelma also were different ( $P=0.005$ ; figure 3).

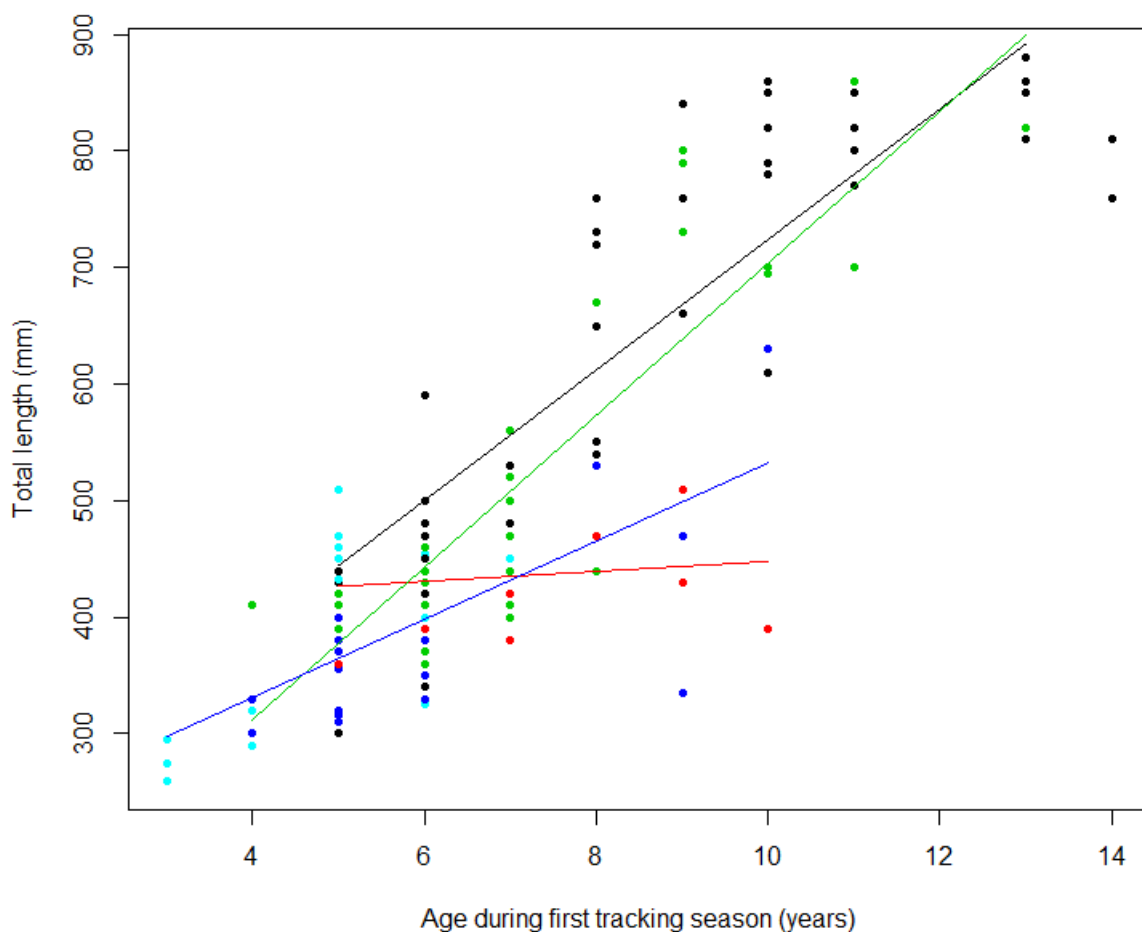


Figure 3: Total length ( $L_T$ ) versus age (length-at-age) of tagged fish from five different watercourses. Botnvassdraget: black, Saltdalselva: green, Misvær: red, Sulitjelma: blue and Valnesfjord: cyan. Solid lines represent the findings from an ANCOVA model, where black is the relationship between age and  $L_T$  for Botnvassdraget, green for Saltdalselva, red for Misvær and blue for Valnesfjord and Sulitjelma combined.

When comparing the difference between watercourses (Kruskal-Wallis and Wilcoxon rank sum test,  $n=175$ ), it was seen that the fish from Botnvassdraget had a higher  $L_T$  than fish from

Misvær ( $P<0.001$ ), Saltdalselva ( $P=0.0017$ ), Sulitjelma ( $P<0.001$ ) and Valnesfjord ( $P<0.001$ ). Fish from Misvær were longer than fish from Sulitjelma ( $P=0.002$ ) and Valnesfjord ( $P=0.038$ ). Fish from Saltdal were longer than fish from Sulitjelma ( $P<0.001$ ) and Valnesfjord ( $P=0.0027$ ).

Tests of body mass (Kruskal-Wallis and Wilcoxon rank sum test,  $n=164$ ) showed that the fish from Botnvassdraget had a higher mass than fish from Misvær ( $P<0.001$ ), Saltdalselva ( $P<0.001$ ), Sulitjelma ( $P<0.001$ ) and Valnesfjord ( $P<0.001$ ). Fish from Misvær weighted more than fish from Sulitjelma ( $P<0.001$ ) and Valnesfjord ( $P=0.033$ ). Saltdalselva weighted more than Sulitjelma ( $P<0.001$ ), and Valnesfjord ( $P=0.017$ ).

Fish tagged in the autumn (in Botnvassdraget and Misvær) did not differ in  $K$  (t.test,  $n=33$ ,  $P=0.08$ ). For the fish tagged in the spring there was a significant effect of watercourse of origin on  $K$  (ANOVA,  $n=131$ ,  $P<0.001$ ) and the fish from Misvær had higher  $K$  than fish from all other watercourses ( $P\leq 0.02$ ).

The age during first tracking season (Kruskal-Wallis and Wilcoxon rank sum test,  $n=146$ ) was higher in Botnvassdraget than in fish from Saltdalselva ( $P=0.004$ ), Sulitjelma ( $P<0.001$ ) and Valnesfjord ( $P<0.01$ ). Fish from Misvær were older than the fish from Sulitjelma ( $P=0.04$ ) and Valnesfjord ( $P<0.001$ ). In Saltdalselva they were older than fish from Sulitjelma ( $P=0.04$ ) and Valnesfjord ( $P<0.001$ ). And the fish in Sulitjelma were older than fish from Valnesfjord ( $P=0.006$ ).

The back calculated smolt age (Kruskal-Wallis and Wilcoxon rank sum test,  $n=137$ ) was higher in Botnvassdraget than in Misvær ( $P=0.001$ ), Sulitjelma ( $P=0.005$ ) and Valnesfjord ( $P=0.005$ ). And the fish in Saltdalselva were older as smolts than the fish in Misvær ( $P=0.001$ ), Sulitjelma ( $P=0.005$ ) and Valnesfjord ( $P=0.005$ ).

Comparisons between watercourses (Kruskal-Wallis and Wilcoxon rank sum test,  $n=120$ ) showed that fish from Botnvassdraget were longer as smolts than fish from Misvær ( $P=0.005$ ), Saltdal ( $P=0.002$ ) and Sulitjelma ( $P=0.03$ ). In Valnesfjord the fish were longer as smolts compared to the fish in Misvær ( $P=0.017$ ) and Saltdalselva ( $P=0.027$ ).

$L_T$  was not different between the fish tagged in autumn in Botnvassdraget (BA16) and fish tagged during the spring in Botnvassdraget (BS16) ( $n=61$ , Wilcoxon rank sum test,  $P=0.06$ ), but fish from BA16 were heavier than fish from BS16 ( $n=52$ , Wilcoxon rank sum test,  $P=0.006$ ).  $K$  was also highest in the autumn group (BA16) ( $n=52$ , t-test,  $P<0.001$ ). Median age of fish during first spring of tracking was higher in the autumn group ( $n=43$ , Wilcoxon rank

sum test,  $P > 0.01$ ). Fish tagged in the autumn also had a longer back calculated length at smoltification than fish in the spring-group ( $n=43$ , t-test,  $P=0.01$ ). Smolt age did not differ between groups ( $n=41$ , Wilcoxon rank sum test,  $P=0.32$ ).

In Misvær no difference was seen between the two groups in any of the measured variables ( $L_T$ , body mass,  $K$ , age during first tracking season, smolt age or smolt length).

In Valnesfjord the two tagging groups (fish from the estuary (Laukåsstraumen), and fish from the lake (Valnesfjordvatnet)), did not differ in  $L_T$  ( $n=23$ , Wilcoxon rank sum test,  $P=0.07$ ), or in mass ( $n=22$ , Wilcoxon rank sum test,  $P=0.32$ ) but the group tagged in the estuary had higher  $K$  than fish from the lake ( $n=21$ , t-test,  $P=0.03$ ). There was no difference in smolt length ( $n=23$ , Wilcoxon rank sum test,  $P=0.26$ ) or difference between groups in age during first tracking season or smolt age.

