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Author: Andrine Emilie Halvorsen

Main supervisor: Professor Asbjørn Vøllestad, Center for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo

Co-supervisor: Associate professor Jan Grimsrud Davidsen, Department of Natural History, NTNU University Museum

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Abstract

Brown trout (BT) and Arctic char (AC) are freshwater species exhibiting a wide array of life history and migration strategies. Populations with free access to the marine environment often display anadromous tendencies, with some individuals undertaking feeding migrations to sea. Recent decades have seen a general decline in anadromous populations of both species across Europe, possibly a consequence of increased marine mortality due to deteriorating conditions at sea. This study aims to increase the knowledge concerning marine migratory behavior of anadromous brown trout and Arctic char through studies of sympatric populations in a fjord system in northern Norway. Acoustic telemetry was used to track the migrations of individual fish (AC: $n = 54$, $L_T = 270\text{-}480$ mm; BT: $n = 111$, $L_T = 169\text{-}880$ mm) and stable isotope analysis was used to identify important prey groups for each species in connection to the marine migration phase (AC: $n = 26$, $L_T = 204\text{-}390$ mm; BT: $n = 110$, $L_T = 185\text{-}720$ mm). Fish were followed in the fjord in 2016, 2017 and 2018. Downstream migration typically occurred in either May or June, with clear differences observed between the species. In 2017, brown trout migrated downstream earlier (median day = 28.05) and displayed greater individual variation on migration timing (interquartile range, IQR = 12 days) than Arctic char (median day = 07.06, IQR = 1.75 days). Timing of marine entry coincided with increased river discharge for Arctic char, but not for brown trout. Brown trout downstream migration timing was negatively correlated with fish body size (L_T). Duration of the marine migration was greater for brown trout than for Arctic char, although large individual variation was observed for both species (AC: mean average = 49.1 ± 32.4 days; BT: mean average = 60.7 ± 31.7 days). For brown trout, migration duration was negatively correlated with Julian day of entry into the fjord. Brown trout utilized the entire fjord system, and had a greater proportion of long-distance (> 20 km) migrants than Arctic char (BT = 65.0%; AC = 28.6%), suggested to be caused by differences in prey choice and spatial distribution of the preferred prey groups. Arctic char mostly utilized the inner fjord areas, and remained in closer proximity to the estuary throughout the marine migration. Stable isotope analysis revealed high proportions of freshwater invertebrates in the diet of Arctic char, suggesting that feeding likely occurred partly in the estuary. Brown trout had mainly been feeding on marine fish and shrimp. The results from this study suggest that Arctic char and brown trout have different marine migratory strategies, driven in part by differences in feeding preferences. However, a significant size difference between the two species is likely to have contributed to some the differences observed in the present study.

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1. Introduction

Migration is a predictable seasonal movement of organisms between habitats, driven in large by the needs of growth, survival, or reproduction (see reviews by Chapman et al., 2011; Dingle, 1996; Shaw, 2016). If migration increases the likelihood of any of these three it is considered to be an adaptive strategy, and because of this underlying adaptive drive, migration is widespread throughout the animal kingdom. For the majority of fishes, migration is considered an essential part of the annual life cycle (Nikolsky, 1963), and three types of migrations in particular are recognized: the spawning-, feeding-, and overwintering migrations (Harden Jones, 1968; Heape, 1931; Nikolsky, 1963).

Some migratory fish move between salt and fresh water as part of their migratory cycle, and these are known as diadromous (Myers, 1949). Two of the main forms of diadromy are anadromy and catadromy. Anadromous fish migrate to saltwater but return to freshwater to spawn, while catadromous fish migrate to freshwater and return to saltwater to spawn (Myers, 1949). Anadromy is most commonly found at temperate and Arctic latitudes, where the marine habitat is more productive than freshwater, yielding an adaptive edge to marine feeding (Gross et al., 1988; review by McDowall, 1988). In contrast, freshwater habitats are more productive at tropical latitudes, creating a greater advantage to freshwater feeding, and catadromy is more commonly observed (Gross, 1987; Gross et al., 1988; McDowall, 1988).

Species of the salmon family, the Salmonidae, are naturally distributed in cool and cold freshwater habitats in the northern hemisphere's temperate and Arctic zones (Klemetsen et al., 2003; McDowall, 1988; Nelson et al., 2016). Most salmonids are believed to show migratory tendencies, some only within freshwater habitats (generally known as freshwater residents), but many also crossing the salinity barrier and entering the sea, i.e. displaying an anadromous life style. Two examples of salmonid species where anadromy is commonly observed is brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*). For populations of these species having free access to the marine environment, it is common for some individuals to undertake feeding migrations to sea, subsequently followed by a return spawning or overwintering migration to the watercourse (Klemetsen et al., 2003). However, not all individuals choose to do this (Hendry et al., 2004; Lucas and Baras, 2001; Northcote, 1997), and brown trout and Arctic char are therefore more accurately known as partial migrants (Chapman et al., 2011; Jonsson and Jonsson, 1993; Klemetsen et al., 2003). For both species the degree of anadromy tend to be correlated with latitude, with increasing occurrences of anadromy towards the north of the species' distributional ranges (Hendry et al., 2004; Johnson, 1980; Klemetsen et al., 2003).

For anadromous fish, many factors underlie the decision to undertake a marine migration, including both external and internal drivers (Dingle, 1996; Hendry et al., 2004). Migration to better feeding grounds at sea leads to increased growth (Gross et al., 1988; Jonsson and Jonsson, 1997; Solomon, 2006), and fecundity in fishes typically increase with body size, especially for females (Hendry et al., 2004). A fish may therefore increase its fitness by migrating to better feeding grounds, assuming this increase is not offset by increased mortality rates and delayed maturation (Gross, 1987; Jensen et al., 2019; Jonsson and Jonsson, 1993), two of the major costs to migration. Migrating is also energy demanding both in terms of distance travelled and in terms of allocating energy for osmoregulation and the smoltification process that prepares the fish for a life at sea (Hendry et al., 2004; Jonsson and Jonsson, 1993; McDowall, 1988). Mortality in the marine environment is typically highest when the smolts enter the sea and decreases as they get larger (Finstad and Ugedal, 1998; Jensen et al., 2019; Jonsson and Jonsson, 1993).

For Arctic char and brown trout choosing to migrate to sea, large individual variation exist concerning the duration and distance of the migration (Eldøy et al., 2015; Klemetsen et al., 2003; McDowall, 1988). Typically, individuals migrate downstream in spring or early summer and return to the watercourse in late summer or fall, although variations exist. Arctic char are usually slow growing and late maturing, and may spend many years in freshwater before their first migration to sea (Johnson, 1980; Klemetsen et al., 2003; McDowall, 1988). They typically overwinter in the freshwater habitat, as low water temperatures increases the difficulty to successfully osmoregulate in the marine environment (at temperatures below 1-2°C; Claireaux and Audet, 2000; Finstad et al., 1989; Jonsson and Jonsson, 2002). Following their first migration, most Arctic char migrate annually until they reach first maturation, after which they may continue to migrate annually or skip migrations for several years before migrating again (Johnson, 1980; McDowall, 1988). Individuals that have adopted a migratory strategy may later choose to become resident, and vice versa (Nordeng, 1983). Arctic char are considered to be rather poor swimmers compared to other salmonids (Beamish, 1980; Johnson, 1980; Lucas and Baras, 2001), and often remain close to their home rivers throughout the migration (Johnson, 1980; Klemetsen et al., 2003; Moore, 1975). Brown trout show equally varied strategies, with some individuals displaying an almost permanent residency in seawater, remaining at sea for two or more years before returning, and others staying out for only a few weeks at a time

(Klemetsen et al., 2003; McDowall, 1988; Thorstad et al., 2016). The duration of the sea sojourn tend to increase with increasing water temperatures in summer, and is therefore shorter further north in the distributional range (Berg and Berg, 1989a; L'Abee-Lund et al., 1989). Brown trout typically migrate further than Arctic char, but usually remain within 100 km of their home rivers (Jonsson, 1989; Klemetsen et al., 2003).

During the marine migration, brown trout are known to feed on crustaceans, polychaetes, fish, and surface insects, with fish becoming an increasingly important food item as the individuals grow larger (Knutsen et al., 2001; Lyse et al., 1998; Pemberton, 1976). They are opportunistic generalist feeders and their diet is expected to reflect changes in food availability, habitat, season, age, and size (Bridcut and Giller, 1995; Klemetsen et al., 2003). On the individual level, however, it is not uncommon to see more specialist feeding behavior, with different individuals preferring different prey items (Grey, 2001). The same is also observed for Arctic char, which may feed on plankton, crustaceans, fish, littoral hyperbenthos, and surface insects while at sea, although a strong individual specialization is common (Grønvik and Klemetsen, 1987; Johnson, 1980; Moore and Moore, 1974).

The biology of both brown trout and Arctic char have been extensively studied, but most of those studies focus on the freshwater part of the life cycle (ICES, 2013). The marine life of these species remains largely unknown, despite the ecological, economic, and cultural importance anadromous forms of these species represent (Fiske and Aas, 2001). In recent decades, population declines have been observed across Europe (Anon, 2018; ICES, 2013; Svenning et al., 2012), possibly a consequence of deteriorating conditions in the marine environment. In order to best know how to preserve these species and their anadromous forms for the future, it is therefore becoming crucial to understand the behavior of these species at sea. Monitoring programs have been increased in Norway to obtain more information on both species, with a particular aim to establish effects of aquaculture on wild stocks (ICES, 2017).

The aim of this thesis is to increase the knowledge concerning marine migration patterns and feeding behavior of anadromous brown trout and Arctic char through studies of sympatric populations in a fjord system in Nordland County, Norway. Acoustic telemetry was used to compare the two species with concern to their marine migration behavior, including migration timing, duration, distance travelled, and use of the fjord system. Stable isotope- and stomach content analysis were used to identify important prey groups for each species in connection to the marine migration phase.

2. Materials and methods

2.1 Study area

This study was conducted from 2016-2018 in a fjord system consisting of four fjords, the Skjerstad-, Saltdal-, Misvær-, and Valnes fjords, located in Nordland county in Northern Norway and shared between the municipalities Fauske, Bodø, and Saltdal (67°*N* 15°*E*, see figure 2.1). In its entirety, the fjord system is 51 km long beginning with the outflow of the river Saltdalselva in the innermost parts of the Saltdal fjord and ending where the Skjerstad fjord meets the Salt fjord in the easternmost parts of the system. Saltstraumen, the strongest tidal current in the world, is located where the Skjerstad- and Salt fjords meet (Plassen et al., 2015). The Valnes fjord stretches to the north and the Misvær fjord to the south of the Skjerstad fjord. Eight Atlantic salmon (*Salmo salar*) fish farms are located in the fjord system.

The watercourse Botnvassdraget drains into the Saltdal fjord on the south-eastern edge of the system (figure 2.1), and is home to sizeable populations of both Arctic char and brown trout. The watercourse consists of two lakes (lake Botnvatnet and lake Litjvatnet) connected to the fjord via the 500 meter long river Botnelva. Lake Botnvatnet has an inflow of water from rivers Knallerdalselva and Ingeborgforsen. Mature fish spawn in Knallerdalsevla during fall.

2.2 Telemetry

2.2.1 *Fish capture and tagging*

Fish were caught in the freshwater parts of the study system, including lake Litjvatnet and rivers Knallerdalselva and Botnelva. Brown trout were caught during spring and fall of 2016 and spring of 2018, while Arctic char were caught during fall of 2016 and 2017. In total, 54 Arctic char and 111 brown trout were caught and equipped with acoustic tags. The fish were caught using fishing rods (single or triple hooks), gill nets (35-45 mm mesh size), or dip nets and flashlights for capture at night. After capture, the fish were kept in holding nets placed in a quiet location of the river/lake until tagging (< 4 hours).

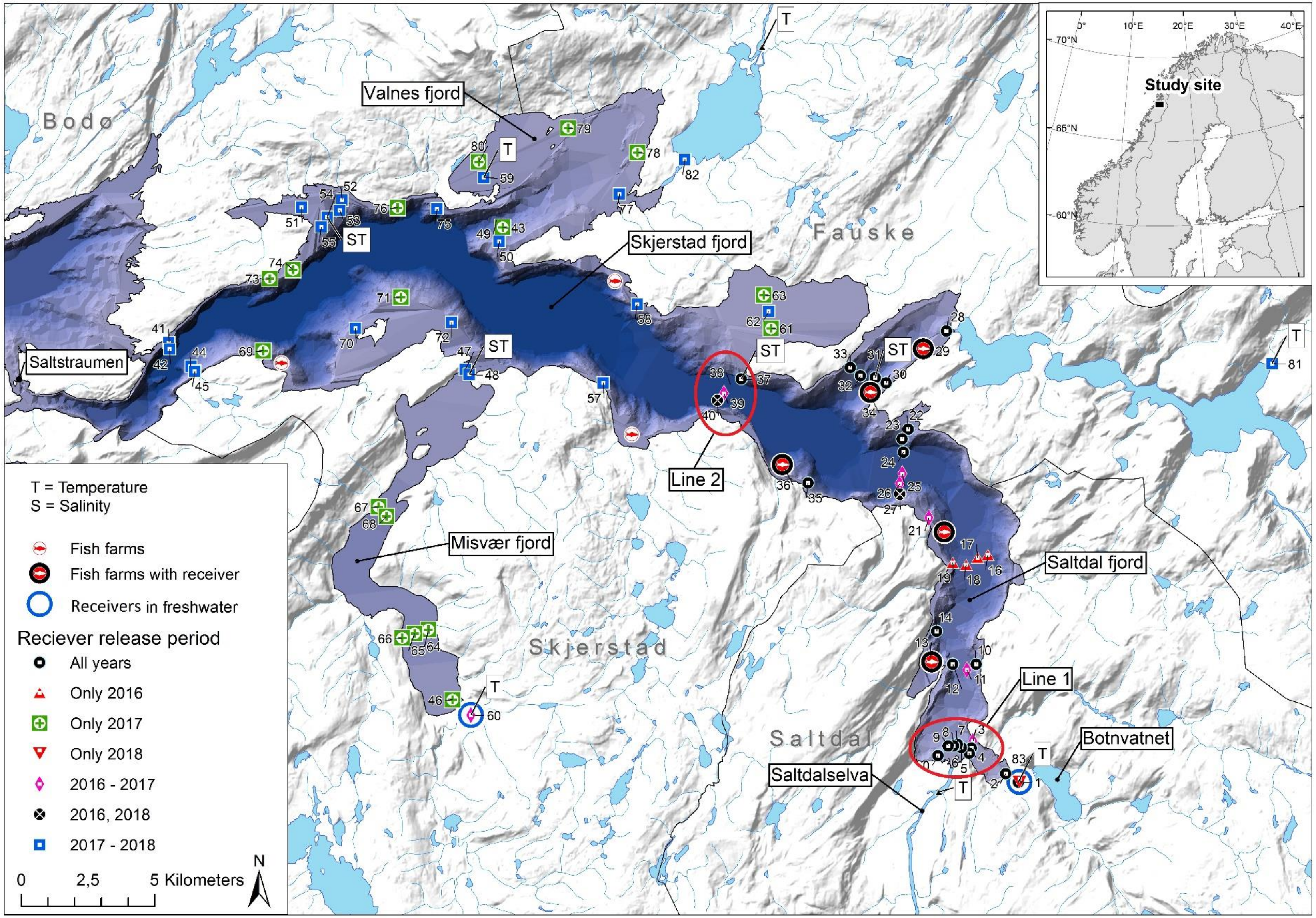

Figure 2.1 Map of the study area (the Skjerstad-, Saltdal-, Misvær-, and Valnes fjords) showing the positions of acoustic receivers, as well as the time period each receiver was operational. The location of temperature and salinity loggers, as well as fish farms with and without acoustic receivers are also labelled. Red circles indicate lines of receivers used in the analyses. The location of Botnvassdraget (Botvatnet), the neighboring river Saltdalselva, and Saltstraumen (the strongest tidal current in the world) are also noted.

Tagging of both brown trout and Arctic char followed the protocol described in full by Eldøy et al. (2015). After capture, the fish were placed in a covered tub containing a solution of phenoxy-ethanol (EEC No 204 589-7, 0.5 mL per L of water), a mixture that sedates the fish after approximately 4 minutes of exposure. Once anesthetized, the length (L_T, from tip of the snout to tip of the longest caudal fin) and weight of the fish were measured, and a 1.5-2 cm long incision was made on the ventral surface of the fish (anterior to the pelvic girdle). A disinfected acoustic transmitter (69 kHz) was gently placed inside the body cavity and the incision sown together with 2-3 sutures (Resolon 3/0). Six tags of differing sizes were used (table 2.1), and the tag chosen for any individual fish was carefully selected based on the L_T of the fish, to avoid any negative influence on the fish's behavior. A modified Carlin tag (Carlin, 1955) was attached to the fish just below the dorsal fin using two cannulas. Lastly, a small piece of the adipose fin was clipped of and placed in ethanol for later DNA sex determination. Throughout the 3-5 min surgery, the gills were gently irrigated to keep the fish hydrated. After surgery, the fish were placed in holding tanks for recovery. Once normal swimming behavior was regained, the fish were released into a calm area of the river/lake, as close as possible to the site of capture.

Table 2.1 Acoustic transmitters used in the study (69kHz). Transmitters with temperature (T) and/or depth (D) sensors had a reduced battery life of about 4-5 months compared to transmitters without sensors. All transmitters have a signal sending interval of about 30-90 seconds. Output is listed as decibel (dB) with the standard reference level for sound in water (re 1µPa) at 1 meter depth. The total number of brown trout (BT) and Arctic char (AC) equipped with each tag is also listed.

Model	**Weight (g, air)**	**Diameter (mm)**	**Length (mm)**	**Battery life (months)**	**Output (dB re 1µPa @1m)**	**Sensor**	**# fish (BT/AC)**
ID-LP7	1.9	7.3	18	5	139	–	50/0
ID-MP9L	5.3	9	29	15	146	–	9/31
T-MP9L	5.5	9	33	10	146	T	0/3
DT-LP13	9.7	13	31	24	150	D/T	19/21
ID-MP13	11.5	13	33	24	153	–	33/2
T-MP13	12.0	13	35	19	153	T	3/0

2.2.2 *Measurement of environmental parameters*

In order to enable accurate descriptions of the environmental conditions faced by the fish during the marine migration, measurements were taken continuously of temperature and depth (water discharge) in Botnelva (figure 2.2), as well as temperature and salinity at several receiver locations in the fjord (appendix A; see figure 2.1 for locations). Depth, temperature, and salinity were measured through the placement of depth-, temperature- and salinity gauges with data loggers (DST milli-TD, DST milli-CT). These were placed during the spring of 2017 and 2018.

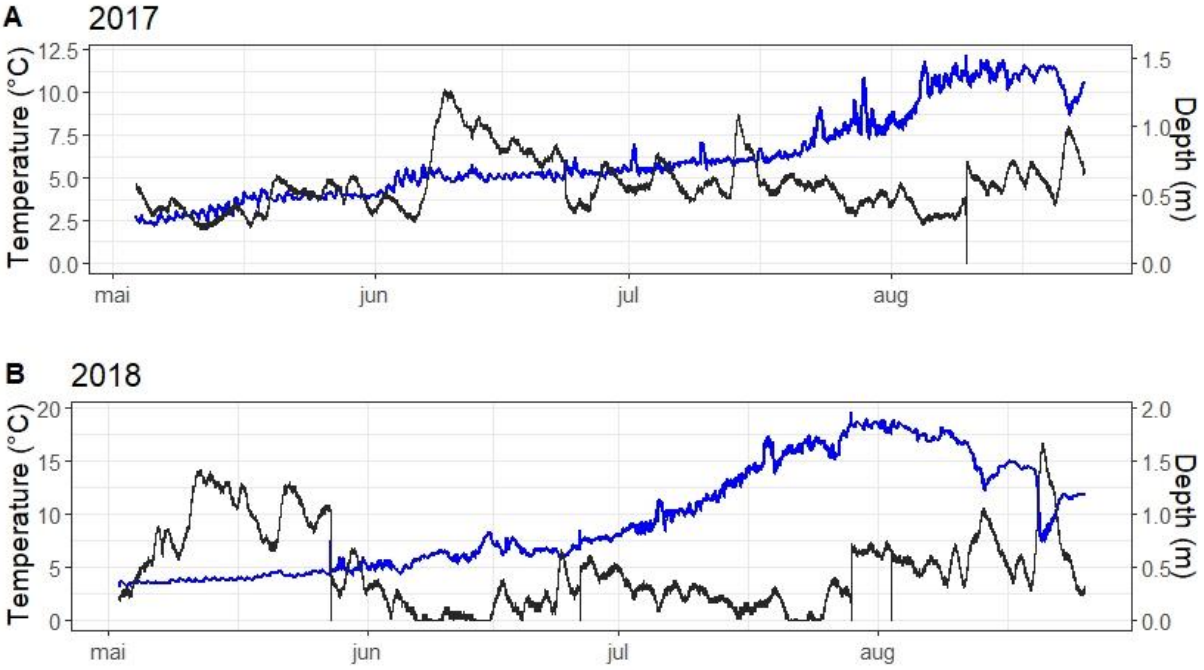

Figure 2.2 Measurements of temperature (blue line) and water depth/river discharge (black line) from May-September in Botnvassdraget. Data from 2017 (plot A) and 2018 (plot B) are displayed.

2.2.3 *Acoustic tracking*

In total, 85 acoustic receivers (Vemco Inc., Canada, models VR2, VR2W and VR2W-AR) were used to track the study populations. Of these, 81 were located in the fjord and four in the watercourses of Botnvassdraget, Misvær, Laksål, and Sulitjelma (receivers 1, 60, 81, and 82, respectively; see figure 2.1). The receiver in Botnvassdraget (Litjvatnet) was fitted to a 20 kg tile and attached to land with a wire. The fjord receivers 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 model AR-60- E). The depths of deployment varied between 0.5-3.0 m in freshwater, while most receivers in the fjord system were moored at five meters depth, with a few at depths of 50-150 m.

The fjord system used in this study is long and complex, exhibiting large spatial and temporal variation in environmental conditions, including wind, salinity, currents, and haloclines. Such variations may affect the detection range of the acoustic transmitters depending on where in the fjord the fish are located, and when. It was therefore necessary to evaluate the reliability of the receiver lines for the analyses performed, and two methods were employed to achieve this. First, the ID of tagged fish registered at the outermost line of receivers (east of Saltstraumen, n = 10 brown trout) were compared to the ID of fish recorded at the first line north of line 1 (figure 2.1). All ten fish were also detected at the inner line, yielding a detection efficiency of 100% for the latter. Secondly, 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 of the tagged fish once every ten minutes. When analyzing data from these signals, detection range was found to be similar to other comparable studies (200-400 m; e.g. Bordeleau et al., 2018; Eldøy et al., 2015). Based on the results from these two performance checks it was concluded that the receiver lines had acceptable performance and were suitable to answer the research questions put forth by this study.

2.2.4 *Genetic sex determination*

Samples taken of the adipose fin of tagged fish were genetically analyzed to determine the sex of each tagged fish. DNA was extracted with the QuickExtract kit (Epigen), according to the manufactures protocol with the exception for the extraction volume, which was reduced to 150 µl. A touchdown PCR amplification of a ~200 bp fragment situated in the first intron of the male specific SDY gene was run on all samples, 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 finished PCR-products were run through a 1% Agarose gel, and the sex determined based on the scores. A number of blind samples with known sex was included to test the quality of the method, and these indicated a 95% positive identification of the sex (J. G. Davidsen, NTNU University Museum, unpublished data).

2.3 Feeding analyses

2.3.1 *Fish sampling*

A trap was set up in the river to record fish returns of both tagged and untagged individuals. This trap was tended to every day, and caught fish released. Due to technical issues with the equipment during the first three days and otters (*Lutra lutra*) feeding on trapped fish, 26 Arctic char and 128 brown trout died in this trap (none of which had been tagged for telemetric analysis). These were frozen down and later analyzed in the laboratory. For each individual, approximately 1 cm^3 of muscle tissue was cut out with a scalpel from the area past the dorsal fin and above the lateral line for stable isotope analysis. The stomach was emptied from the upper end of the oesophagus to the pyloric sphincter and the contents frozen for further analysis. Additionally, length and weight were measured, scales and otoliths collected for age identification, and the gender and stage of maturation was determined. Scales were collected from the area along the lateral line between the dorsal and adipose fins, as is standard for salmonid fishes. All equipment used for sample-taking was dipped in ethanol and burned between each round of sampling to avoid contamination between individual fish.

2.3.2 *Capture of prey species*

To determine the marine diets of Arctic char and brown trout, potential prey species were collected from the fjord to be used for stable isotope analysis. Prey species were collected in the Saltdal fjord in June (5th-8th) and August (21st-23rd) 2018. Different methods were employed to collect different prey items.

In June, two hauls with a fine mesh seine net were conducted on the beach near the outlet of Botnvassdraget. Captured prey species included three-spined stickleback (*Gasterosteus aculeatus*), sand gobies (*Pomatoschistus minutus*), sand shrimps (*Crangon sp.),* amphipods (Amphipoda), European plaice (*Pleuronectes platessa*), and common dab (*Limanda limanda*).

In August, bottom gillnets (25 meter long, 1.5 meter tall) of differing mesh sizes (6-25 mm) were placed in the fjord in several near-shore areas in the Saltdal fjord. Captured prey species included saithe (*Pollachius virens*), Atlantic herring (*Clupea harengus*), Atlantic mackerel (*Scomber scombrus*), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and lesser sand eel (*Ammodytes tobianus*).

Seven to eight hours were also spent fishing for larger fish species in the fjord, as these had the potential of carrying additional prey species in their stomachs. This was done using fishing rods with a rubber shad jig as bait. Both krill (Euphausiacea) and crabs (*Hyas* sp.) were sampled in this manner (both found in the stomachs of Atlantic cod). Krill and flying insects found in the stomachs of Arctic char and brown trout (see section 2.3.1) were also used in the analysis.

2.3.3 *Stable isotope analysis*

The prey items collected were identified to the lowest taxonomic group possible before a muscle sample was taken. As with the brown trout and Arctic char samples (see section 2.3.1), up to about 1 cm^3 of tissue was collected from each specimen; however, due to small prey sizes, this quantity was often much less than 1 cm^3. For the prey fish species, the sample was taken from the side of the fish between the dorsal and caudal fins. For the smaller species, a larger area was sampled to obtain a similar volume of sample as for the larger species. For the crustaceans, the exoskeleton was removed and the tissue inside used as the sample. In some instances, parts of the exoskeleton was used as well, due to small prey size. This also holds true for the insect samples. When possible, 3-5 samples were taken from each species, although some were only sampled once or twice. Each sample was put in an aluminum foil can and placed in a drying oven for 48 hours.

Once dried, each sample was crushed to a fine powder using a mortar. Approximately 1 mg of sample was weighed up for analysis and placed in 5×9 mm tin containers. Each container was closed and placed in a "Thermo Scientific FLASH 2000 HT Elemental Analyzer" with columns set up for "NC with Flash IRMS". The samples were burned with O_2 in a carrier gas of He, at 1020°C. NO_x was reduced to N_2 with Cu at 680°C. The products were then separated in a glass column and transferred to a "Thermo Electron DELTA V Advantage IRMS" via a "Thermo Fisher Scientific Confo IV Universal Interface" for analysis of carbon and nitrogen isotope ratios (for the full procedure, see Davidsen et al., 2018b). Carbon and nitrogen stable isotope compositions are measured as the ratio of the heavier isotope to the lighter isotope ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) and are reported in standard delta (δ) notation as parts per thousand (per mil, ‰) relative to internationally defined standards for carbon (Vienna Pee Dee Belemnite; Craig 1953) and nitrogen (Ambient Inhalable Reservoir; Mariotti 1983) (Fuller et al., 2012). Every third sample run was a gelatin fish mix with already known variables (G7041 GelatineFish), and the first and last samples in a series of 32 were empty samples, i.e. blank control samples.

2.3.4 *Stomach content analysis*

Stomach content samples were analyzed using a stereoscopic microscope, and the content identified to the lowest taxonomic level possible. Most samples were well digested and could only be identified to high taxonomic levels (fish, crustaceans, flying insects). For every sample, the approximate percentage each taxonomic group contributed volumetrically to the total was estimated by eye (subjective methods; see Hyslop, 1980), and the total contribution of each food group to the stomach content of all sampled fish was determined.

2.3.5 *Scale and otolith sample analysis*

Scales and otoliths were used to determine the age of individual fish. Scales were used for age determination of brown trout while otoliths were used for Arctic char (char scales are small and difficult to read (Nordeng, 1961), hence otoliths were used instead).

Each scale sample was analyzed using a stereoscopic microscope. Scales suitable for age identification were retrieved and copied onto 1 mm Lexan plates using a pressing iron. Replacement scales and scales with damages were avoided as they are difficult to read accurately. The printed Lexan plates were then analyzed with a computer-controlled stereoscope (Leica M165C with camera Leica MC170 HD) and its connected software, LAS V4.5 (Leica, 2014). In order to avoid among-observer effects, the majority of the scales were read by the same person. Results were later discussed, and quality checked with a person of long experience with brown trout scale reading.

Otoliths from Arctic char were analyzed with a stereoscopic microscope for the presence of translucent and opaque macrozones (Nordeng, 1961). The translucent zones were counted as far as possible. All otoliths were read twice, one time each by two different people, and age was determined based on the counts. In the case of an uncertainty in the estimate, the lowest age estimate was used for the analysis.

2.5 Data analysis

2.5.1 *Telemetry data*

2.5.1.1 Filtration and removal of registrations

Registrations of tagged fish used in this study spanned a period of two and a half years (three summer seasons; April 2016 – October 2018). Registrations were downloaded each year, and the data stored and managed in VUE [version 2.6.0, VEMCO, 02.2019]. The last download was conducted in October 2018, when the receivers were removed from the fjord system.