### 3.2 Overview of telemetry results

Of the 175 fish tagged in the study, 111 (63%) were recorded in the fjord (table 4), however from these four fish was excluded from further analysis because they were recorded last recorded during the autumn of 2016 and were therefore not relevant for the scope of the study. The number of fish that were never recorded was 28 (16%; table 4).

In the three watercourses that contained acoustic receivers it was seen that parts of the populations were only recorded there, and never entered the fjord ( $n=36$ , 21%; table 4). In Botnvassdraget 10% of the tagged fish displayed this strategy ( $n=6$ ), whereas 47% of the tagged fish had this strategy in Sulitjelma ( $n=16$ ) and 61% in Valnesfjord ( $n=14$ ). In Sulitjelma all of the 16 individuals were detected during the month of June, and for half of them the last registration also happened in June. For the remaining eight, one had the last registration in July, three in August, six in September and three in October. In Valnesfjord, eleven of the fish had their first recording in June, whilst the three other fish were not detected until August, September and October, respectively. Two of the fish had their last recordings in June, four in July, one in August, four in September and three in October. Of the six individuals in Botnvassdraget that only were registered in the lake of the system, two of them were repeatedly recorded at the receiver near the outlet of the lake during most months of 2017. The four other individuals were also recorded on the same station during the month of May, but then never again.

Table 4: Overview of the telemetry data, and aspects of the marine migration for the fish that were detected in the fjord during the study. Some of the fish were registered during both years, and the total number of fish recorded in the fjord might therefore not sum up with the number of fish in the fjord in 2016 and 2017. Based on the how far out into the fjord the fish had been registered it was classified as either a short, medium or a long-distance migrator. Fish that disappeared from the study before a specified cut-off point were excluded.

Watercourse	Botnvassdraget	Misvær	Saldalselva	Sulitjelma	Vahnesfjord
Tagged fish	61	17	40	34	23
Never recorded	16 (26%)	0 (0%)	5 (13%)	0 (0%)	7 (30%)
Only recorded in the watercourse	6 (10%)	0 (0%)	0 (0%)	16 (47%)	14 (61%)
Recorded in the fjord	39 (64%)	17 (100%)	35 (88%)	18 (53%)	2 (9%)
2016	24	6	35	na	na
2017	16	16	2	18	2
<b>Timing of migration</b>					
<b>Outward migration</b>					
2016	01.05-27.06	na	30.04-24.06	na	na
2017	20.05-08.06	03.05-28.07	20.05	04.06-30.06	23.05-09.07
<b>Inward migration</b>					
2016	10.07-29.09	na	11.06-18.08	na	na
2017	19.07-20.09	22.07-29.08	na	25.07-31.08	25.06
<b>Returning to the watercourse</b>					
In total	12	9	8	7	1
In 2016	6	na	8	na	na
In 2017	6	9	0	7	1
<b>Migration distance in fjord</b>					
Short	1	16	1	1	1
Medium	4	0	2	0	1
Long	25	0	29	16	0
Excluded	6	0	2	1	0

### 3.4 Migration characteristics of fjord migrating fish

#### 3.4.1 Migration timing

In 2016 the median day of outward migration into the fjord for all fjord migrating fish was 03.06 ( $n=55$ , range=01.05-06.07, IQR=18.72) and the median day of inward migration for all fjord migrating fish was 25.07 ( $n=14$ , range=11.06-29.09, IQR=33.12). Fish from Saltdalselva migrated outwards at an earlier date than fish from Botnvassdraget (figure 4; Wilcoxon rank sum test,  $n=55$ ,  $P<0.001$ ), and had median day of migration the 19.05, whilst the fish in Botnvassdraget had median migration date on the 29.05. No difference between watercourses was detected in the timing of the return back to the rivers (Wilcoxon rank sum test,  $n=14$ ,  $P=0.14$ )

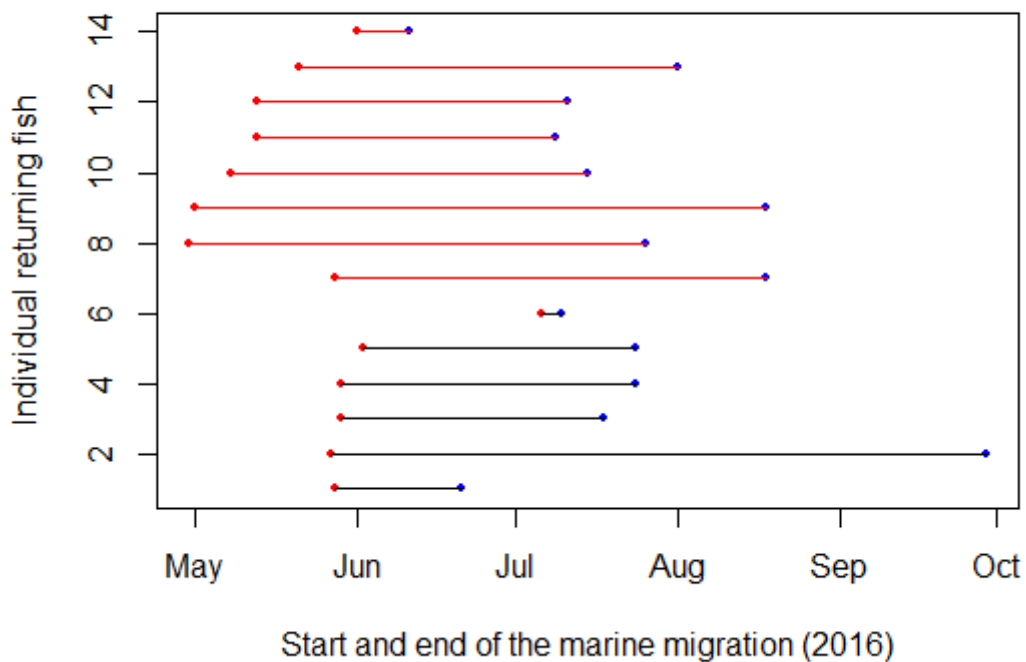


Figure 4: The duration of each marine migration from migrants that entered the fjord in 2016 and returned to the watercourses. Fish from Botnvassdraget are marked with black and fish from Saltdalselva with red lines. Red dots mark the start of the migration and blue dots the last day of the migration.

In 2017 the median day of outward migration for all fjord migrating fish was 24.05 ( $n=51$ , range=03.05-28.07, IQR=18.38) and the median day of inward migration for all fjord migrating fish was 07.08 ( $n=22$ , range=25.06-20.09, IQR=26.47). Fish from Misvær migrated out earlier (figure 5; median day of migration: 06.05) than fish from Botnvassdraget (median day of

migration: 28.05;  $n=51$ , Pairwise comparisons Wilcoxon,  $n=51$ ,  $P=0.01$ ), and also earlier than fish from Sulitjelma (median day of migration: 09.06; Pairwise comparisons Wilcoxon,  $n=51$ ,  $P<0.001$ ). Fish from Botnvassdraget also migrated out into the fjord earlier than fish from Sulitjelma ( $n=51$ , Pairwise comparisons Wilcoxon,  $P<0.001$ ). The time of return migration from the fjord in 2017 did not show any difference between watercourses ( $n=22$ , Kruskal-Wallis,  $P=0.37$ ).