Acoustic telemetry is a method based on sound, and sound pollution and tag collisions are therefore two common sources of error. Sound pollution occurs when the receiver interprets a sound as an acoustic signal from a transmitter, even when it is not. This can include sounds from waves, wind, boat traffic, etc., and may result in a series of random ID registrations. These errors are mostly negligible as they are eliminated simply by removing tag IDs that were not used in the study. Tag collisions occur when the receiver receives signals from more than one transmitter simultaneously, causing the receiver to interpret the combination of these signals as an own, separate signal. These erroneous signals can be harder to filter out, as the combination of two tag IDs often resemble existing IDs used in the study. A consequence of this is so-called false registrations, i.e. when a fish has been falsely detected in a location it has not actually been in (Pincock, 2012). This is a problem that can never be completely eliminated (Pincock, 2012), only reduced through careful filtration of the data. The receiver situated in Botnvassdraget was chosen for such filtration as this is an area where fish are residing in large numbers, and hence tag collisions are expected to occur. The filtration process consisted of removing all registrations that were not followed by a second registration of the same tag ID on the same receiver within 10 minutes. False registrations typically differ temporally from real registrations as they usually do not occur several times within a short time frame, as would be expected from real registrations (Pincock, 2012).

Registrations from transmitters that had become stationary (i.e., that had remained in place without movement for longer than a week, suggestive of tag expulsion) were also removed from the database. Additionally, individual fish that disappeared at a very early stage of the migration (within three days of entry into the fjord) were excluded from analyses. Reasons for such an early disappearance may include death shortly after entering the fjord, tag expulsion or tag malfunctioning, or these fish may have been freshwater residents traveling only to the estuary before returning to the watercourse. As the focus of this study is on marine migrations, these individuals (11 brown trout in total) were subsequently excluded from further analyses.

2.5.1.2 Duration of marine migration

Duration of individual migrations were calculated based on the following criteria:

- The beginning of the migration was set at the first registration of the fish in the fjord. In some instances, first registration did not occur at the first receiver in the fjord. However, these were still registered at receivers close to the watercourse, and the lapse in time was therefore considered to be negligible.
- Fish were assumed to have returned if the last registration of the fish in the fjord occurred at the receiver closest to the watercourse. If a fish was last detected at a different receiver in the fjord, the last detection in the fjord was substituted for the first registration in the watercourse. The time it took fish to swim from the first-in-fjord to the watercourse receiver was observed to be short, hence allowing for this substitution (brown trout = 8.0 ± 4.6 hours; Arctic char = 8.4 ± 5.1 hours). If a fish had its last registration at the last-in-fjord receiver outside another watercourse, it was assumed to have travelled up that watercourse instead, and that registration was used as the last registration for the fish.
- If a fish returned to the watercourse several times during a migration phase, the time spent in the watercourse was subtracted from the overall migration duration.

2.5.1.3 Distance travelled in the fjord

Each fish registered in the fjord was classified as either a short-, medium-, or long-distance migrant, based on a set of criteria for what would constitute a short-, medium-, or long-distance migration. Travel distance measured is a minimum estimate of the true migration distance, as it is an aerial distance measure, not a track of the path of the fish in the fjord.

- Short-distance: Fish recorded at, but never beyond, the closest line to the watercourse (line 1, figure 2.1) were classified as short-distance migrants. Minimum distance travelled for short-distance migrants was ~2 km.
- Long-distance: Fish recorded at or past line 2 were classified as long-distance migrants. This line was selected because it was the last line to cross the main body of the fjord system. Minimum distance travelled for long-distance migrants was ~20 km.
- Medium-distance: Fish recorded beyond line 1 but never at or past line 2 were classified as medium-distance migrants. Minimum distance travelled for medium-distance migrants was ~5 km.

2.5.2 *Feeding data*

The stable isotope values obtained were analyzed with the simmr-package in RStudio (Parnell, 2016; RStudio Team, 2016). simmr is a stable isotope mixing model based on the siar-package (Parnell and Jackson, 2013).

Mean average and standard deviations of $\delta^{15}N$ and $\delta^{13}C$ isotopic values for both Arctic char and brown trout (the consumers) and the prey species sampled (the sources) were loaded into simmr as described by Parnell and Inger (2016). Prey $\delta^{15}N$- and $\delta^{13}C$-values were further corrected for trophic enrichment using fractionation factors of 3.23 and 1.03 for brown trout (H. Jensen et al., 2012) and 3.80 and 0.66 for Arctic char, respectively (Linnebjerg et al., 2016; Søreide et al., 2006).

2.5.3 *Statistical analysis*

All statistical analyses were conducted in RStudio (RStudio Team, 2016) with a chosen statistical significance level of $p = 0.05$.

When comparing means of Arctic char and brown trout, the Welch two-sample t-test was used when the assumption of normality was met, and the Wilcoxon rank sum test when the assumption of normality was not met. Correlations were tested for using Pearson's product-moment correlation (normality) and Spearman's correlation test (non-normality). Normality was tested for with functions ggqqplot(), ggdensity(), plotNormalHistogram(), and shapiro.test() (required packages include dplyr (Wickham et al., 2018), ggpubr (Kassambara, 2018), and rcompanion (Mangiafico, 2019)).

To test for a difference in the proportions of short-, medium-, and long-distance migrants between the two species, a χ^2-contingency test was conducted.

3. Results

3.1 Study populations

3.1.1 *Telemetry group*

In total, 111 brown trout and 54 Arctic char were captured and tagged for telemetry analysis. Arctic char were tagged in the fall of 2016 and 2017 and brown trout in the spring and fall of 2016 and the spring of 2018. Tagged brown trout in 2018 mainly consisted of smolts (with the exception of three individuals). Total length (L_T) of the individuals varied between 270-440 mm (with a mean average of 335 mm) for Arctic char and 169-880 mm (with a mean average of 453 mm) for brown trout (see figure 3.1, plot A). Brown trout L_T was significantly higher than Arctic char L_T when excluding the spring 2018 brown trout smolts (Wilcoxon rank sum test, $W = 124$; $p < 0.001$), but not when including them in the analysis ($W = 2823$; $p > 0.05$). Body mass varied between 140-660 g (mean average = 314 g) for Arctic char and 36-6300 g (mean average = 1672 g) for brown trout (figure 3.1, plot B). Of the 111 brown trout tagged, 58 were females, 44 males, and nine were of unknown gender. Of the 54 Arctic char tagged, 22 were females and 32 were males.

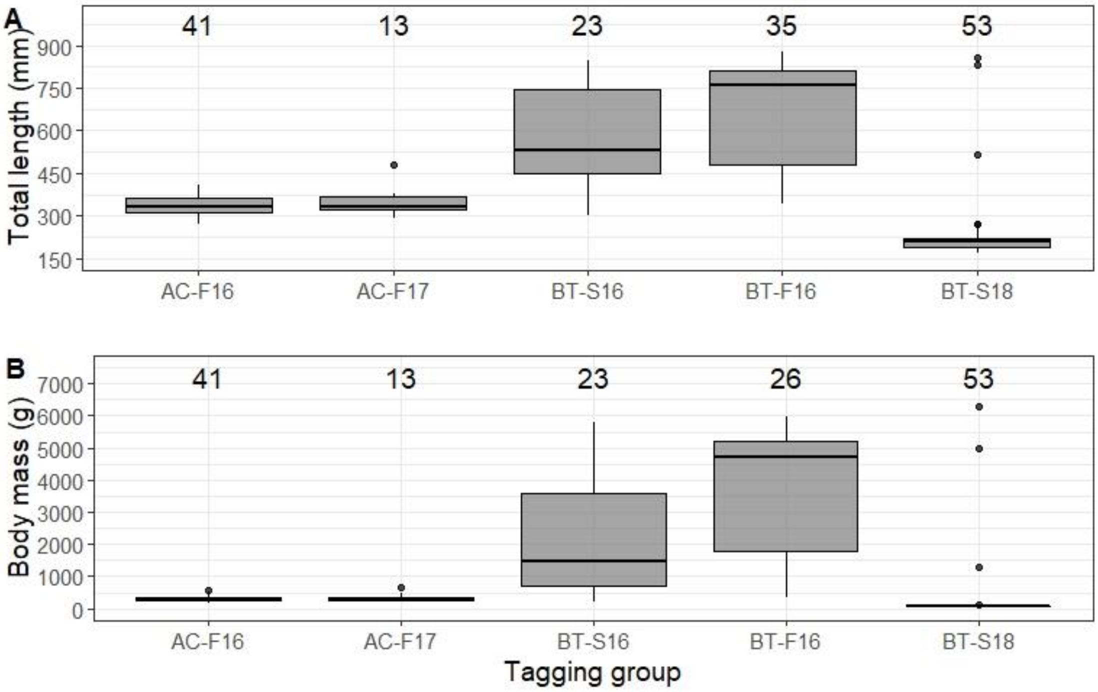

Figure 3.1 Total length (plot A) and body mass (plot B) of all tagged fish participating in the telemetry study. Tagging groups are named after species (AC = Arctic char, BT = brown trout), season (Spring/Fall) and year they were tagged in. The box-and-whisker plots display the median values (bold lines), the interquartile ranges (boxes), the 5th and 95th percentiles (whiskers), as well as outliers (dots). Numbers above each plot indicate sample size of each tagging group.

3.1.2 *Stable isotope group*

In total, 154 fish died in the traps set out in the watercourse in 2017. Of these, 138 were analyzed for stable isotopes, including 26 Arctic char and 112 brown trout. Two of the brown trout samples had to be excluded due to a fault with the system as they were being analyzed, leaving the total number of brown trout samples at 110. Total length (L_T) of the individuals participating in the stable isotope study varied between 204-390 mm (with a mean average of 276 mm) for Arctic char and 185-720 mm (with a mean average of 336 mm) for brown trout. Brown trout L_T was significantly higher than Arctic char L_T (Wilcoxon rank sum test, $W = 1021$; $p < 0.01$). Body mass varied between 66-599 g (mean average = 209 g) for Arctic char and 27-2292 g (mean average = 479 g) for brown trout. Age varied between 4-8 years (mean average = 5.4) for Arctic char and 3-10 years (mean average = 4.3) for brown trout. Of the 26 Arctic char, nine were identified as males, 11 as females, and the remaining six were unidentified. Seventeen were immature (65.4%), six mature, and three of unknown maturity. Of the 110 brown trout, 51 were males, 47 females, and the remaining 12 unidentified. As with the Arctic char, most brown trout were immature: 103 (93.6%) compared to six mature (one was unknown).

3.2 Migratory behavior

3.2.1 *Overview of telemetry results*

Of 165 fish tagged for telemetry analysis, 81 were recorded in the fjord at some point during the study (49.1%). This includes 21 out of 54 Arctic char (38.9%) and 60 out of 111 brown trout (54.1%) (see table 3.1). The remaining fish were either never recorded at all (36 individuals in total, 21.8%) or only recorded in the watercourse (48 individuals in total, 29.1%). The high proportion of fish only registered in freshwater is due to both Arctic char and brown trout displaying partial migration in this system. Of the 81 fish that went out, 29 were registered as having returned to the watercourse after the marine migration (39.5%). Tagged Arctic char went out in 2017 and -18, while tagged brown trout went out in 2016, -17, and -18. Of the three adult brown trout tagged in 2018 (see tagging group BT-S18 in figure 3.1), two never left the watercourse and the third was never registered at all. Hence, all migrating brown trout in 2018 were smolts.

Table 3.1 Overview of telemetry data, including aspects of the marine migration phase for the individuals that were recorded in the fjord (timing, rate of returns, duration of marine migration for returnees, and migration distance). Depending on how far out in the fjord system the fish had been registered, they were classified as either short-, medium-, or long-distance migrants Individuals that disappeared from the study within three days of entering the fjord were excluded from the study.

Species	**Arctic char**	**Brown trout**
Tagged fish	54	111
No recordings	13 (24.1%)	23 (20.7%)
Only recorded in watercourse	20 (37.0%)	28 (25.2%)
Recorded in fjord	21 (38.9%)	60 (54.1%)
2016	–	14
2017	18	13
2018	3	22
Excluded	–	11 (18.3%)
Timing of migration		
Outward migration		
2016	–	22.05-06.07
2017	30.05-16.06	20.05-08.06
2018	08.05-31.05	30.05-12.07
Inward migration		
2016	–	18.07-10.09
2017	12.06-27.09	20.07-20.09
2018	15.05-21.07	04.07-08.09
Returning to the watercourse		
In total	9 (42.9%)	20 (33.3%)
2016	–	6 (42.9%)
2017	7 (38.9%)	6 (46.2%)
2018	2 (66.7%)	8 (36.4%)
Duration of marine phase		
2016	–	65.2 days (± 16.7)
2017	50.2 days (± 37.2)	76.5 days (± 24.1)
2018	45.2 days (± 8.4)	68.0 days (± 26.7)
Migration distance in fjord		
Short (>2 km)	6 (28.6%)	5 (10.2%)
Medium (>5 km)	9 (42.9%)	10 (20.4%)
Long (>20 km)	6 (28.6%)	34 (69.4%)

3.2.2 *Migration timing and duration*

In 2016 (figure 3.2, plot A), the median date of outward migration for brown trout was 29.05 (n = 14; range = 22.05–06.07; interquartile range, IQR = 29 days), while the median date for inward migration by returning individuals was 24.07 (n = 6; range = 18.07–10.09; IQR = 45). One of these migrated again during fall, from 07.09-29.09. In total, 57.1% of the fish entered the fjord for the first time in May, 35.7% in June, and 7.1% in July. Of the returning individuals, 66.7% returned for the first time in July, 16.6% in August, and 16.6% in September. On average, returning brown trout spent 65.2 days in the fjord in 2016 (n = 6; range = 49.9–92.8; SD = 16.7).

In 2017 (figure 3.2, plot B), the median day for outward migration by fjord-migrating brown trout was 28.05 (n = 13; range = 20.05–08.06; IQR = 12) and the median day for inward migration was 07.08 (n = 6; range = 20.07–20.09; IQR = 23.8). In total, 69.2% entered the fjord in May and 30.8% in June. Of returning individuals, 33.3% returned in July, 50.0% in August, and 16.7% in September. The median date for outward migration by migrating Arctic char in 2017 was 07.06 (n = 18; range = 30.05–16.06; IQR = 1.75), while the median day for inward migration was 31.07 (n = 7; range = 12.06–27.09; IQR = 30.5). One Arctic char entered the fjord in May (5.6%) while the remaining entered in June (94.4%). Of returning individuals, 28.6% returned in June, 28.6% in July, 28.6% in August, and 14.2% in September. Arctic char spent less time on average in the fjord than did brown trout; 50.2 days (n = 7; range = 4.2 – 112.4; SD = 37.2) and 76.5 days (n = 6; range = 43.3–112.7; SD = 24.1), respectively.

In 2018 (figure 3.2, plot C), the median day for outward migration by fjord-migrating brown trout was 17.06 (n = 22; range = 30.05–12.07; IQR = 6) and the median day for inward migration was 29.08 (n = 8; range = 04.07–08.09; IQR = 12.3). One individual entered the fjord in May (4.6%), 81.8% in June, and 13.6% in July. Of returning individuals, 12.5% returned in July (one individual), 50.0% in August, and 37.5% in September. The median date for outward migration by fjord-migrating Arctic char in 2018 was 25.05 (n = 3; range = 08.05–31.05; IQR = 11.5), while the median day for inward migration was 12.07 (n = 2; range = 03.07–31.07; IQR = 9). All Arctic char entered the fjord in May and both returnees returned in July. Also this year, Arctic char spent less time on average in the fjord than brown trout; 45.2 days (n = 2, range = 39.3 – 51.2, SD = 8.4) and 68.0 days (n = 8, range = 10.6 – 92.3, SD = 26.7), respectively.

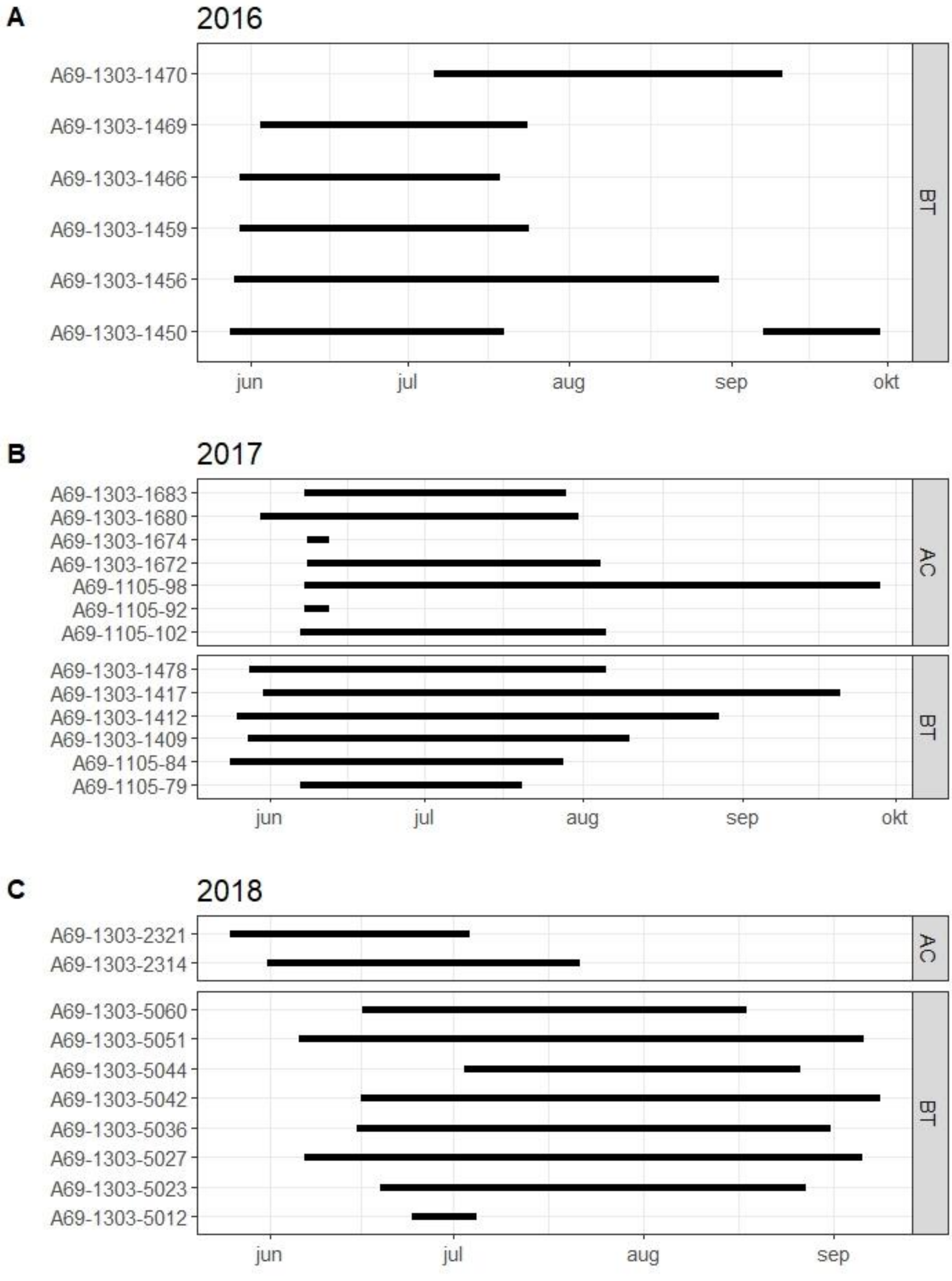

Figure 3.2 Timelines depicting marine duration and timing of downstream and upstream migration for returning individuals in 2016 (A), 2017 (B), and 2018 (A). Unique IDs for each individual fish are listed to the left. Both brown trout (BT) and Arctic char (AC) were followed in the fjord in 2017 and 2018, while brown trout only were followed in 2016.

Overall, returning individuals of brown trout spent a marginally significant longer time in the fjord than returning Arctic char (Welch two-sample t-test; t = -2.0; df = 27; p = 0.057). Duration times for returning fish are summarized in figure 3.3, plot A.

When including individuals that did not return, brown trout spent an average of 57.8 days in the fjord in 2016 (n = 14; range = 5.6–121.0; SD = 29.7), 62.6 days in 2017 (n = 13; range = 11.3–112.7; SD = 32.3), and 55.1 days in 2018 (n = 22; range = 10.6 – 115.6; SD = 28.6). All Arctic char spent in 2017 an average of 36.1 days in the fjord (n = 18; range = 4.2 – 112.4; SD = 36.1), and 32.6 days in 2018 (n = 3; range = 7.3 – 51.2; SD = 22.7). When including non-returnees, brown trout spent a significantly longer time in the fjord than did Arctic char (Wilcoxon rank sum test; W = 277; p < 0.01). Duration times for all fish (returnees and non-returnees) are summarized in figure 3.3, plot B.

Julian day of outward migration was found to be negatively correlated with fish L_T for brown trout (Spearman's rank correlation; rho = -0.62; p < 0.001) but not for Arctic char (rho = -0.05; p > 0.05) (see figure 3.4, plots A and B). Additionally, migration duration was found to be negatively correlated with Julian day of outward migration for brown trout (rho = -0.37; p < 0.01) but not for Arctic char (rho = -0.38; p > 0.05) (see figure 3.4, plots C and D).

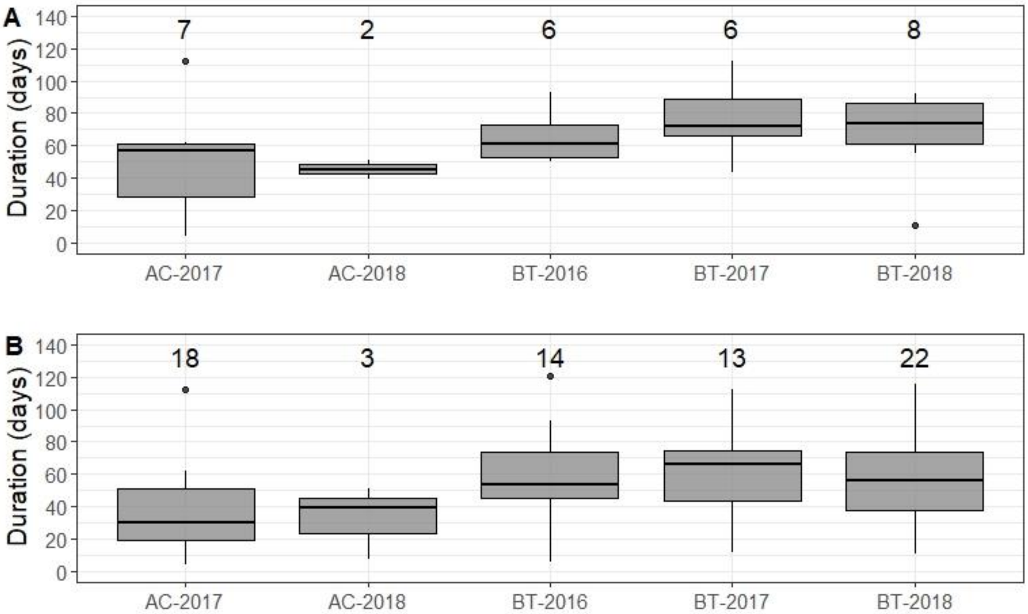

Figure 3.3 Duration of the marine migration phase for returning individuals only (plot A) and all fish (returnees + non-returnees; plot B) for both species and all years. Group names indicate the species and year they were followed in the fjord. Numbers above the groups indicate sample size. The box-and-whisker plots show the median values (bold lines), the interquartile ranges (boxes), the 5th and 95th percentiles, as well as outliers (dots).

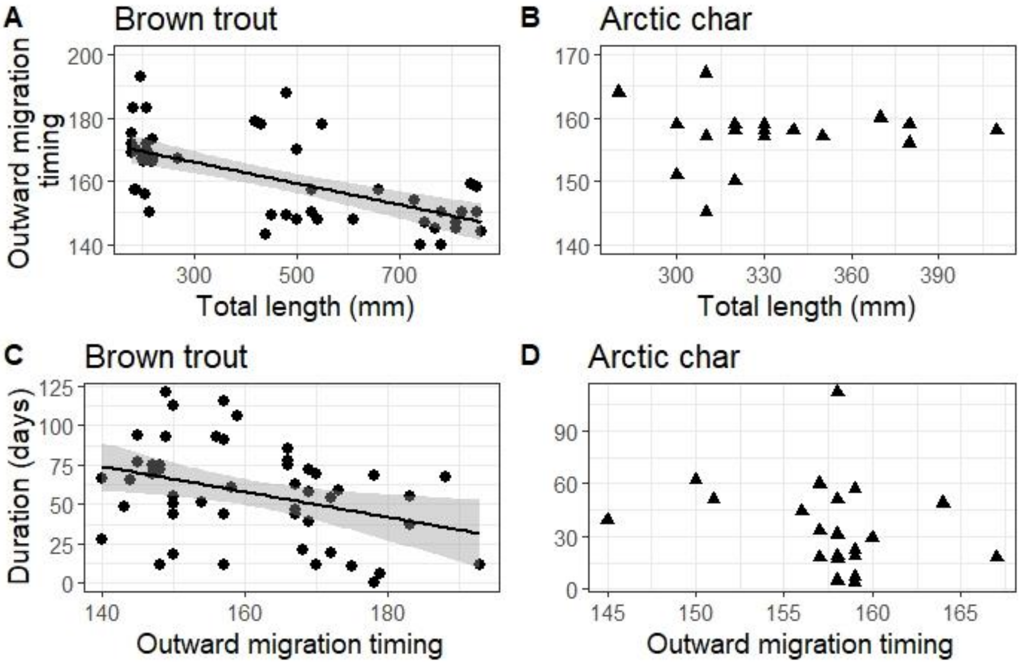

Figure 3.4 Figures showing the relationship between total length (mm) and Julian day of outward migration for brown trout (plot A) and Arctic char (plot B), as well as the relationship between Julian day of outward migration and migration duration for brown trout (plot C) and Arctic char (plot D). The relationships are depicted with regression lines (+ 95% confidence intervals). Length is negatively correlated with day of outward migration for brown trout but not for Arctic char. Julian day of outward migration is negatively correlated with duration for brown trout but not for Arctic char.

3.2.3 *Migration distance and use of the fjord system*

Adult brown trout defined as long-distance migrants used on average 2.9 (± 2.9) days to reach the defined boundary qualifying them for long-distance migration. Brown trout post-smolts (2018) spent 18.5 (± 8.3) days on average on the same journey. Arctic char individuals only qualified for long-distance migration in 2017, and these spent an average of 13.3 days (± 8.7) on qualifying for long-distance migration.

Among the 49 brown trout that entered the fjord (after excluding the 11 that disappeared at an early stage), 34 (65.0%) were classified as long-distance migrants, 10 (18.9%) as medium-distance migrants, and five (15.1%) as short-distance migrants (see figure 3.5). Of the 21 Arctic char that entered the fjord, six individuals (28.6%) were classified as long-distance migrants, nine as medium-distance migrants (42.9%), and six as short-distance migrants (28.6%) (figure 3.5). Overall, therefore, proportionally more brown trout than Arctic char undertook long-distance migrations (χ^2 contingency test, $\chi^2 = 9.4$; df = 2; $p < 0.01$).

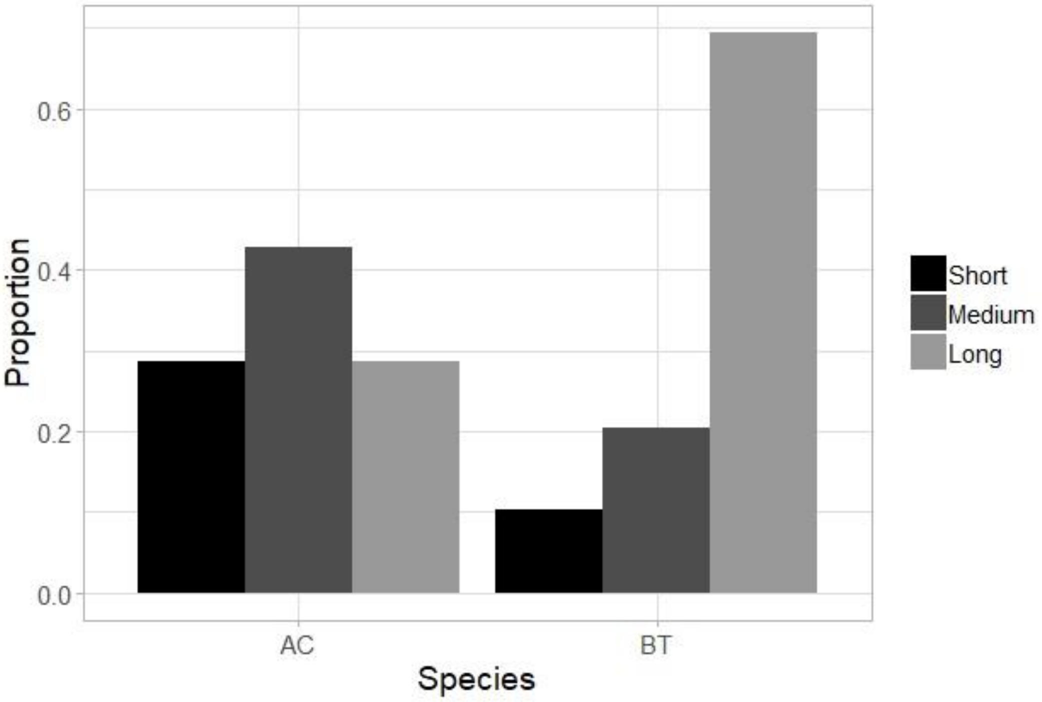

Figure 3.5 Proportion of individuals of both Arctic char (AC) and brown trout (BT) that were classified as either long-, medium- or short-distance migrants. *n* = 21 for Arctic char, and *n* = 49 for brown trout.

Brown trout utilized the entire fjord system and was frequently recorded at receivers in the outer regions of the fjord system (see figure 3.6). Arctic char, in contrast, mostly utilized the inner areas, and were never registered at the outermost line of receivers (see figure 3.7).

3.3 Prey choice

3.3.1 *Overview of feeding results*

The combined results from analyses of stable isotopes and stomach content revealed a higher propensity for piscivory in brown trout, while Arctic char had a more varied diet consisting of a range of different invertebrate prey groups. Fish was also found in the stomachs of Arctic char, however, although to a lesser degree than for brown trout, and fish was not one of the main prey groups for Arctic char based on the stable isotope analysis. Overall, Arctic char had a more freshwater- and brown trout a more marine-based diet. Small crustaceans (krill/shrimp) and flying insects were found in the stomachs of both species. Stable isotope analysis revealed shrimp to be important for brown trout and amphipods for Arctic char, while flying insects made up only a small portion of the respective diets. For an overview of stable isotope and stomach content results, see table 3.2.