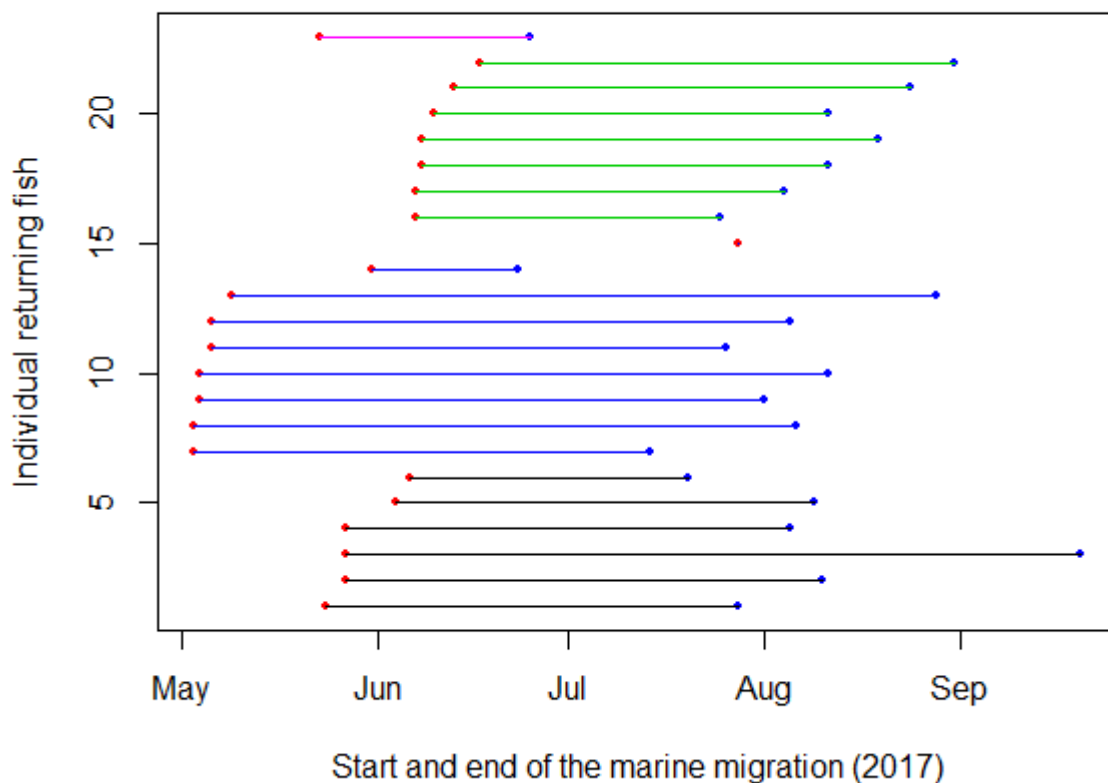


Figure 5: The duration of the marine migration of fish that entered the fjord in 2017 and returned to the watercourses. Fish from Botnvassdraget are marked in black, Misvær in blue, Sulitjelma in green and Valnesfjord in pink. Red dots mark the start of the migration and blue dots the last day of the migration.

The timing of the outward migration did not differ between years for fish from Botnvassdraget (Wilcoxon test,  $n=37$ ,  $P=0.44$ ), and neither did the inward migration (Wilcoxon test,  $n=12$ ,  $P=1$ ).

Only one fish from Saltdalselva and two from Valnesfjord migrated out in 2017, and these are therefore not included in the statistical analysis, but their migration time can be found in table 4.



The total return rate in the study, defined as the number of fish that were registered as having returned to the watercourse after the migration, was 33% ( $n=37$ ). In Botnvassdraget, the return rate was 31% ( $n=12$ ) (table 4), in Misvær 53% ( $n=9$ ), in Saltdalselva 23% ( $n=8$ ), in Sulitjelma 39% ( $n=7$ ) and in Valnesfjord 50% ( $n=1$ ). During the winter of 2016 two of the fish from Misvær, along with a fish from Saltdalselva were recorded residing in the Misvær estuary instead of returning to the watercourses.

### 3.4.2 Migration distance

In 2016 55 fish from Saltdalselva and Botnvassdraget migrated into the fjord, and of these 39 (71%) qualified as “long distance migrants” (table 4). Median migration time (time from fjord until the point that qualified as “long migration” was reached) was 3.6 days ( $n=39$ , range= 0.3-55.6 days, IQR=9.6 days). Of these fish, ten were from Botnvassdraget and 29 from Saltdalselva. Fish from Botnvassdraget was faster than fish from Saltdalselva (Wilcoxon rank sum test,  $n=39$ ,  $P=0.01$ ), with a median migration time of 1.0 day (IQR=2.2) while Saltdalselva had a median migration time of 5.6 days (IQR=11.23).

In 2017 16 fish from Sulitjelma had a migration strategy that qualified as “long” and these had a median migration time, calculated from last recording in the river to first recording on a receiver defining long distance migration, of 8.5 days ( $n=15$ , range=1-42 days, IQR=6.59). In the same year one fish from Saltdalselva classified as a long-distance migrant (migration time=5.8 days) together with 16 from Botnvassdraget. These had a median outward migration time of 2.3 days ( $n=17$ , range=0.6-33.5 days, IQR=6.1 days). Fish from Botnvassdraget had a lower median time for long distance migration than fish from Sulitjelma (Wilcoxon rank sum test,  $n= 31$ ,  $P=0.017$ ).

To explain the differences in speed of the long-distance migrants an analysis of covariance (ANCOVA) was done on migration speeds in 2016 ( $n=35$ , adjusted  $R^2=0.3$ ). The full model contained watercourse, sex,  $L_T$ ,  $K$ , age and Julian day of outward migration, and the response variable (time to long distance migration) was log transformed. After model selection the best model to explain the speed of outward migration contained sex (ANOVA,  $P=0.008$ ) and Julian day of outward migration (ANOVA,  $P=0.006$ ). Males used longer time than females and increasing Julian day of outward migration was negatively correlated with time until long migration.

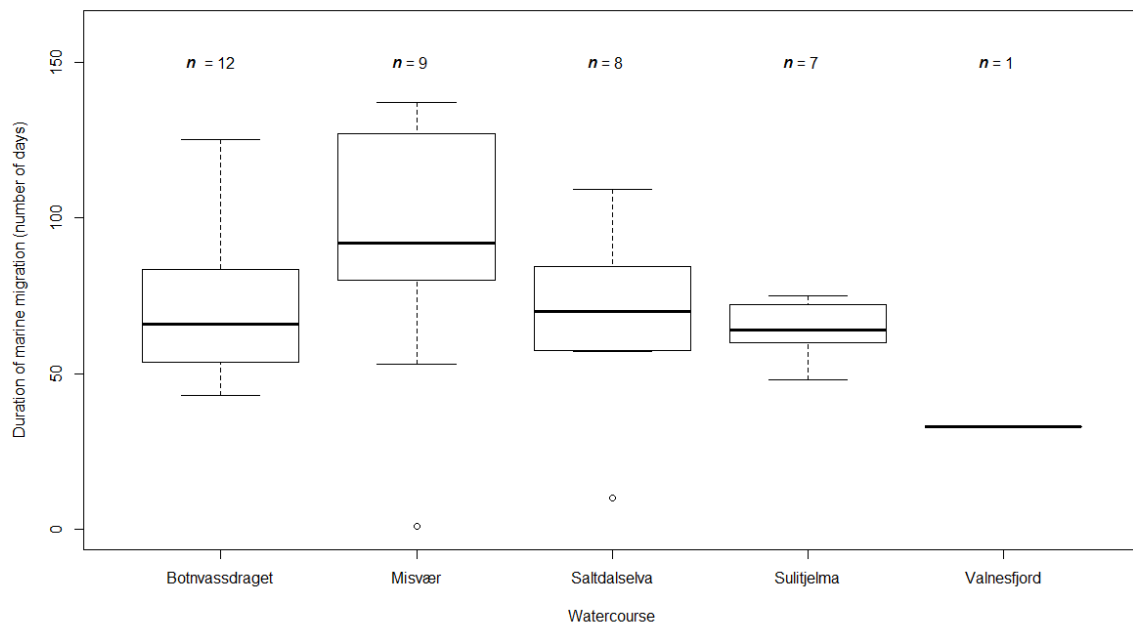
The full model analysing migration speeds in 2017 contained watercourse, sex,  $L_T$ , age and Julian day of outward migration, and had the response variable in log. The best model ( $n=26$ ,

adjusted  $R^2=0.12$ ) only contained  $L_T$  (ANOVA,  $P=0.049$ ), in which increasing  $L_T$  was correlated with shorter time used on the long-distance migration.

Seven fish had a medium distance migratory strategy (table 4), and this type of migration was only recorded in 2016. Twenty were categorised as “short distance migrants”, two in 2016 and 18 in 2017. Fish from Misvær exclusively had short distance migrations and made up 80% of this group ( $n=16$ ). The other four short distance migrants were from each of the other watercourses (table 4).