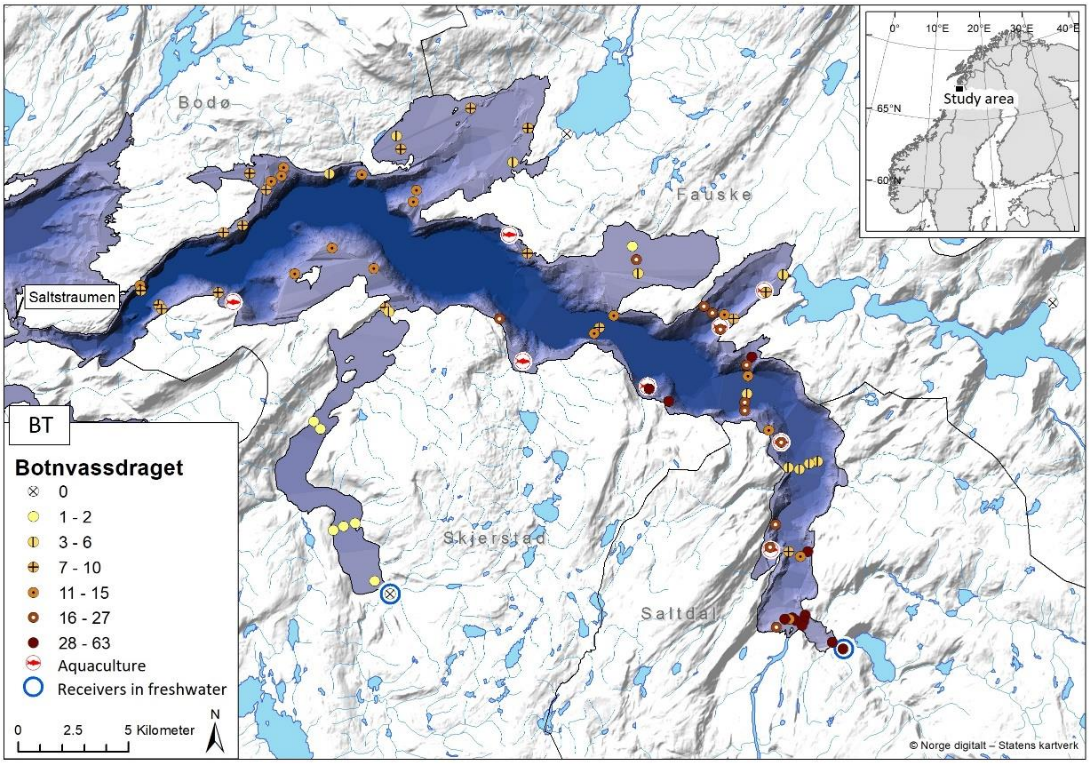

Figure 3.6 Map depicting area use by brown trout (BT) originating from Botnvassdraget. Data is the accumulated data from all years of study. The colored circles indicate individual receivers in the fjord system, and the darker the color the more frequently fish has been registered at the receiver.

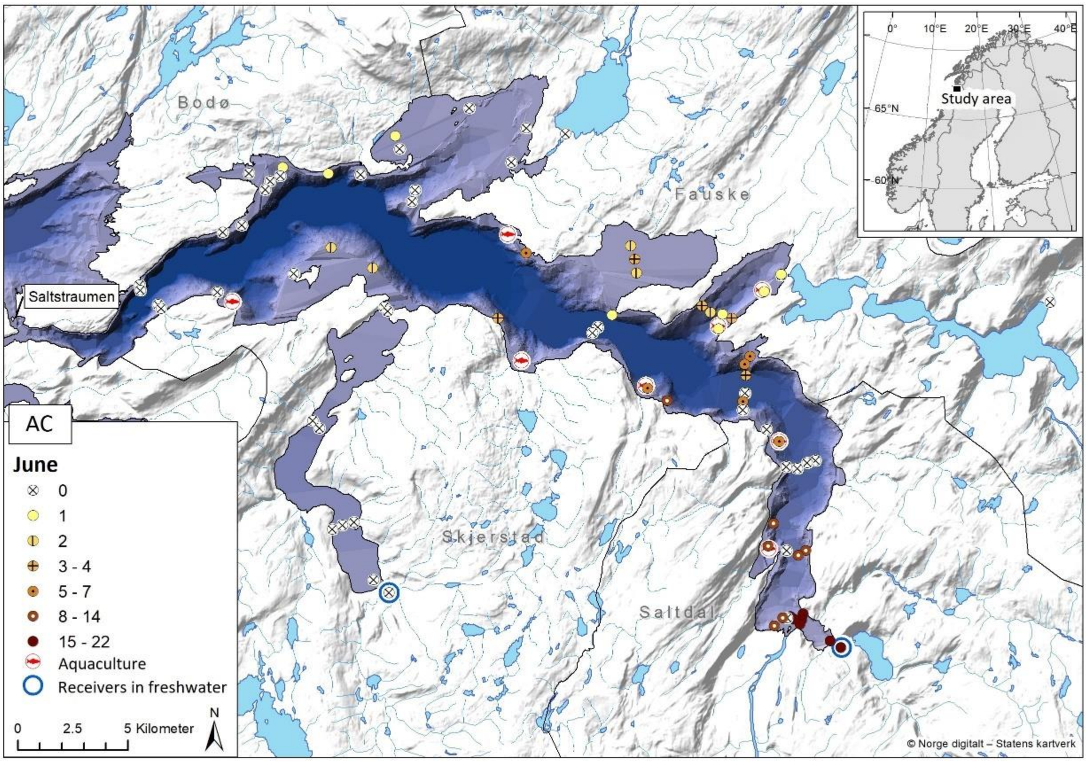

Figure 3.7 Map depicting area use by Arctic char (AC). Depicted is the accumulated data from the month of June, which is the month most Arctic char were in the fjord. The colored circles indicate individual receivers in the fjord system, and the darker the color the more frequently fish have been registered at the receiver.

Table 3.2 Overview of stable isotope data, including range and mean average δ15N- and δ13C-values for both species. The prey groups identified from stomach content samples are also listed with the percentage they made up of the total stomach contents of each species.

Species	**Arctic char**	**Brown trout**
# that died in traps	26	128
# sampled for stable isotopes	26 (100.0%)	110 (86.0%)
# sampled for stomach content	11 (42.3%)	21 (16.4%)
Stable isotopes (mean avg. ± SD)		
δ^{15}N	9.1 ± 1.3	12.3 ± 1.3
δ^{13}C	-23.2 ± 1.7	-20.2 ± 1.2
Stomach content (%)		
Fish	36%	61%
Crustaceans	9%	5%
Insects	50%	31%
Unidentified	5%	3%

3.3.2 *Stable isotope prey species*

In total, 19 groups of prey items were collected for stable isotope analysis (see appendix B). Fourteen of these were collected from the marine environment in the area outside the river mouth of the watercourse. The remaining five are freshwater groups whose isotopic values were extracted from existing literature (Eloranta et al., 2010; Hayden et al., 2013). The 19 groups of prey were further assembled into 10 groups used in the analysis: Flying insects, freshwater zooplankton, freshwater profundal benthos, freshwater littoral benthos, freshwater amphipods, marine amphipods, marine shrimp, marine crabs, marine krill, and marine fish.

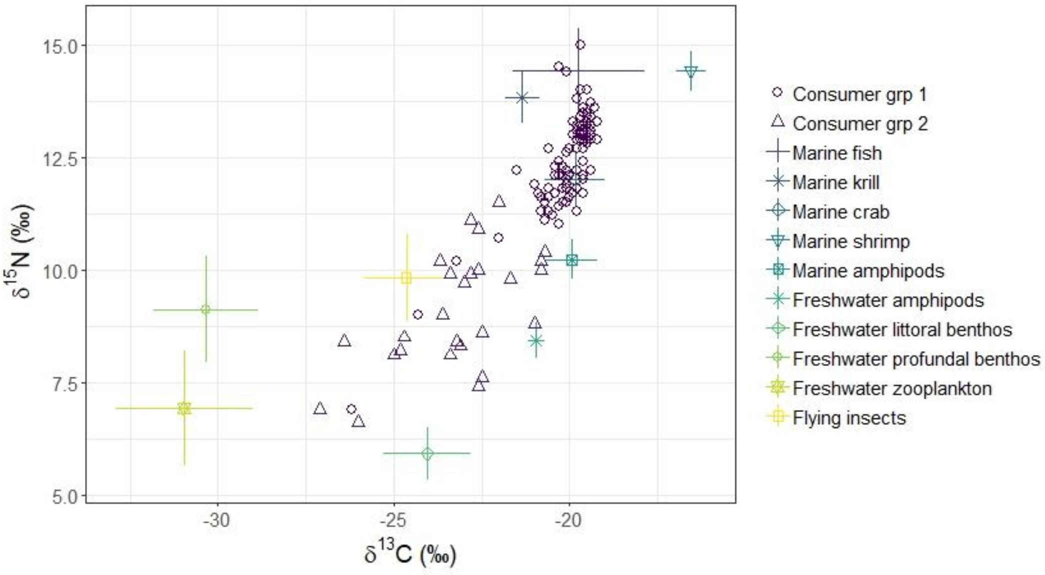

Figure 3.8 Isospace plot of brown trout (Consumer grp 1 - circles) and Arctic char (Consumer group 2 - triangles), and the 10 groups of prey collected for stable isotope analysis. Symbols represent the average mean isotopic value of each group, while lines represent standard deviations. Values have been corrected for trophic enrichment. X-axis display carbon isotope values and y-axis nitrogen isotope values.

3.3.3 *Stable isotope analysis*

Results from the simmr analysis showed that Arctic char and brown trout form two quite isotopically distinct groups. Arctic char had δ^{15}N isotopic values ranging from 6.6 to 11.9 (mean average = 9.1) and δ^{13}C-values ranging from -27.1 to -20.7 (mean average = -23.2). Brown trout had δ^{15}N-values ranging from 6.9 to 15.0 (mean average = 12.3) and δ^{13}C-values ranging from -26.2 to -19.2 (mean average = -20.2) (see figure 3.8 and table 3.2). However, there was a spread in individual values, especially for Arctic char, and some overlap between the two species was observed. The difference in isotopic signatures between the two species was statistically significant (Wilcoxon rank sum test: δ^{15}N; W = 112; $p < 0.001$, and δ^{13}C; W = 136; $p < 0.001$). Running simmr revealed that Arctic char had mainly been feeding on freshwater littoral benthos and freshwater amphipods (see figure 3.10), while brown trout had a diet dominated by marine shrimp and fish (figure 3.11).

A correlation test between δ^{15}N-values and L_T was conducted to check for the possibility of fish length being an influencer of observed δ^{15}N-values (see figure 3.9) and this correlation was found to be significant (Spearman's correlation; rho = 0.67; $p < 0.001$). When separating the species, the correlation was still significant for brown trout (rho = 0.75; $p < 0.001$) but not for Arctic char (rho = -0.32; $p > 0.05$). If looking only at low-δ^{15}N individuals (those with $\delta^{15}N < 12$ – this includes all Arctic char), there was no significant difference between the two species in terms of length (Wilcoxon rank sum test; W = 563; $p > 0.05$) but still a statistically significant higher δ^{15}N-value for brown trout compared to Arctic char (W = 112; $p < 0.001$). Therefore, even when of similar lengths, there is a propensity for brown trout to have higher δ^{15}N-values than Arctic char.

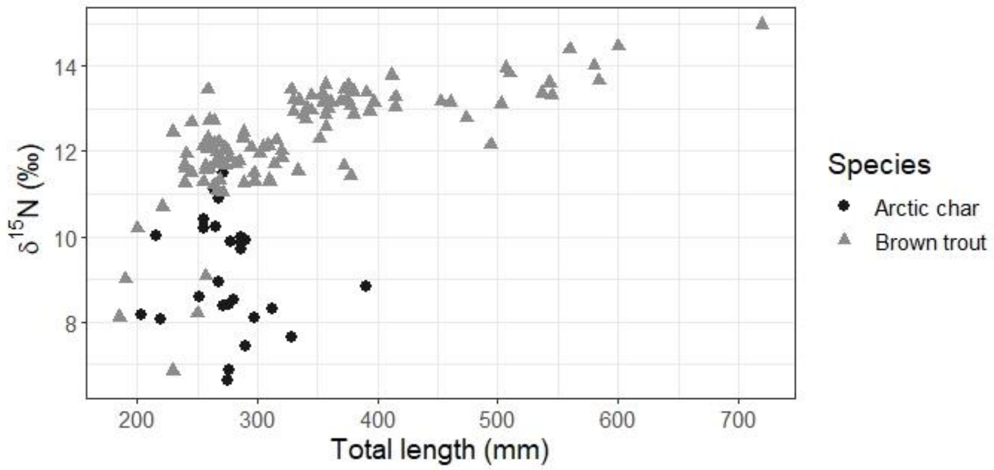

Figure 3.9 Total length (in mm) plotted against δ^{15}N-values for both Arctic char (black circles) and brown trout (grey triangles). δ^{15}N-value increases with size for brown trout but not Arctic char.

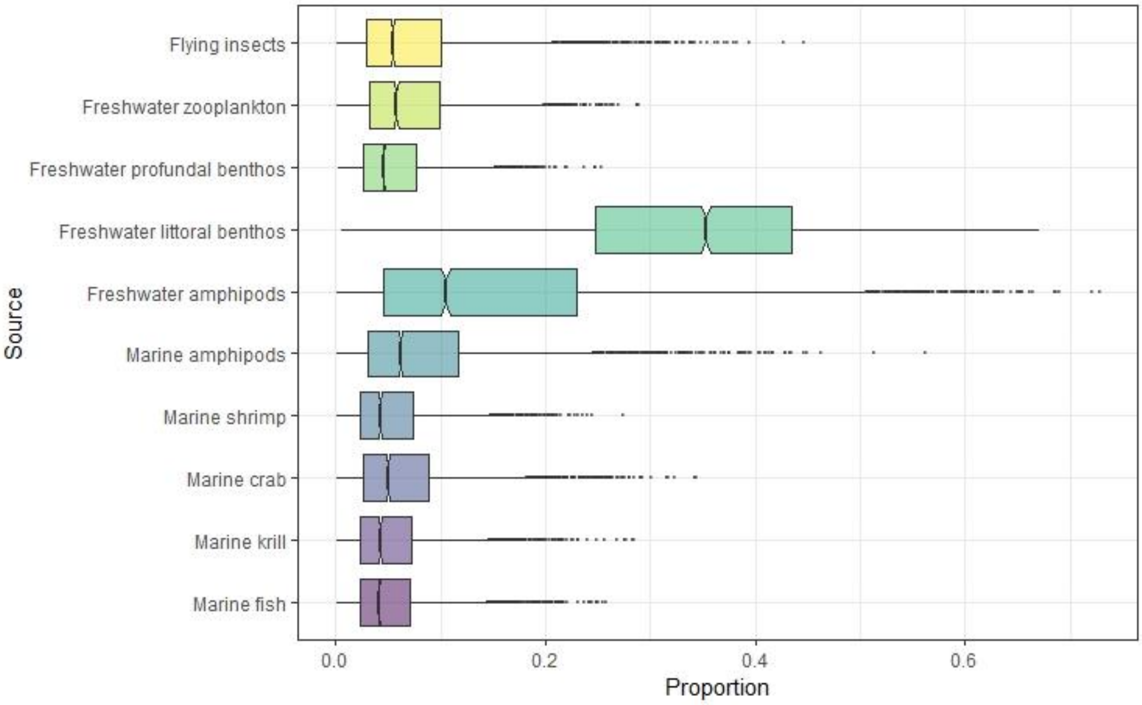

Figure 3.10 The proportions each prey group make up of the total diet of Arctic char, based on the simmr-analysis. Main prey sources for Arctic char are freshwater littoral benthos and freshwater amphipods.