### 3.4.3 Duration of marine migration

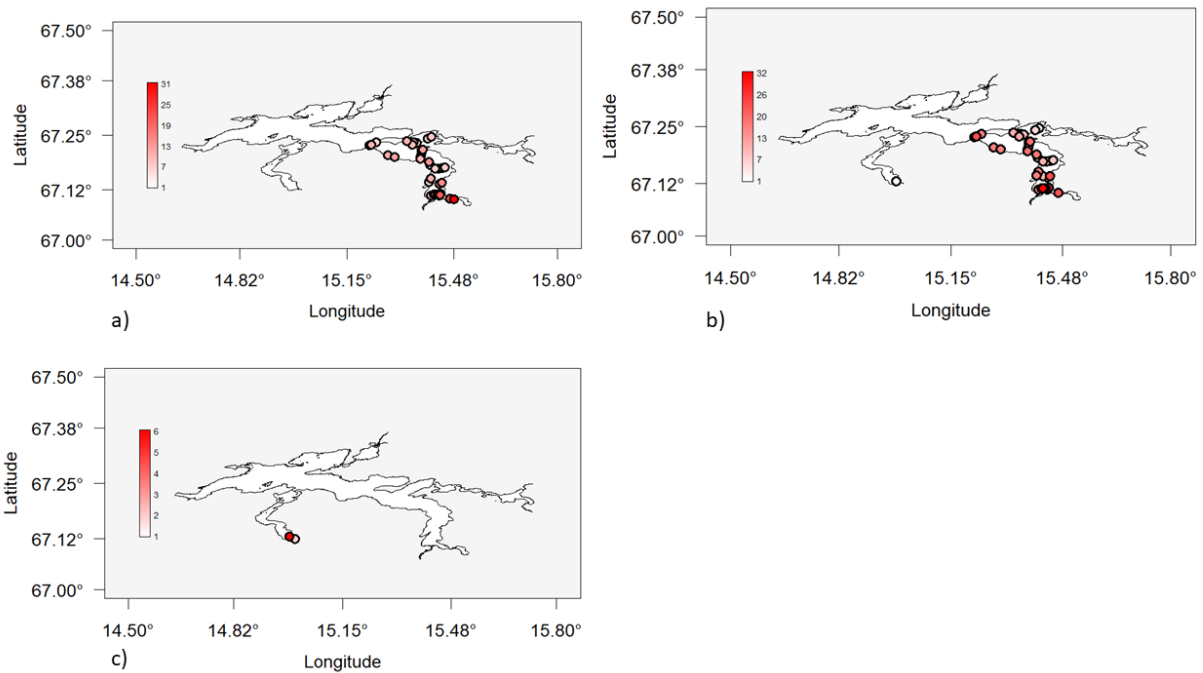
In 2016 the mean duration of a marine migration was 65 days ( $n=15$ , range=9.5-109.4,  $SD=23.5$ ), and in 2017 it was 75 days ( $n=23$ , range=1-137 days,  $SD=32.25$ ). Figure 6 summarises the data for both years, for each of the watercourses. There was no significant difference between years (t-test,  $n=38$ ,  $P=0.3$ ), and therefore all data was pooled to do an ANCOVA ( $n=29$ , adjusted  $R^2=0.35$ ). The full model contained sex, watercourse,  $L_T$ , age and Julian day of outmigration. After model selection, the best model to explain duration of marine migration contained Julian day of outward migration and watercourse as explanatory variables, with watercourse consisting of two levels, Saltdalselva or not-Saltdalselva (all other watercourses pooled). Julian day of outward migration had a negative correlation on the duration of marine migration ( $P<0.001$ ) and fish from Saltdalselva had a shorter duration of migration than fish from the other watercourses ( $P=0.017$ , estimated effect=-24.6 days).



Figur 6: Duration of the marine migration is calculated from the first and last registration of the fish in the fjord. If a fish returned to freshwater and back to the fjord again, the time spent in the watercourse is subtracted from the migration duration. The box-and-whisker plots show median values (bold lines), the interquartile ranges (box) and the 5th and 95<sup>th</sup> percentiles (whiskers) and outliers (O).

### 3.4.4 Geographic use of the fjord system

Fish from Misvær were never recorded outside the Misvær fjord during the course of the study (figure 7-8), and in Valnesfjord only two individuals were detected in the fjord (figure 8). Fish from the three other watercourses all displayed a more varied use of the entire fjord system (figure 7-8).



Figur 7: Plots showing the number of individual fish registered at each acoustic receiver in 2016. Includes both receivers in the fjord and in the watercourses. Figure a) show the fish from Botnvassdraget, b) the fish from Saltdalselva and c) the fish from Misvær. Receivers with no registrations are not pictured. Note that fewer acoustic receivers were present in the fjord in 2016 than in 2017 (figure 1). Colour intensity denotes number of fish registered at each receiver.

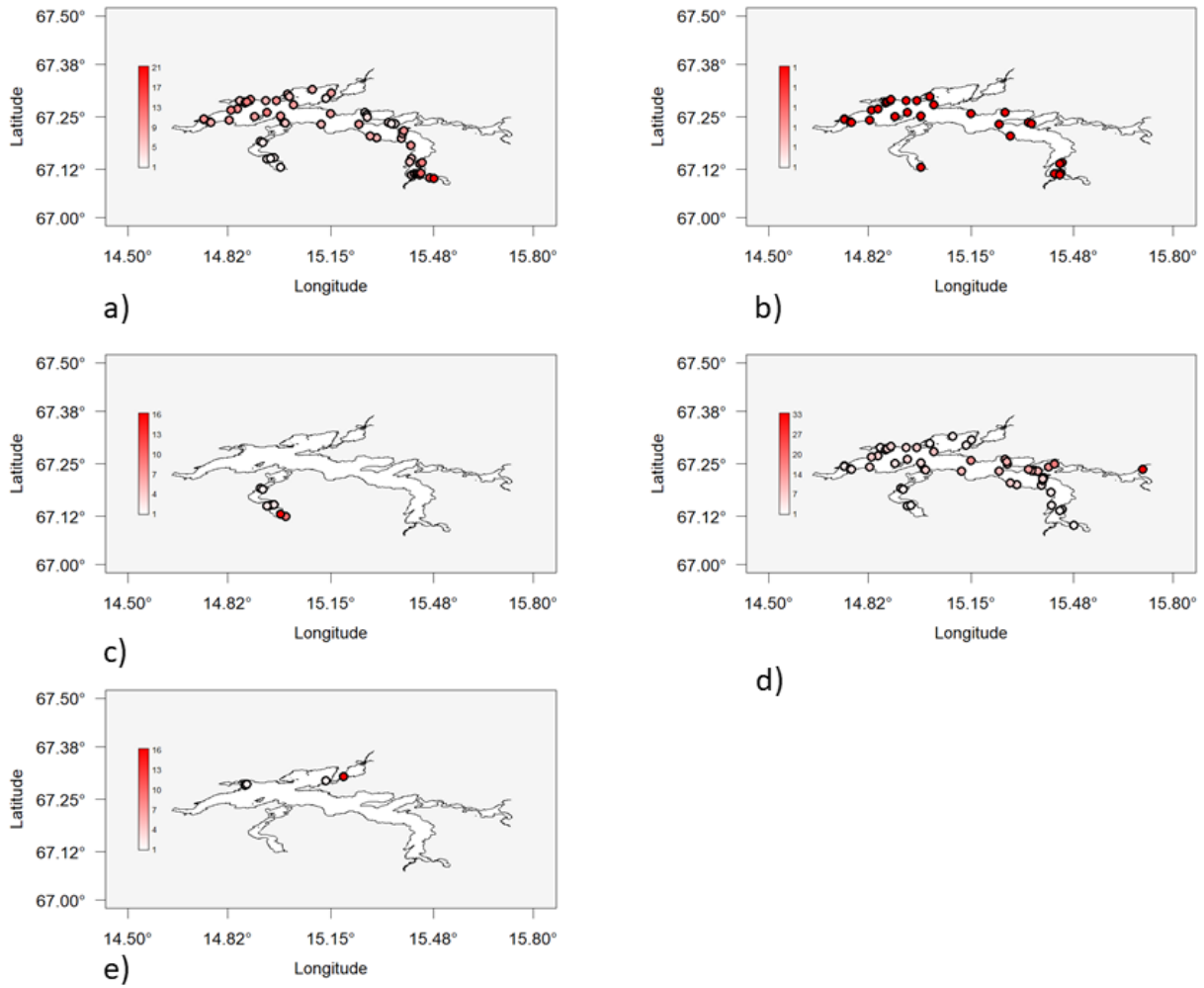


Figure 8: Plots showing the number of individual fish registered at each acoustic receiver in 2017. Includes both receivers in the fjord and in the watercourses. Figure a) show the fish from Botnvassdraget, b) the fish from Saltdalselva, c) the fish from Misvær, d) the fish from Sulitjelma and e) the fish from Valnesfjord. Receivers with no registrations are not pictured. Note that fewer acoustic receivers were present in the fjord in 2016 than in 2017 (figure 1). Colour intensity denotes number of fish registered at each receiver.