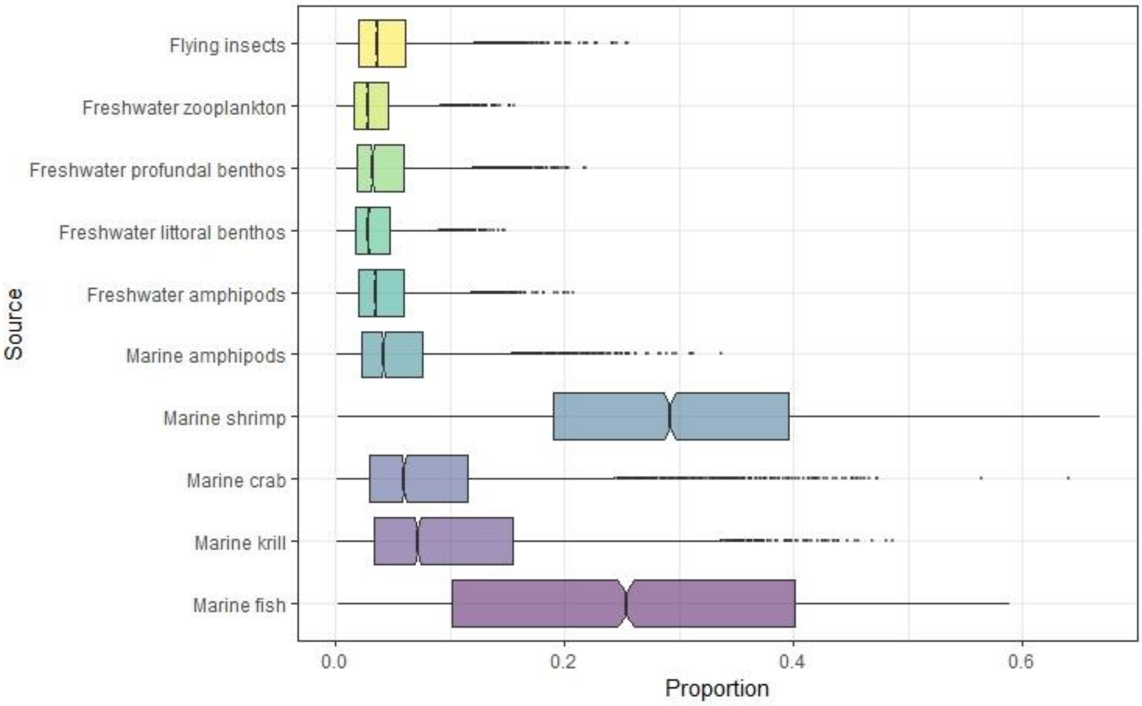

Figure 3.11 The proportions each prey group make up of the total diet of brown trout, based on the simmr-analysis. Main prey sources for brown trout are marine shrimp and marine fish.

3.3.4 *Stomach content analysis*

Of the 126 fish analyzed for stomach content, 32 had food in their stomachs at the time of death, including 11 Arctic char and 21 brown trout. Most of these samples were well digested and identification was therefore only possible at a high taxonomic level. Of the three food-groups identified, flying insects dominated the samples from Arctic char (50% of the total stomach content), while fish dominated the samples from brown trout (61% of the total stomach content) (see figure 3.12). Fish as a food source came in second for Arctic char (36%) and flying insects came in second for brown trout (31%). Nine and 5% of the content of Arctic char and brown trout, respectively, consisted of crustaceans, while the remaining 5% and 3% were unidentified.

From these numbers, and from figure 3.12, it can be observed that both species displayed generalist feeding behaviors on the population level. However, when viewing the stomach content samples individually, it also became clear that both species tended to have a more specialist feeding behavior on the individual level. Typically, only one food item dominated the samples per individual fish (see appendix C).

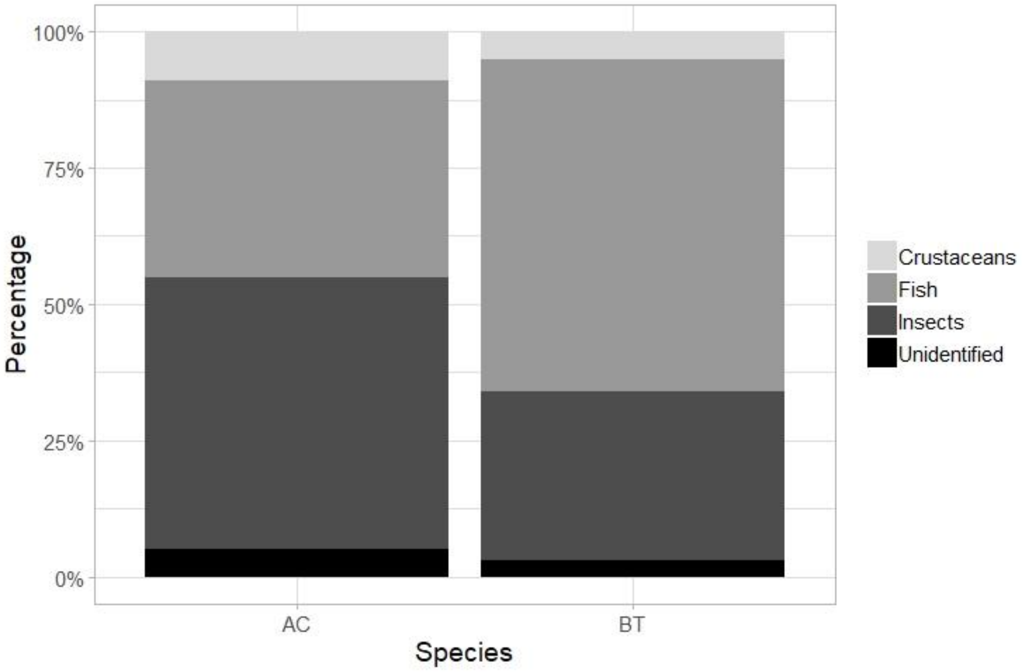

Figure 3.12 Accumulated stomach content from Arctic char (AC) and brown trout (BT). Prey were divided into four groups: Crustaceans, fish, insects, and an unidentified/mixed group. The percentage represent the total contribution of that prey group to all stomach content samples analyzed.

4. Discussion

The results of this study further describes the marine migration behavior of anadromous brown trout and Arctic char. Variations were seen both between and within species on chosen outward and inward migration dates, with adult brown trout migrating earlier than adult Arctic char the one year they were both followed in the fjord (2017). Larger individuals of brown trout, but not Arctic char, migrated earlier than smaller ones. Brown trout typically remained longer at sea than did Arctic char, and migrated further into the fjord system as well. Arctic char tended to keep more in proximity to the estuarine area throughout the migration, and were found to have fed heavily on freshwater invertebrates. Brown trout were more piscivorous; however, they were also larger, on average, which may explain some of the observed differences.

4.1 Migratory behavior

4.1.1 *Timing and duration*

Migration timing and duration varied somewhat between species and between years. Typically, most adult brown trout (from 2016/2017) entered the fjord in May, some early in June, and returned in either July (2016) or August (2017). The brown trout smolt tagged in 2018 entered the sea almost exclusively in June and most returned in August or September. Overall, larger individuals of brown trout, but not Arctic char, entered the fjord at an earlier date than did smaller ones (see figure 3.4). A size-dependent effect in Arctic char might have been obscured by the narrow time frame they migrated within, as well as the narrow size range they displayed. Previous studies have found larger and older individuals of both species to migrate earlier than smaller and younger ones (Bohlin et al., 1996, 1993; Johnson, 1980), possibly due to better hypo-osmoregulatory capacity by larger individuals (Finstad and Ugedal, 1998; Jonsson and Jonsson, 2002; Parry, 1958). Ionic regulation at low sea temperatures is thought to be difficult for many salmonids, and especially for smaller individuals that have a larger surface area to volume ratio (Claireaux and Audet, 2000; Finstad et al., 1989; Jonsson and Jonsson, 2002). Increasing temperature and decreasing salinity in the fjord later in the season (see appendix A) might therefore explain why smolts migrated later than adults in the present study.

Arctic char entered the fjord in either May (2018) or June (2017) and typically returned in late July/early August. The only year where adults of both Arctic char and brown trout were followed in the fjord at the same time was 2017, and this year the median date for outward migration by brown trout was 28.05, ten days prior to the median date for outward migration by Arctic char (07.06). All but one Arctic char entered the fjord in June (94.4%) while 69.2% of brown trout entered in May, showing a clear discrepancy between the species on chosen outward migration timing that year. Arctic char also had a much higher degree of coherence in chosen entry date than brown trout, with all brown trout entering the fjord during a 19-day period (IQR = 12 days), and all but three Arctic char entering within a four-day period (IQR = 1.75 days). However, the three Arctic char that entered the fjord in 2018 showed a greater level of variance, with 23 days passing from first to last entry date. That year, all three Arctic char entered the fjord in May, contrasting it to the previous year where almost all entered in June. Such inter-annual variation was also observed for adult brown trout, but to a lesser degree than for Arctic char: the median date of entry for 2016 brown trout fell close to the date for 2017 (29.05 and 28.05, respectively).

Sympatric Arctic char and brown trout are often found to migrate at slightly different times (Carlsen et al., 2004; A. J. Jensen et al., 2012). Initiators of downstream migration, such as increased river discharge, temperature, and photoperiod, are hence likely to influence the two species in slightly different ways (Aarestrup et al., 2002; A. J. Jensen et al., 2012; Jonsson, 1991). Photoperiod is thought to act as a synchronizing factor determining the time after which migrations can occur (Aarestrup et al., 2002). Previous experiments with Arctic char, for example, have shown increased day length to induce increased osmoregulatory capacity, and hence increased marine survival (Finstad et al., 1989; Gulseth et al., 2001). River discharge and temperature work instead as rapid initiating factors, determining the time at which migrations do occur (Aarestrup et al., 2002; Jonsson, 1991). In this study, Arctic char downstream migration coincided with increasing levels of river discharge both years they were followed in the fjord (around June 7th in 2017 and throughout May in 2018; see figure 2.2). To migrate during periods of greater discharge is energy-efficient, as well as providing some measure of protection against predation, as high discharge increases turbidity and lowers the visibility of the water (Aarestrup et al., 2002; Hvidsten and Hansen, 1988; Jonsson and Jonsson, 2002). Carlsen et al. (2004) found Arctic char smolt migrations to coincide with increased discharge caused by snowmelt, and freshwater temperature at the time of migration was therefore low. Brown trout smolt from the same study migrated instead two weeks later, when flow was high and temperatures increasing. In the current study, brown trout smolts did not migrate during the time of highest discharge (May), as did Arctic char, possibly due to low temperatures at that time (3-4°C; see figure 2.2). Instead, most migrated in the latter half of June, when temperatures were around 7-8°C and flow had increased slightly compared to the first half of that month. A lower threshold of 2-4°C has often been observed for brown trout smolt migrations, and few individuals will migrate if the temperatures drop below this threshold despite high discharge (Carlsen et al., 2004; Hembrel et al., 2001). Both river discharge and temperature therefore seem to be important in determining downstream migration timing of brown trout smolts. No clear pattern of either discharge or temperature was found for adult brown trout, possibly due to the larger size of these individuals. Both discharge and temperature have generally been found to affect adults less than smolts (Davidsen et al., 2014; Jonsson and Jonsson, 2002; Östergren and Rivinoja, 2008), as predation risk is lower and hypo-osmoregulatory capacity is better for larger individuals.

Large variation was also observed on inward migration timing for both species. In 2017, the span for returning brown trout stretched across two months (20.07-20.09), with 07.08 being the median date. Arctic char return dates spanned an even longer period (12.06-27.09), with the median date falling on 31.07. Overall, however, Arctic char tended to return earlier than brown trout (all but one returned before the median date for returning brown trout) and they typically had shorter migration durations. Brown trout migration duration was shortest in 2016 (mean average = 65.2 days) and longest in 2017 (= 76.5 days), with the 2018 post-smolts displaying an intermediate duration (= 68.0 days). These numbers are in accordance with brown trout migration durations generally observed from studies in northern Norway, which have found a stay of 45-70 days to be common (Berg and Berg, 1989a; Bordeleau et al., 2018; Jensen et al., 2014). Variations between seasons are commonly observed as well (Berg and Berg, 1989a), as duration is strongly influenced by water temperature. This is seen both on a latitudinal and an annual basis, with migration duration decreasing with increasing latitude (L'Abee-Lund et al., 1989) and decreasing summer temperature (Berg and Berg, 1989a). Arctic char displayed less inter-annual variation on migration duration, with only a slightly longer migration in 2017 (mean average = 50 days) compared to 2018 (= 45 days), but not significantly so. Also these numbers are in accordance with previous studies from northern Norway: Berg and Berg (1989b) found a stay of 48 days in the Vardnes River and Jensen et al. (2014) of 42-53 days in the Hals watercourse. Brown trout from these watercourses had marine durations of 68 and 64-65 days, respectively, again suggesting a longer migration by brown trout compared to Arctic char. This pattern was also seen by Davidsen et al., (2018a), who found average stays of brown trout and Arctic char in the Tosen fjord to be 52 and 34 days, respectively.

Anadromous fish migrate to sea to experience increased growth in a better feeding environment, and Arctic char are known to prefer lower temperatures for growth than do brown trout (9-12°C and 12-16°C, respectively; Larsson, 2005). Berg and Berg (1989b), for example, found growth of Arctic char to decrease with increased time spent at sea, with most growth occurring early in the migration when temperatures were below 10°C. In the current study, sea temperatures usually reached 10°C in early July, with maximum temperatures occurring in late July/early August (see appendix A). Growth potential is traded off against increased mortality risks at sea, and individuals should return to freshwater when the potential for additional growth becomes less than the risks of predation, diseases or parasites. All but one returning Arctic char returned either before or around the time of maximum temperature in the fjord. Temperature, and the way temperature influences the trade-off between growth potential and mortality, might therefore be important in determining inward migration timing for Arctic char.