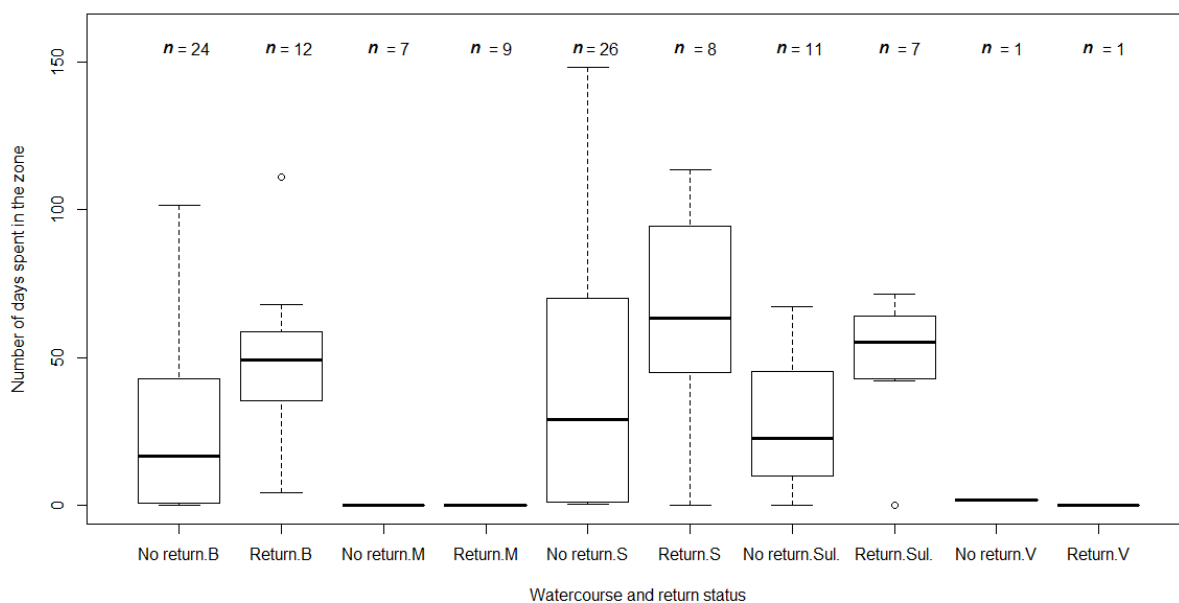


Figure 9: The total number of days spent in the fjord zone. Watercourse of origin is noted by the first letter (B=Botnvassdraget, M=Misvær, S=Saltdalselva, Sul=Sulitjelma and V=Valnesfjord. Fish that were confirmed returned from migration are marked “Return” whilst the fish that never returned are marked as “no return”. The box-and-whisker plots show median values (bold line), the interquartile ranges (box) and the 5th and 95<sup>th</sup> percentiles (whiskers) and outliers (O).

The returning fish from Botnvassdraget spent on average 49 days in the fjord zone ( $n=12$ , range=4.2-111.2 days, SD=26.1 days; figure 9), and were significantly longer in the fjord zone than the non-returning fish from Botnvassdraget ( $n=36$ , Wilcoxon rank sum test,  $P=0.016$ ), which had a median time in the fjord zone of 16.6 days ( $n=24$ , range=0-101.6 days, IQR=41.8). Time spent in inner fjord zone (figure 10) did not differ between the returners and non-returners from Botnvassdraget ( $n=36$ , Wilcoxon rank sum test,  $P=0.14$ ). Median time spent here was 0.5 days ( $n=36$ , range=0-120 days, IQR=2.1 days).

The returning fish from Saltdalselva spent 64.9 days on average in the fjord zone ( $n=8$ , range=0-113.7 days, SD=37 days; figure 9) and were not longer in the fjord zone than the non-returning fish ( $n=34$ , Wilcoxon rank sum test,  $P=0.10$ ). Time spent in the inner fjord zone (figure 10) did not differ between returners and non-returners from Saltdalselva ( $n=34$ , Wilcoxon rank sum test,  $P=0.077$ ). Time in this zone had a median time of 2.1 days ( $n=34$ , range=0-31.8 days, IQR=7.95).

The returning fish from Sulitjelma had a mean time in the fjord zone of 48.5 days ( $n=7$ , range=0-71.4 days, SD=24.3 days; figure 9), and did not differ from non-returners ( $n=18$ , t-test,  $P=0.07$ ). There was no difference between returners and non-returners in the time they spent in

the Fauske zone (figure 10). The median time spent in this zone was 1.1 days (range=0-74.6 days, IQR=4.61).

There was no difference in fjord zone residency between the three populations that spent most time in the fjord zone (Botnvassdraget, Saltdalselva and Sulitjelma, figure 9; Kruskal-Wallis and Wilcoxon rank sum test,  $n=99$ ,  $P>0.05$ ).

In Misvær the returning fish spent 94.4 days on average in the near-Misvær zone ( $n=9$ , range=46-137 days, SD=33.3 days; figure 10), while the non-returners spent on average 83 days, but this difference was not significant ( $n=16$ , t-test,  $P=0.58$ ).

Brown trout from Valnesfjordvassdraget were followed in the estuary for a median time of 8.2 days. ( $n=16$ , range= 1.2-101.7 days, IQR=16.1).

### 3.4.5 Fjord and non-fjord migrating fish in Sulitjelma

In Sulitjelma 47% of the tagged fish migrated to the fjord, while the other 53% were only recorded on the receiver by the river of origin. In the fjord migrating group females made up 61% ( $n=11$ ), while the group of fish that were not recorded in the fjord consisted of 87.5% males ( $n=14$ ). The fish that were recorded in the fjord were longer (mean length=423 mm;  $n=34$ , t-test,  $P=0.001$ ), than fish that didn't go to there (341 mm). The mass was also higher in the fjord migrating group (515 g;  $n=34$ , Wilcoxon rank sum test,  $P=0.004$ ), than in the other group (330 g). The condition factor was higher amongst the non-fjord migrating fish ( $n=34$ , t-test,  $P=0.01$ ), where the mean in the non-fjord group was a condition factor of 0.86, and the fjord-migrators had a mean condition factor of 0.81. The two groups did not differ in age during first season of tracking ( $n=32$ , Wilcoxon rank sum test,  $P=0.09$ ) or smolt length ( $n=25$ , t-test,  $P=0.06$ ). Smolt age was however lower amongst the non-fjord migrating group ( $n=25$ , Wilcoxon rank sum test,  $P=0.005$ ), where median age of smolting was four years, with four years as the median in the other group.

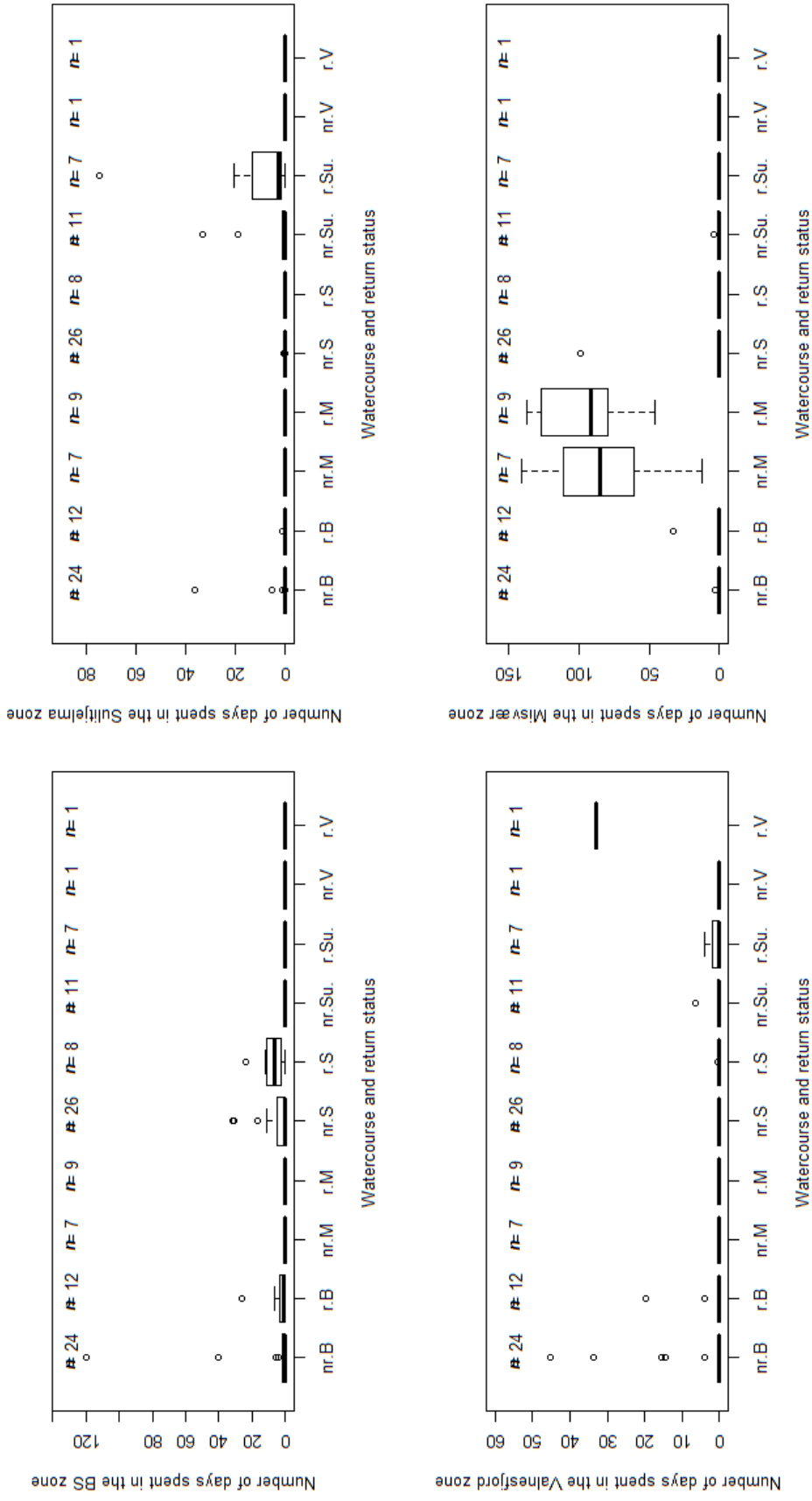


Figure 10: The number of days spent in the four near-watercourse zones; the inner-fjord zone (top left), the Sultjelma zone (top right), the Valnesfjord zone (bottom left) and the Misvær zone (bottom right). Groups are labelled after return status (nr=not returned, r=returned) as well as the first letter of the watercourse of origin (B=Botnvassdraget, M=Misvær, S=Saltåselva, Su.=Sultjelma, V=Valnesfjord). The box-and-whisker plots show median values (bold line), the interquartile ranges (box) and the 5th and 95<sup>th</sup> percentiles (whiskers) and outliers (O).



## 4 Discussion

The results from this study further describes the variation in migration strategies and the varied life histories of brown trout. Brown trout from five different watercourses, assumed to be five distinct populations, were compared on some important life history traits like length-at-age and age and length at smoltification, as well as marine migration strategies. Because these five populations had access to the same fjord system for their feeding migrations this study could compare these traits and strategies between populations on the same latitude, in contrast to many of the previous studies (e.g. L'Abée-Lund *et al.* (1989) and Jonsson *et al.* (1991)) that has been done on these topics. The differences in life history and marine migration strategies tells about the different selection pressures that have shaped these five populations.

### 4.1 Difference between length-at-age, smolt characteristics and condition

Investigation of the relationship between total length ( $L_T$ ) and the age of the fish (figure 3) showed that the five populations studied had three different growth curves, where fish from Saltsalselva and Botnvassdraget had the steepest growth curve, and fish from Misvær the slowest. The difference in length-at-age of these populations can be an indication of different feeding opportunities, or different life-history strategies (whether energy is allocated towards somatic growth or reproduction).

That the model explained 82% of the variation in  $L_T$  by watercourse of origin and age shows that the included variables are important, but also that there are other factors also at play.

The back calculated smolt age was higher in Botnvassdraget and Saltdalselva than in Misvær, Sulitjelma and Valnesfjord. This could be a reflection of the nutrient status of these watercourses, as it has been seen that nutrient availability is negatively correlated with smolt age (Thomson & Lyndon, 2018). The back calculated smolt length was highest in Botnvassdraget, and here the fish were longer than in all other populations, except Valnesfjord. In Valnesfjord the smolt was longer than the smolt in Misvær and Saltdalselva. Smolt age is influenced by the growth rate of the parr (Økland *et al.*, 1993), and fast-growing parr will normally smoltify younger than slower-growing parr. However, earlier studies of brown trout smolts (Davidsen *et al.*, 2014; Davidsen, unpublished results) have also indicated that individuals that grow up with access to a lake may have higher growth rate and older smolt age than individuals from a pure riverine habitat. This difference can be attributed to the observation that marine mortality for smolts is size-dependent (Dieperink *et al.*, 2001; Kallio-Nyberg *et al.*,

2007; Flaten *et al.*, 2016) and that the smolts with access to better feeding conditions in the lake utilize this to gain more growth before the migration. Another factor in smolt age is the temperature in the river, which is heavily dependent on water temperature. As Botnvassdraget and as Saltdalselva both contain glaciers in their watersheds it is as expected that these contain the oldest smolts.

The length of smolts are positively correlated with the age of the smolt (Økland *et al.*, 1993) which explains the long smolt in Botnvassdraget, but not in Valnesfjord. The smolt in Valnesfjord must pass a freshwater estuarine habitat which has been described as an important habitat for birds (NVE, 2018) on their way to the lake, and it is therefore possible that the long length as smolt is a reflection of to the high predation pressure they likely experience. The smolts in Misvær are in a similar situation, and also have to pass a predator-rich area, with the estuary in Misvær also being a popular area for cod (personal observation). A study (L'Abée-Lund *et al.*, 1989) found that low sea temperatures and high predation risk selects for high age and large size for smolts.

Condition factor, which is a reflection of the fish's weight independent of its length, vary throughout the year. The freshwater residency during winter is associated with weight loss, and the feeding migration in the fjord with weight gain (Berg & Jonsson, 1990). Therefore, the tagged groups were compared based on time of capture, and this analysis showed that the condition factor of fish tagged in the spring in Misvær were significantly higher than the fish tagged in the spring in the other watercourses. In Valnesfjord it was also seen that the fish tagged in the lake had a lower condition factor than fish tagged in the estuary. Both of these results, that fish from the estuary in Misvær and fish from the estuary in Valnesfjord had a higher condition factor, shows that these fish already were using productive feeding areas at time of capture.

#### 4.1.1 Validity of population assumptions

One of the assumptions behind this study has been that the five groups of fish tagged have represented five different populations, and that the tagged groups represent the population as a whole.

During the study it was observed fish from other watercourses in Misvær (in total five, from Botnvassdraget ( $n=2$ ), Saltdalselva ( $n=1$ ) and Sulitjelma ( $n=2$ )), and as some of the fish tagged in Misvær had been caught in the estuary, it was a possibility that fish originating from other watercourses could have been tagged by accident. This was however deemed improbable, as

the telemetry results showed that all of the tagged fish from Misvær displayed similar behaviour, with high fidelity to the Misvær fjord.

In Botnvassdraget fish tagged during the autumn (the BA16-group) were older, had higher body mass and had a longer back calculated smolt length than fish tagged the spring of 2016 (BS16). In the spring the fish were caught in the lake, and the fish that were tagged might have been immature fish that resided in the lake instead of returning to the river to spawn, whilst the fish tagged in the autumn most likely were spawning fish. In Botnvassdraget it therefore seems that the tagging during the autumn 2016 happened to target a different, older, part of the population than what was tagged in the spring. When fish return to the river for spawning there has been seen that the size of the fish influence where in the river it stays, and that they select for a specific substrate and water current (Jonsson & Jonsson, 2006b). The tagging effort this season might have focused on a stretch of river which was preferred by large fish.

When designing studies aiming to describe differences in migratory behaviour between different brown trout populations it is important to include as much variation within the studied population as possible, e.g. by capturing individual fish at different seasons and habitats within the watercourse. However, practical limitations may compromise this. In this study, the populations from Botnvassdraget, Misvær and Valnesfjord were probably better represented due to greater variation in time and place for capture, than the populations from Saltdalselva and Sulitjelma. Hence, it is possible that e.g. differences in size and age between the populations were caused by this difference in tagging effort.

## 4.2 Observed migration strategies

Overall, three different types of migration strategies stood out in the telemetry data (figure 7-8): marine migration that utilized the entire fjord system, marine migrations confined to estuaries and assumed marine migrations inside the watercourses.

Fish from Saltdalselva and Botnvassdraget mainly utilized the whole fjord system, while the fish from Misvær confined their migrations to the estuary in Misvær and fish from Valnesfjord were mostly found in the lowermost part of the estuary or in the lake, influenced by the tide and marine waters. Tagged brown trout from Sulitjelma were divided between the two: 53% migrated to the fjord system while 47% were only recorded in the watercourse. This watercourse contained areas that similarly to Valnesfjord was strongly influenced by the marine environment.

#### 4.2.1 Marine migration inside the watercourses

Fish with assumed marine migrations were only recorded in their watercourses, but as these had access to marine-influenced areas in the watercourse it was assumed, based on the idea that animals will seek to maximize fitness over evolutionary time, that these animals had evolved to use these areas of higher productivity in their watercourses, instead of residing in freshwater the entire year.