Growth potential could also explain why brown trout post-smolts typically returned later than the adults of 2016 and 2017. Previous studies have found a tendency for older and larger individuals to return earlier in the season than younger and smaller ones (Davidsen et al., 2018a; Johnson, 1980; Jonsson and Gravem, 1985). Smaller individuals have greater potential for additional growth than larger individuals, and should therefore remain longer at sea to maximize this. On a similar note, fish with poor body condition are likely to return later than fish with good body condition, again to maximize the potential for increased growth (Bordeleau et al., 2018). No data is available on size and condition after the marine migration in this study, as these were only measured at the time of tagging (which, in the case of all Arctic char and some brown trout, occurred 7-8 months prior to the migration). Brown trout tagged in spring soon before the migration (2016/2018), however, revealed a possible effect of length and condition on chosen return date in 2016, but not 2018 (appendix D). Even so, the number of returnees in 2016 was very small (n = 6), and nothing conclusive can be said based on these results alone. Overall, large variation on inward migration timing suggest several influencers of chosen return date for both species. Gender was not found to influence inward migration timing.

4.1.2 *Distance, movement, and use of the fjord system*

Brown trout had a higher proportion of long-distance migrants than did Arctic char, and were frequently recorded at the outermost receivers placed in the fjord system. Adult brown trout spent on average 2.9 days reaching “line 2” (figure 2.1), qualifying them for long-distance migration (>20 km). In contrast, Arctic char and brown trout post-smolts spent 2-3 weeks reaching the same point. Swimming ability might partly account for this: Arctic char are known to be poorer swimmers than brown trout, (Beamish, 1980; Johnson, 1980; Lucas and Baras, 2001), and post-smolts generally have poorer swimming abilities than adult individuals (Remen et al., 2016). Despite the slower pace of brown trout post-smolts, however, the overall pattern of migration for this group was more similar to that of adult brown trout than to that of Arctic char, with most individuals undertaking long-distance migrations. Arctic char mainly remained in the inner parts of the fjord system, in closer proximity to the estuary. This migratory behavior of Arctic char is consistent with previous studies (Anras et al., 1999).

The stable isotope analysis (see section 4.2.1) indicated that brown trout were more piscivorous than Arctic char. Feeding opportunity might therefore be important in determining distance travelled in the fjord by brown trout, as they are likely to seek out areas with high occurrences of smaller fish species to prey on. Saltstraumen, the strongest tidal current in the world, lies at the entrance to the fjord system (see figure 2.1). This current creates a highly nutritious and oxygen-rich environment with high species richness and diversity, and fish (including Atlantic cod, saithe, Atlantic halibut (*Hippoglossus hippoglossus*) and Atlantic wolfish (*Anarhichas lupus*)) are numerous and known to grow to large sizes in the area[1]. Brown trout from Botnvassdraget and the neighboring river Saltdalselva, both located in the innermost parts of the fjord system (figure 2.1), have been found to migrate farther than brown trout originating from other watercourses in the same system (Meyer, 2018). This could be explained by poor feeding conditions for brown trout in the innermost parts of the system, prompting them to swim farther to reach the better feeding grounds created by Saltstraumen. Growth rate was also high for these individuals compared to others in the system, suggesting that the former are experiencing good feeding conditions while at sea (Meyer, 2018). Arctic char, on the other hand, were less piscivorous and might therefore not need to travel as far in order to feed. Additionally, they were generally smaller than brown trout and would likely be more vulnerable to predation by the piscivors found in the areas around Saltstraumen. As with migration timing, gender was not found to influence distance travelled in the fjord for either species.

4.1.3 *Survival*

Arctic char had an overall return-rate of 42.9% and brown trout of 40.8%. These minimum survival rates are quite low – Berg and Jonsson (1990), for example, found minimum annual survival rates of adult Arctic char and brown trout in the Vardnes River to be 57% and 50%, respectively. However, survival does vary greatly between watercourses, and anything between 15%-86% have been reported for adult brown trout (Bordeleau et al., 2018; Jonsson and Jonsson, 2009; Kristensen et al., 2019). Mortality at sea is typically highest soon after the fish enter the marine environment as smolts, (Jensen et al., 2017; Klemetsen et al., 2003; Thorstad

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[1] http://www.saltstraumen.info/saltstraumen-marine-verneomrade

et al., 2016) and subsequently decrease as the fish get larger. This is reflected in the lowest brown trout return-rate occurring for the 2018 post-smolts: 36.4% compared to 42.9% and 46.2% in 2016 and 2017, respectively. First-time migrants of brown trout from the Vardnes River had a similar estimated marine survival of about 37% (Berg and Jonsson, 1990).

Marine mortality (predation, capture by game fishers, etc.), tag expulsion or battery depletion may all explain the observed return-rates. Some individuals might have overwintered in the fjord or other watercourses, causing their batteries to deplete before they returned to Botnvassdraget. Brown trout are known to overwinter in seawater, but do so more commonly further south in the distributional range (e.g. Knutsen et al. 2004). Many salmonids find it harder to osmoregulate efficiently in colder waters (Berg and Berg, 1989b; Finstad et al., 1989), and Arctic char have only been observed to overwinter in estuaries if they do not have access to a lake (Jensen and Rikardsen, 2008). Straying into other watercourses is known to happen for both species, however, and one brown trout was registered as having done so in the current study. Some exchange of individuals between Botnvassdraget and Saltdalselva might also have occurred, although this cannot be confirmed. Berg and Jonsson (1990) found a straying percentage of 15.5% for brown trout in the River Vardnes, and Arctic char often display even higher percentages of straying than this (Armstrong and Morrow, 1980; Davidsen et al., 2018a; Johnson, 1980). Even so, homing in salmonids is generally quite strong (Nordeng, 2009; Nordeng and Bratland, 2006) and brown trout and Arctic char most commonly return yearly to overwinter and potentially spawn in their home rivers (Berg and Jonsson, 1990).

4.1.4 *Tagging groups*

When designing studies aiming to describe migratory behavior, it is important to include individuals representing variation within populations, e.g. by capturing and tagging them in differing seasons and habitats. Practical limitations might compromise this, however, and Arctic char were only caught in the river during fall, as they are difficult to catch on their downstream migration in spring. Both tagging groups of Arctic char were fairly uniform in terms of L_T and weight, while more variation was seen for brown trout, which were tagged during one fall and two spring periods. Body condition is likely to be better after the marine feeding migration in fall, which may account for some of the variation observed between the 2016 fall and spring brown trout tagging groups (0.97 and 0.84, respectively). Tagged Arctic char were consistently smaller than tagged brown trout (excluding the 2018 smolts), which is unsurprising given the slower growth and hence smaller size at any given age for Arctic char (see appendix E). Additionally, anadromous Arctic char from northern Norway are generally known to be quite small (30-40 cm; Klemetsen et al., 2003; Kristoffersen et al., 1994; Svenning et al., 1992).

Both populations of brown trout and Arctic char in this study display partial migration, and some of the tagged individuals might therefore have been freshwater residents. Acoustic receivers placed in Botnvatnet, used for another study on overwintering behavior, was checked to see if some of the individuals never recorded in the fjord, or at the receiver in Litjvatnet, could have been residents moving around in the larger lake. This turned out to be the case for 15 individuals. When excluding these, 20.7% brown trout and 24.1% Arctic char remained as never having been recorded at all during the course of the study. The reasons behind this are not known, but it may be that the tagging procedure itself caused some fish to die prematurely (no such effects were observed at the time of tagging, but tagging could cause a higher mortality for tagged compared to untagged individuals later in life). Otherwise, some might have died of natural causes, or tag malfunctioning or tag expulsion might have occurred. Of brown trout never recorded, 63.6% were smolts (2018), which could be explained by a general higher mortality for these individuals (Berg and Jonsson, 1990; Jonsson and Jonsson, 1993).

4.2 Feeding behavior

4.2.1 *Brown trout and Arctic char diet*

Brown trout had significantly higher δ^{15}N- and δ^{13}C-values than Arctic char. A higher δ^{15}N-value is suggestive of feeding occurring at a higher trophic level, while higher δ^{13}C-values are indicative of marine as opposed to freshwater feeding (Fuller et al., 2012; Hobson, 1999; Van der Zanden and Rasmussen, 1999). As suggested by this, brown trout had a marine diet consisting mainly of fish and shrimp, while Arctic char had a freshwater diet consisting of littoral benthos and amphipods. Stomach contents additionally revealed that brown trout and Arctic char both had been feeding on surface insects, fish, and crustaceans prior to capture.

The brown trout diet observed here is in accordance with other studies that have found fish, crustaceans, polychaetes, and surface insects to be important prey groups for this species at sea (Davidsen et al., 2017; Knutsen et al., 2001; Lyse et al., 1998). More surprising is the finding that Arctic char had been feeding on freshwater species. All individuals examined were presumed to be anadromous individuals returning from a marine feeding migration (they were caught in the watercourse moving upstream in August and September 2017). Muscle tissue is a metabolically active tissue that will equilibrate to diet within the order of a few months in rapidly growing salmonids (Perga and Gerdeaux, 2005; Tieszen et al., 1983; Trueman et al., 2005). For anadromous individuals of brown trout and Arctic char, this would typically reflect the summer period of somatic growth, which is the period where most growth occurs (Perga and Gerdeaux, 2005). Although the telemetry data revealed that some individuals performed long-distance migrations, the majority of Arctic char individuals remained in the inner parts of the fjord system, in close proximity to the estuary. In addition to containing both marine and estuarine species, estuaries often contain freshwater species having drifted down with the currents from the river (e.g. Roper et al., 1983). It is possible, therefore, for Arctic char to feed on freshwater species when they are in the estuary. Additionally, as the fish analyzed for stable isotopes had not been tracked telemetrically, there is no certain way of knowing how long or where they had been in the fjord. They could have moved only to the estuary for a short time before returning, which is sometimes observed for immature Arctic char (Johnson, 1980).

Both brown trout and Arctic char are opportunistic generalist feeders whose diets are expected to reflect changes in food availability, habitat, season, age, and size (Bridcut and Giller, 1995; Klemetsen et al., 2003; Knutsen et al., 2001). Arctic char sampled for stable isotopes were significantly smaller than sampled brown trout. Moreover, both brown trout and Arctic char sampled for stable isotopes were smaller than brown trout and Arctic char tagged for telemetry (60 mm shorter on average for Arctic char). Feeding is typically size-dependent for fish, and fish in particular is known to become an increasingly important food item as individuals grow larger (Amundsen, 1994; Damsgård, 1993; L'Abée-Lund et al., 1992). Observed differences in isotopic values might therefore be a reflection of a difference in size.

It is common for δ^{15}N-values to increase with size, as larger individuals usually feed higher up in the food chain than do smaller ones (an increase of ~3‰ per trophic level is commonly observed; e.g. Fuller et al., 2012; Schoeninger and DeNiro, 1984). However, no pattern of increased δ^{15}N-values with size was observed for Arctic char in this study, possibly due to the small size range of fish caught. All Arctic char were smaller than 400 mm and had a δ^{15}N-value less than 12. When comparing Arctic char with brown trout of equal length and δ^{15}N-value ($L_T < 400$ mm, $\delta^{15}N < 12$), size is eliminated as a factor describing the observed differences between the species. Even so, brown trout of this length still had a significantly higher δ^{15}N-value than did Arctic char. A difference in feeding behavior between the two species, even when of similar length, is therefore apparent, with brown trout feeding higher up in the food chain than Arctic char. When found in sympatry in freshwater, it is commonly observed that brown trout are more piscivorous and typically begin to feed on fish at a smaller size than Arctic char (e.g. 13 cm contra 16 cm in freshwater in Björnsson, 2001; L'Abée-Lund et al., 1992). Stomach content analysis did reveal, however, that Arctic char had been feeding on fish prior to capture, even though this was not apparent in the stable isotope analysis. Brown trout movement patterns in the fjord system indicate that piscivorous food conditions might be poor in the innermost, near-estuarine parts of the fjord. Arctic char have been known exploit lower trophic levels if suitable prey fish abundance is low, including plankton and littoral hyperbenthos (Grønvik and Klemetsen, 1987). As Arctic char are poorer swimmers than brown trout, they may choose to feed on the less nutritious invertebrate fauna found closer to the estuary, rather than expend too much energy moving far into the fjord in search of suitable fish prey. The latter strategy likely entails greater mortality risks as well, as large piscivores are known to gather at the rich feeding grounds created by Saltstraumen. Overall, more research on similar-sized Arctic char and brown individuals in this system would be needed to determine the degree to which feeding patterns observed in the current study is a consequence of a difference in size or behavior.

4.2.2 *The simmr-model*

Although the stable isotope analysis indicated a distinction between brown trout and Arctic char in terms of habitat source of food, the actual food-groups observed as most important has to be taken with some precaution. The simmr-model works best when investigating diets consisting of only a few food-groups. More accurately, for the model to run right, no more than $n + 1$ food groups should be included, n representing the number of isotopes analyzed (Phillips et al., 2014). Only isotopes of carbon and nitrogen were used for analysis in this study, and the ideal would therefore have been to run the analysis with only three food groups. However, both brown trout and Arctic char are generalist feeders and have the potential to feed in both freshwater and at sea, and the final count of food groups ended up at ten. This makes the analysis less accurate, and too much weight should not be put on the individual food groups. Rather, the focus should be on the separation of a more marine brown trout diet at a higher tropic level as opposed to a more freshwater Arctic char diet at a lower tropic level. Additionally, it is likely that some food groups that could have been important food sources for both brown trout and Arctic char were not sampled for analysis. Most notably of these are freshwater sticklebacks and marine zooplankton and benthos. Mixing models such as simmr are known to be sensitive to missing sources, as excluded sources necessarily will lead to a bias in the estimates of the dietary contributions of the other sources, as they still must sum to 100% (Phillips et al., 2014). Therefore, the results might have looked different if these sources had been included, and this should be taken into consideration. For a more extensive review of the best practices for use of simmr and other isotopic mixing models, please refer to Phillips et al. (2014).

5. Conclusion

This study revealed clear differences in the marine migratory behavior of anadromous brown trout and Arctic char in terms of migration timing, duration, and marine area use. Stable isotope analysis of muscle tissue and analysis of stomach content suggested that brown trout had a more marine, more piscivorous diet at a higher trophic level compared to Arctic char. Combined, the telemetry results and the feeding analyses suggest that species specific differences in prey choice influence the observed marine migratory strategies. Such differences in prey choice and areal use of the marine habitat may cause human activities, which are known to vary in both time and space, to influence the species in somewhat different ways. This should be taken into consideration when working towards the conservation of these species. However, Arctic char in the present study were consistently smaller than brown trout, which could have influenced the observed differences between the species. Further research should therefore be conducted on individuals of more similar size, in order to further eliminate size as a factor explaining the migratory behaviors of these two species.

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Appendices

Appendix A: Salinity and temperature in the fjord system

Salinity and temperature were measured at several receiver locations in the fjord, in the time period 2017-2018. Measurements from two stations, one in the outer area (station 54, plot B and C, figure A) and one in the inner area of the Skjerstad fjord (station 31, plot A, figure A) are plotted in figure A. Overall, summer temperatures were higher in 2018 than in 2017. Peak temperatures occurred in late July/early August both years. Salinity was typically lowest in June/July, having decreased significantly in the period from May until June.