In Sulitjelma, the fish were tagged in the freshwater habitat Lake Øvrevatnet and from there have access to Lake Nervatnet, which is located at sea level and connected to the fjord through a small tidal current, and therefore a marine area. Local inhabitants in the area report that large brown trout and Arctic charr can be caught here (Kristensen *et al.*, 2012). The area is popular area for fishing, and it is therefore not an unlikely assumption that some of the tagged fish from Sulitjelma spent the season here, although it cannot be confirmed.

In Valnesfjord the one receiver was placed where the lake exited into the estuary, and it was not possible to determine the exact location of the fish throughout the season, but it could be confirmed that the fish continued to reside in the area. As the lake is tidal influenced, the fish in Valnesfjord would spent time in a marine environment whether they were in the lake or the estuary, and all the 14 individuals recorded on this receiver therefore had a type of marine migration.

That a high proportion of brown trout in Valnesfjord and Sulitjelma did not migrate to the fjord, but stays in the estuaries or in areas of the watercourse with brackish water are in agreement with the thoughts of Cucherousset *et al.*, (2005) which argued for a view of migration strategies as a continuum, rather than a resident/migrant dichotomy. The fish in Sulitjelma and Valnesfjord have productive marine areas in close proximity, and a long and perilous marine migration is therefore most likely not beneficial to them (Wysujack *et al.*, 2009). That the fish caught in the estuary in Valnesfjord had a higher condition factor than the fish caught the same season in the lake also indicate that the estuary is a productive area the fish migrates to in order to feed. The same strategy was seen in the fish from Misvær, which also confined their migration to their nearby productive areas, instead of migrating to the outer fjord. Further support for this was found by examining the difference between the fish in Sulitjelma. The marine migrants were mostly females while the group that migrated within the watercourse consisted mostly of males. This difference illustrates the running theme in this study that migration strategy is a reflection of the size of the costs and the benefits of migration for the

individual in question: as females have a higher pay-off from increased body mass on fecundity than what males have (Ferguson, 2006), they have a stronger incentive for performing longer (and assumedly) more dangerous migrations. The fact that the fjord migrants from Sulitjelma were longer and heavier than the other group underpins the argument.

The four fish that were recorded only in the watercourse of Botnvassdraget were assumed to be freshwater residents, as the closest receiver to Botnvassdraget in the fjord had an 89% detection rate for the out-migrating fish, and it is therefore unlikely that these four fish only observed in Botnvassdraget all migrated to the fjord undetected.

#### 4.2.2 Marine migrations to the fjord system

During the two years of the study, 111 (63%) fish were recorded in the fjord system, and these fish originated from all watercourses, with a majority from Botnvassdraget (35%,  $n=39$ ) and Saltdalselva (32%,  $n=35$ ). The other watercourses made up 16% (Sulitjelma;  $n=18$ ), 15% (Misvær;  $n=17$ ) and 2% (Valnesfjord;  $n=2$ ) of the fjord migrating group.

##### 4.2.2.1 Migration timing

The fish in Saltdalselva and Botnvassdraget had different dates of median migration in 2016, with fish from Saltdalselva being the first to migrate. In 2017 fish from Misvær migrated the earliest, followed by Botnvassdraget and ended with Sulitjelma (migration time for the one and two fish that migrated from Saltdalselva and Valnesfjord in 2017 is found in table 4).

Previous studies investigating the initiation of the downstream migration have found that increasing waterflow and temperature in the river initiates the first-time migrants of smolts (Aldvén *et al.*, 2015a), but the same patterns have not been seen for veteran migrants (e.g. Davidsen *et al.* (2014)). In a study on Atlantic salmon kelts, Halttunen *et al.* (2013) found that the timing of outward migration was a trade-off between the energetic state of the individual, and that the need for access to food was weighted against the safety of the river. It is possible that the same mechanisms operate in brown trout, and that it is the energetical state of the animal that initiates outward migration.

It has also been seen (Jonsson & Jonsson, 1998) that the time fish spend in the river after the spawning migration is a trade-off, influenced by the quality of the watercourse as a overwintering habitat (temperature, water level, ice, food access), the sex of the fish (the different sexes have difference energy expenditure during spawning) and the conditions in the marine environment. In Misvær the fish encounter high quality habitat on immediate entry into

the fjord, while the fish from Botnvassdraget and Saltdalselva have a long migration before they reach the desired feeding grounds, and the fish from Misvær seems then to have a higher benefit of migrating to the fjord earlier than the other fish. An additional pull-factor for the fish in Misvær is that the river might be a poor overwintering habitat for larger fish, making an early marine migration even more beneficial.

There was no difference between watercourses, or between years, in the timing of the up-stream migration, but this could be because of the low sample size (in total, 14 returned in 2016 and 23 in 2017). However, previous studies have also failed to find such correlations (e.g. Davidsen *et al.* (2014)). Time of spawning varies between populations (Berg & Jonsson, 1990), and the timing of arrival to the spawning grounds may vary from several months before, to arriving just before spawning (Pemberton, 1976; Berg & Jonsson, 1990), creating a large natural variation.

The return rates in this study were low compared to two previous studies in other northern-Norwegian rivers. In River Vardnes an annual minimum survival of 37% for second-time migrants, and 50% for all older fish were observed (Berg & Jonsson, 1990), while a return rate of 68% was observed in lake Urvoll (Bordeleau *et al.*, in press). More similar results were seen in the river Imsa, wherein the veteran migrants had a mean survival of 33% (Jonsson & Jonsson, 2009).

There are several possible explanations for why a fish was not recorded returning to the river. Likely reasons are predation or other courses of natural mortality at sea, capture and removal from the fjord by game fishers, technical failures in the acoustic tag, tag expulsion or battery depletion (table 3). However, it could also be that the individual fish overwintered in or outside the fjord system or migrated to another freshwater system outside the study area. To skip the spawning migration one year has been observed elsewhere (Pemberton, 1976; Knutsen *et al.*, 2004) in favour of residing in the fjord until next autumn, or possibly even longer, although it is yearly returns to the river to spawn or overwinter that is most common (Jonsson, 1985; Berg & Jonsson, 1990). Skipped breeding was observed in this study when a fish from Saltdalselva overwintered in the Misvær fjord instead of returning to the river. Two of the brown trout from Misvær were also recorded overwintering in the Misvær fjord instead of in the river.

The last possibility is that the fish returned after the last download of data. Based on previous experience from similar studies (Davidsen *et al.*, 2014; Bordeleau *et al.*, in press) it was not expected that the fish would reside in the fjord so late in the autumn as they did in this study,

and consequently receivers were possibly downloaded too early to give data about all returning fish. In Botnvassdraget, the “first in fjord” receiver (figure 1) was downloaded in the end of August 2017 (23.08.2017) while the receiver in the lake was downloaded on the 24.10.2017 and should therefore have recorded any late returning fish. In Saltdalselva, there was a range of receivers that acted as the “first in fjord” receiver (figure 1), and some of these were downloaded late in the season (24.10.2017 and 31.01.2018) while some were downloaded for the last time on the 03.05.2017 and the 22.08.2017, and it is therefore possible that some fish may have migrated back to the river without being detected. In Misvær the receivers were downloaded on the 20.09.2017, but at that time only one fish was still residing in the estuary, and it is therefore not an important factor here. In Sulitjelma the two receivers (the “first in fjord receiver” and the one by the river; figure 1) were downloaded as late as 23.10.2017 and 31.01.2018 and therefore most likely registered all the fish that returned. In Valnesfjord only two fish were recorded in the fjord, and the one that did not return disappeared from the study only a short time after migrating out, and the downloading scheme is therefore thought to be irrelevant here.

During the calculation of marine residency, it was detected that some fish from Botnvassdraget and Saltdalselva could have returned to each other’s rivers, but it was not possible to confirm these suspicions, and no fish from other watercourses were detected on the receiver in the lake of Botnvassdraget, nor on the receivers in lake Valnesfjordvatn or Lake Øvrevatn.

#### 4.2.2.2 Migratory distance in the fjord

The results show that the majority of fjord migrating fish in Botnvassdraget (69%), Saltdalselva (85%) and Sulitjelma (89%) were long distance migrants. In total 66% of the fjord migrating fish in the study were long distance migrants (table 4).

A similar telemetry study from the fjords Hemnfjord and Snillfjord (Trøndelag, Norway) (Eldøy *et al.*, 2015) found that 40% had a short distance migration (defined as <4 km), 18% migrated a medium distance (4~13 km) and 42% of fish had a long distance migration (>~13 km), and Bordeleau *et al.* (in press), which also was a telemetry study, found that in the fjords Tosenfjorden and Bindalsfjorden (Nordland, Norway) 14% migrated <2 km, 33% between ~13 to 28 km (to the inner fjord area) and 52% <21 km (to the outer fjord area). Migration distance has also been studied through mark and recapture, e.g in the Vardnes river by Berg & Berg (1987). Here 53% of the tagged fish were recaptured within 3 km of the river mouth. In the same study the mean distance travelled daily by the fastest adults (non-smolt) was 6 km and 5 km a day, respectively (but these numbers are minimum estimates, as mark and recapture-

studies normally are not as precise as telemetry studies and cannot quantify exactly when a fish arrives into an area).

The fact that so many of the fish from these three watercourses Botnvassdraget, Saltdalselva and Sulitjelma were long distance migrants, compared to other studies, indicates that the area furthest into the fjord were not desirable for the fish, with the fish instead preferring the outer areas of the fjord. This preference can be caused by the strong tidal current (Saltstraumen) which is located in the exit of the fjord, and which ensures that large volumes of water is transported in and out of the fjord two times a day, indicating a habitat with high food access. The steep growth curve seen in the populations from Botnvassdraget and Sulitjelma, compared to the other watercourses, is a further indication of that these populations have access to more productive areas than the other populations. Jonsson and Jonsson (2006a) also found a positive correlation between migration distance and body mass and length at maturation for brown trout, indicating that the large size of fish in these watercourses could be a reflection of their long migration route. For fish with long migration routes, it therefore seems beneficial to postpone maturation until a larger body size has been attained, while fish with shorter migration routes prioritise maturation and thereby energy allocation to reproduction instead of growth. This matches the results from the growth-at-age for Misvær, which shows a slow growth curve, perhaps indicating greater focus on reproduction rather than somatic growth. This however assumes that all fish in the study have reached maturation, and since we have not data on this within the current project no conclusion can be drawn.

For the long-distance migrators, the time from start of migration until the criteria for long migration was reached differed between the populations. In 2016 the fish from Botnvassdraget was faster than the fish from Saltdalselva, with a median time of long migration of 1.0 day, while the fish from Saltdalselva used 5.6 days. In 2017 32 fish had a “long distance migration”, and this year the 16 fish from Botnvassdraget used 2.25 days, while the 16 long distance migrants from Sulitjelma used 8.5 days. The significant effects on migration speed in 2016 were sex and the Julian date of outward migration, where females were faster than males, and fish that migrated out later used shorter time than fish that migrated earlier in the season. The best model accounted however for only 30% of the variation in migration speed, and important effects therefore seems to be missing.

That the fish used longer time in 2017 than in 2016 was as expected, as the distance that had to be travelled in 2017 to be registered as a long migrant was longer. Line 3 (figure 1) was not



operational in 2017, and instead the first detection on a receiver in the outer fjord area (all receivers past line 3) counted as a long-distance migration. The difference between Botnvassdraget and Saltdalselva in 2016 was not expected, as they have approximately the same distance to travel. In 2017 only the  $L_T$  of the fish had a significant effect on migration speed, where increasing length was associated with faster migration speed. Difference in length accounted for 12% of the variation seen in migration speed, indicating that important effects are missing also this year.

That  $L_T$  is influencing migration speed was expected, as swimming speed in brown trout is traditionally stated as body length per second ( $BL\ s^{-1}$ ; e.g. Aldvén *et al.*, (2015b)), and the effect of Julian day of outward migration could be an indication that the fish that enter the fjord later are in more dire need of food than the earlier migrators, and therefore swim faster to begin the feeding. Fish from Sulitjelma were the slowest to reach the point of long distance migration, and this could maybe be an effect of swimming past the assumed productive areas of Lake Nervant, in which they maybe take the time to feed before entering the fjord.

All fish in Misvær had short distance migrations (table 4), and apart from these only four individuals were recorded as a short migrant, one from each of the other four watercourses. Only seven fish were classified as medium migrants, indicating that it was the two extremes that were the most common strategies.

In the studies of Eldøy *et al.* (2015) and Bordeleau *et al.* (in press) it was seen that individuals that had a long migration had a lower condition factor before migration than the individuals that had a short migration. This could indicate that the energetic state of the animal influences the migration distance. This was also seen in this study, where the fish in Sulitjelma that migrated into the fjord had a lower condition factor than the fish that did not migrate to the fjord. If this also could explain why some fish from Saltdalselva, Botnvassdraget and Sulitjelma had short or medium migrations instead of long ones could not be tested because of lack of individuals with the short and medium strategies in these watercourses.

The reason for the short migrations of the fish from Misvær is assumed to be the same as the reason why some of the fish never migrated into the fjord (described in chapter 4.2.1): as they have access to productive marine areas in close proximity of their watercourses, a long and perilous marine migration is therefore most likely not beneficial to them (Wysujack *et al.*, 2009).

#### 4.2.2.3 Duration of marine migration

The mean duration of a marine migration was 65 days in 2016 and 75 days in 2017, but the difference between years was not significant and the only significant factors on the duration of marine migration was Julian day of outward migration and watercourse (with the only difference being between fish from Saltdalselva and the other four watercourses pooled together). Fish from Saltdalselva spent shorter time in the fjord than the other fish, and the fish that entered the fjord later in the season also had a shorter duration of the marine migration. Eldøy *et al.* (2015) found the same: that the duration of marine migration was negatively correlated with the date of first sea entry. Here it was also seen that body length and smolt age had a positive correlation with duration, which was not seen in this study. Bordeleau *et al.* (in press) did not find any correlation between duration of marine migration and population of origin, condition factor,  $L_T$  or mass.

In a study from the Vardenes river in northern-Norway it was found that the duration of the marine migration was positively correlated with seawater temperature (during April-June) (Berg & Berg, 1989). In this study it was also seen that females stayed longer in the fjord than males did, an effect that was not seen in this study.

#### 4.2.2.4 Geographic use of the fjord system

For the fjord migrating fish from Botnvassdraget, Saltdalselva and Sulitjelma, >70% of the migration time was spent in the fjord zone. In Botnvassdraget and Saltdalselva the fish spend 73% and 72% of their recorded time at sea in the “fjord” zone while the fjord migrants from Sulitjelma 76% of their recorded time in this zone.

Difference between returning and non-returning fish was examined to test the hypothesis that low return rate was caused by fish “skipping” the return migration, choosing instead to remain in the fjord. As it was seen that fish that not returned stayed shorter in the fjord than returners in Botnvassdraget, it did not seem that this at least was a prevailing strategy, and that fish instead do not return because they disappear from the study. Still, it cannot be a completely abandoned idea, as the boxplots from Botnvassdraget and Saltdalselva (figure 9) have some positive outliers, indicating that while many fish disappear early in the non-return group, some also stay for a longer time than returners.

The close to watercourse-areas (the inner fjord-zone) did not seem important to fish from Botnvassdraget and Saltdalselva, measured in time spent there, but were very important to the fish from Misvær.

### 4.3 Lost fish

Of the tagged fish, 16% ( $n=28$ ) were never recorded during the course of the study (table 4), and the reasons behind this is unknown. No tagging mortality was detected during tagging, but it is possible that some of the fish tagged died at a later time because of tag effects, or because of natural reasons. The fish might simply also be a resident fish that never resided near the receiver in its watercourse, or it might never have been registered because of tag malfunctioning or tag expulsion. As 57% ( $n=16$ ) of the fish that were never recorded belonged to the same tagging group (the group tagged in Botnvassdraget the autumn of 2016; table 2) this could indicate a problem with the tagging procedure during this tagging event, and not with the method as a whole.

## 5 Conclusion

This study found further support for the view of brown trout migration being better represented as a continuum, rather than the dichotomic view of brown trouts as either residents in the river or migrants at sea. The fish from the five watercourses studied display a range of different marine migration behaviour, in which it seemed like the location of the feeding opportunities was central for the extent of the different strategies.

That the marine migration strategy is so flexible and adapted to local conditions, indicate that changing conditions, either the freshwater habitat or the marine, can lead to different strategies being favoured by evolution, and that the populations therefore could change over time. Further studies could go into this and investigate if there are brown trout populations that can be seen to have changed over historic time in response to changing conditions.

The recent declines in brown trout populations indicate that the marine conditions could be deteriorating, leading to increased mortality. The implications of this could be that brown trout populations that presently display extensive marine migrations could shift towards less marine migration, and more residency or short-distance migrations. The populations could still be sustained, but at a lower level. A such development can be assumed to be negative for the social and economic benefits brown trout provide, as this would favour a type of fish that is presently less popular, and attracts less revenue and tourism, than sea trout fishing.

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