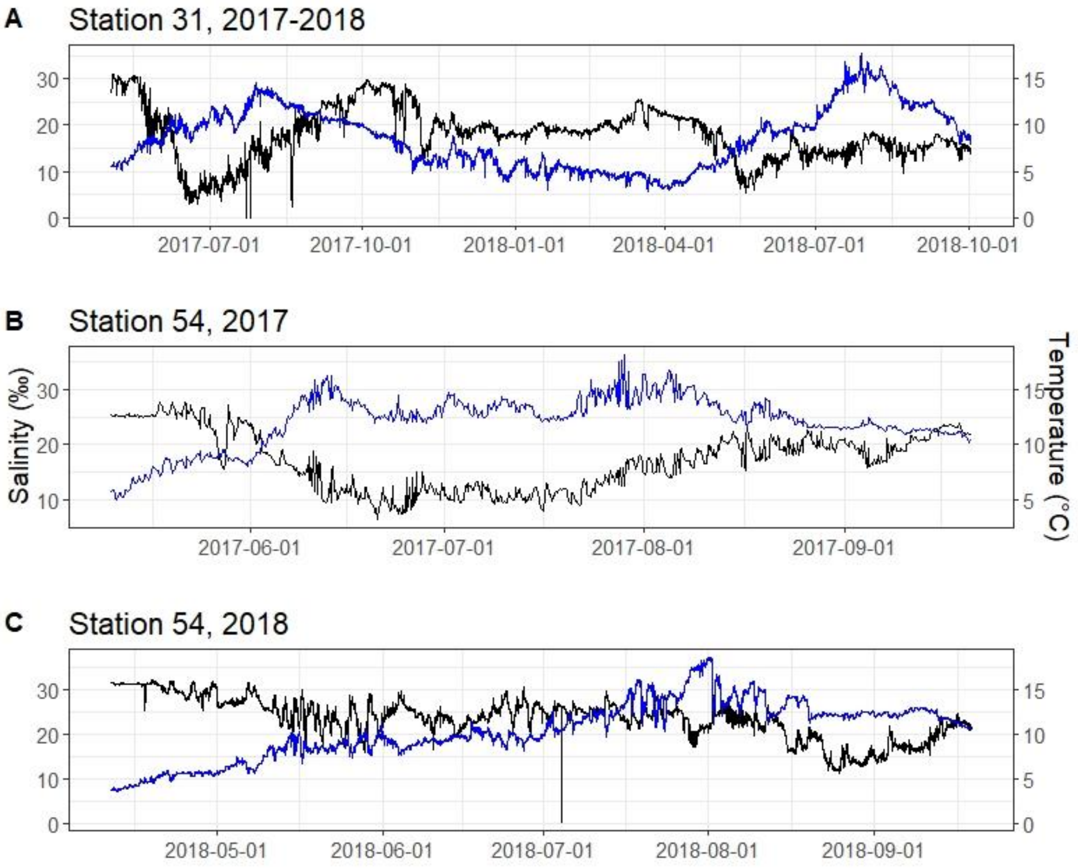

Figure A Measurements of temperature (blue line) and salinity (black line) at two different stations in the fjord system; station 31 (plot A) and station 54 (plot B and C) (see figure 2.1). Measurements are from 2017 and 2018.

Appendix B: Prey items collected for stable isotope analysis

A list of all prey groups sampled for stable isotope analysis is provided, including groups sampled from existing literature (see table B).

Table B Prey items sampled for stable isotope analysis, including number of individuals caught per prey item, capture method, and date of capture. Isotopic values of some prey items had to be collected from existing literature, as they were not sampled specifically in this study. Habitat source of each prey item is also noted (marine (M) or freshwater (F)).

Prey	**#**	**Capture method**	**Date of capture**	**Marine/ Freshwater**
Amphipoda	5	Seine net	06.06.2018	M
Atlantic cod (*Gadus morhua*)	7	Bottom net	21-23.08.2018	M
Atlantic herring (*Clupea harengus*)	2	Bottom net	22.08.2018	M
Atlantic mackerel (*Scomber scombrus*)	2	Bottom net	22.08.2018	M
Common dab (*Limanda limanda*)	3	Seine net	06.06.2018	M
European plaice (*Pleuronectes platessa*)	1	Seine net	06.06.2018	M
Flying insects	4	From stomach samples of brown trout and Arctic char	–	F
Gammarus lacustris	–	From literature (Eloranta et al., 2010)	–	F
Haddock (*Melanogrammus aeglefinus*)	1	Bottom net	22.08.2018	M
Hyas sp.	3	Found in the stomach of an Atlantic cod	23.08.2018	M
Krill (Euphausiacea)	8	Found in the stomachs of other fish	–	M
Lesser sand eel (*Ammodytes tobianus*)	1	Bottom net	23.08.2018	M
Littoral benthic animals	–	From literature (Hayden et al., 2013)	–	F
Profundal benthic animals	–	From literature (Hayden et al., 2013)	–	F
Sand goby (*Pomatoschistus minutus*)	5	Seine net/bottom net	06.06.2018/ 21-23.08.2018	M
Sand shrimp (*Crangon crangon*)	5	Seine net	06.06.2018	M
Saithe (*Pollachius virens*)	10	Bottom net	21-23.08.2018	M
Three-spined stickleback (*Gasterosteus aculeatus*)	5	Seine net/bottom net	06.06.2018/ 21-23.08.2018	M
Zooplankton	–	From literature (Hayden et al., 2013)	–	F

Appendix C: Individual stomach contents

Brown trout and Arctic char were found to be generalist feeders on the population level. Even so, individuals often display more specialist feeding behavior, which was also observed in the present study (figure C). One prey item typically dominated the stomach content sample of each individual.

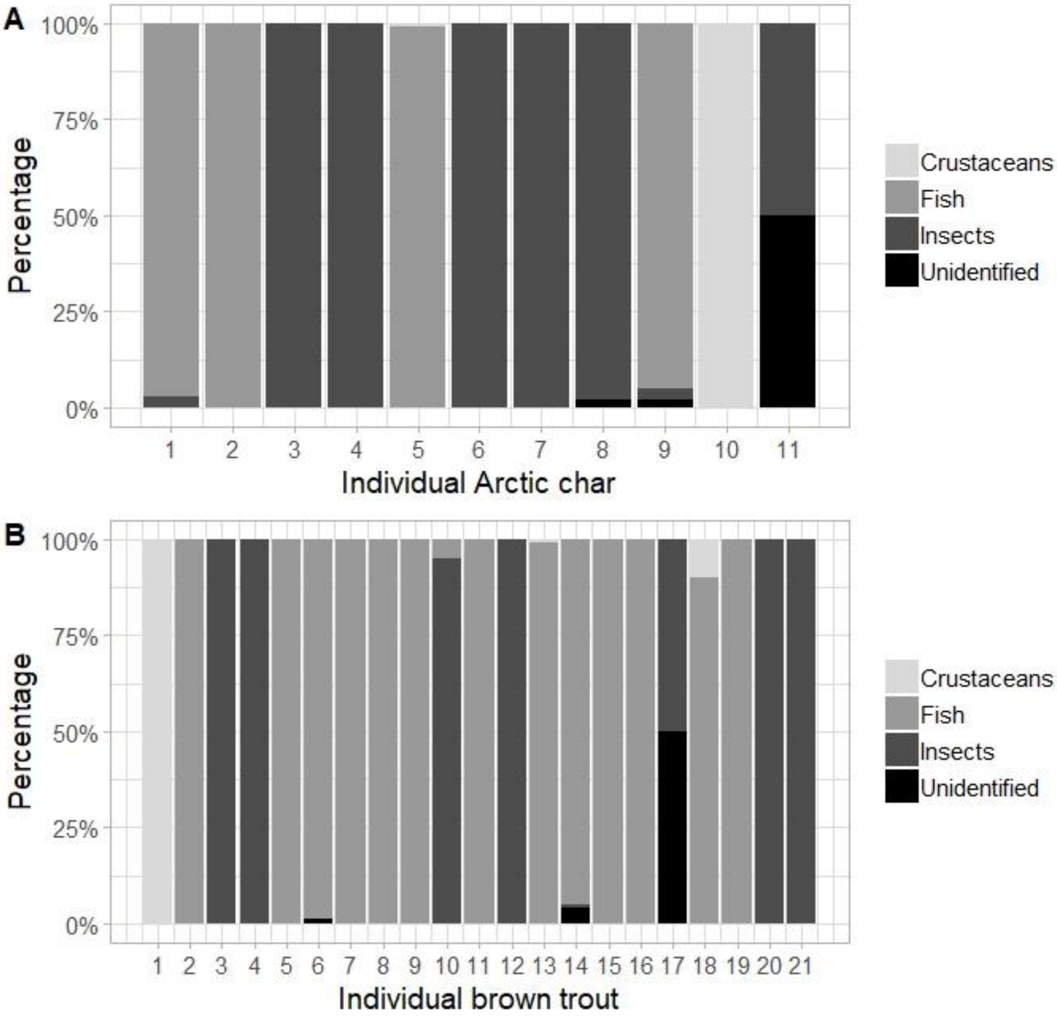

Figure C Individual stomach content samples from Arctic char (plot A) and brown trout (plot B). Prey were divided into four groups: Crustaceans, fish, insects, and one unidentified/mixed group. Eleven Arctic char and 21 brown trout were sampled for stomach contents in total.

Appendix D: Length and condition vs. Julian day of inward migration

Length and body condition of fish have sometimes been found to influence the inward migration timing of returning fish, as smaller fish/fish with lower body condition should remain longer at sea to maximize the potential for additional growth (Bordeleau et al., 2018). In this study, length and condition were only measured at the time of tagging, which for many individuals occurred 7-8 months prior to the migration. These length and condition measurements can therefore not inform about the effect of these two factors on chosen inward migration timing, as they might have changed over the course of the winter season. Two tagging groups of brown trout, however (S16 adults and S18 smolts) were tagged soon before the migration. The S16 tagging group suggest a possible negative relationship between length/condition and chosen inward migration date (Spearman's rank correlation; rho = -0.84; p < 0.05, and rho = -0.81; p = 0.05, respectively; plot A and B, figure D). No such pattern was observed in 2018 (rho = 0.19; p > 0.05, and rho = -0.07; p > 0.05, respectively; plot C and D, figure D). However, sample size was very small for both groups, and nothing conclusive can therefore be said.

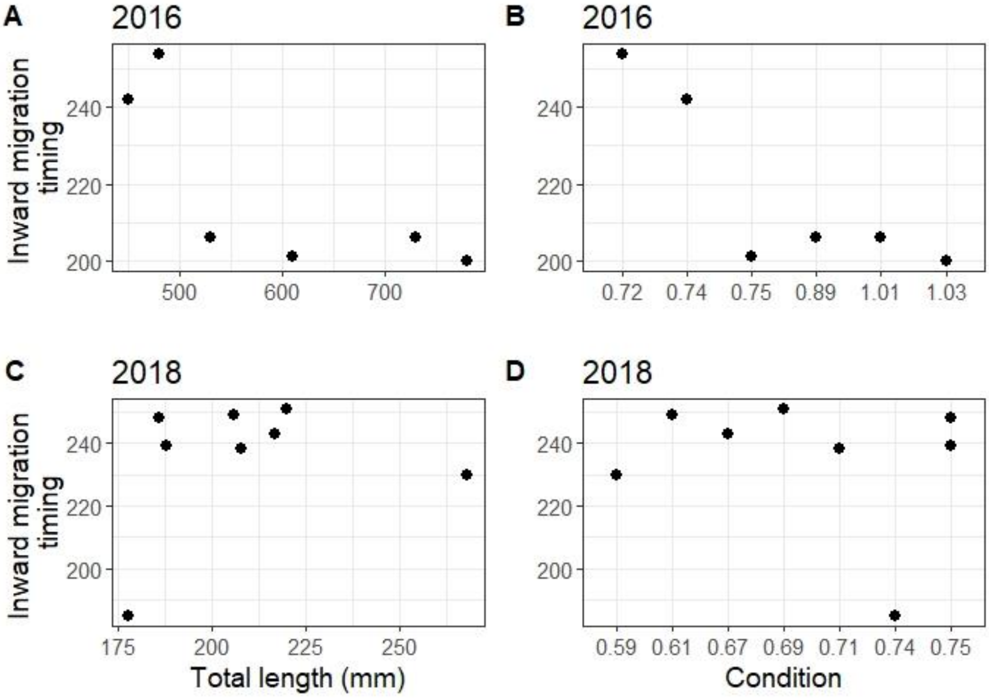

Figure D Total length (A, C) and condition (B, D) plotted against Julian day of inward migration for 2016 (A, B) and 2018 (C, D) brown trout. Length and condition were negatively correlated with inward migration timing in 2016, but not 2018.

Appendix E: Growth curves of stable isotope fish

Age estimated from scales of brown trout and otoliths from Arctic char used in the stable isotope analysis was plotted against their respective lengths. The resulting growth curves revealed a steeper growth rate, and a larger size at any given age for brown trout compared to Arctic char (see figure E).

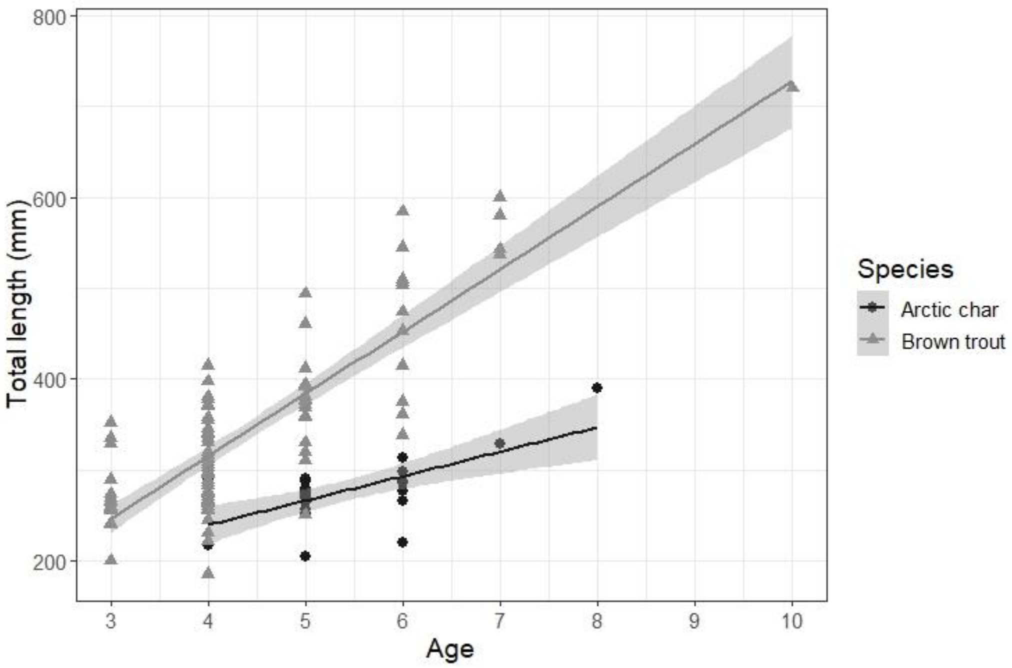

Figure E Age data for both brown trout (grey triangles) and Arctic char (black circles) plotted against their respective lengths. Growth is represented here by the projected regression lines (+ 95% confidence intervals), and is seen to be slower for Arctic char than for brown trout. Additionally, at any given age, brown trout is typically larger than Arctic char.