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Area use of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in an Arctic fjord system —a two-year acoustic telemetry study

Odin Lagerborg Kirkemoen

Photo: Odin Lagerborg Kirkemoen (top), Jenny Jensen, Akvaplan-niva (bottom)

Preface

This master thesis is written as a part of an Akvaplan-niva project which with a purpose to increase the information about salmonid migrations in the Neiden and Bøk fjord system. The project was funded by Norterminal, Sydvaranger gruve AS, Sør-Varanger kommune, Akvaplan-niva, Framsenteret og Fylkesmannen i Finnmark.

Firstly I would like to thank my supervisor, Professor Thrond Oddvar Haugen at NMBU. You have been helped me thought this crazy world of statistics! Your office almost feels like mine after the last six months.

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Abstract

The Arctic charr *Salvelinus alpinus* (L.) and the brown trout *Salmo trutta L.* are fish species with complex and comparable life strategies. However, there are also differences between the two species. The migratory behavior of Arctic charr and brown trout at sea is poorly understood compared to their far more studied behavior in fresh water. Because of the declining populations of anadromous Arctic charr the last decades, this species is particularly important to understand in order to mitigate possible human influence and climate change effects that may affect it in a negative way. The Neiden and Bøk fjord system is a complex fjord system in north-eastern Norway that host both Arctic charr and brown trout. New coastal industrial areas are planned where the marine environment today has a relatively low degree of human impact. In this setting, documentation of the anadromous salmonids behavior in the fjord system is needed.

This study aimed to document the fjord area use of Arctic charr and brown trout and the differences between them. From spring 2014 to autumn 2015, the marine migratory behavior of the two species was studied by use of acoustic telemetry. A total of 33 Arctic charr and 86 brown trout were tagged with acoustic transmitters during the study period. The average number of days at sea for the Arctic charr was 32 and 43 for 2014 and 2015 respectively, while the brown trout was documented to stay at sea for 60 and 54 days.

The major findings in this study was the difference in fjord area use between the two species. The Arctic charr used the areas far away from the river outlets more frequently than the brown trout. Arctic charr also used the Braselv bay, especially early and late in the season. Large brown trout was found to migrate the furthest. The brown trout which was tagged in the long and narrow Lang fjord in the inner parts of the fjord system, did not migrate out of this fjord to a large degree. Smolt length of brown trout was found to be an important factor in modelled predictions of the fjord area use, but it was not as important as day of season or the size of the fish. Size and day of season was important predictors also for the Arctic charr fjord area use.

Both species used the planned harbor areas, but only a low proportion used these areas throughout the whole summer season. However, some individuals of brown trout caught and tagged in the Høybukt bay close to the planned harbor areas used these areas during the entire

summer. To protect the brown trout in the Høybukt bay and the Arctic charr in the Braselv bay, fishing regulations have been proposed. These suggested regulations include a maximum size catch limit and a reduction in fishing pressure in important feeding areas like the estuaries.

Content

1 Introduction

The Arctic charr *Salvelinus alpinus* (L.) and the brown trout *Salmo trutta* L. are two salmonids with important ecological, recreational and economical functions (Jonsson & Jonsson 2011; Klemetsen et al. 2003; Svenning et al. 2012). Both species have a complicated life cycle, with many different life strategies based on migration, diet, growth rates and size at spawning (Jonsson & Jonsson 2011). One central life strategy for both species is the adaptation to feeding in saltwater and spawning in freshwater, which is called anadromy. Anadromous fish migrate to the sea in order to increase their body size, which is strongly related to reproductive success in salmonids (Gross 1987).

Arctic charr has a northern circumpolar distribution and is the world's northernmost freshwater fish species, while the brown trout has a more global distribution (Frost & Brown 1967 Klemetsen et al. 2003). Anadromous Arctic charr populations are located north of 65°N in Norway (Anon. 2011), whereas anadromous brown trout populations are found in most coastal streams and rivers along the Norwegian coast whereas. The annual catches of anadromous fish of both species have declined during the last one to two decades. The anadromous brown trout is declining in many parts of Norway, but is stable or increasing in the northernmost parts. Arctic charr populations are declining all over the country, and this applies to anadromous populations in particular (Anon. 2011).

Both Arctic charr and brown trout in northern Norway generally migrates to the sea to feed during summer, and return to freshwater to spawn and/or overwinter during late summer or fall (Klemetsen et al. 2003). They generally stay in coastal areas close to their natal river during their marine residency. There are also differences in migratory behavior between the two species. For example, the Arctic charr's sea residency normally lasts 45 to 55 days (Berg & Berg 1989; Finstad & Heggberget 1993; Jensen & Rikardsen 2012) while the brown trout stays at sea between 45 and 70 days (Berg & Jonsson 1990; Jensen & Rikardsen 2012).

Human activity is an increasingly important factor influencing the ecological state of both the lacustrine and marine environment (Halpern et al. 2008; Syvitski et al. 2005). Runoff from land-based human activities alters the composition of the waters and might change the behavior or reduce populations of fish and other marine animals and plants (Vitousek et al. 1997). In addition, developments along coastal shorelines, such as harbor areas, dredging and other coastline modifications may temporarily or permanently remove suitable habitats for species utilizing these areas (Kroglund et al. 2012; Wen et al. 2010). In this context, there is a need to study the species living in areas influenced by human developments in order to understand the organism's responses to the alterations and the impact the developments have on them.

The Neiden and Bøk fjord system in the north-east corner of Norway is defined as "Norwegian national salmon fjords" because of the Atlantic salmon population in the Neiden River (St.meld. nr 32 (2006-2007)). In the national salmon rivers and fjords, the aim is to keep new human activity to a minimum in order to protect the Atlantic salmon populations. The Neiden and Bøk fjord system have been exposed to human activity in form of dumping of marine mine tailings for decades. Four new harbor areas for oil reloading and other industrial activities are planned on Tømmerneset (Figure 1, Material and methods) north-west of Kirkenes (Sør-Varanger kommune 2014).

When a large building project is planned in Norway, the Planning and Building Act require an impact assessment (Plan- og bygningsloven § 4-2 & § 14) which should predict the environmental consequences the project will lead to. As part of the impact assessment, the migratory behavior of all naturally occurring anadromous salmonids in the fjord system will be studied as a baseline survey of the species use of the planned industrialized areas.

Acoustic telemetry is one of many biotelemetry methods used when studying animal movements (Cooke et al. 2004). As well as the position of the animal, acoustic telemetry can provide important behavioral traits like temperature- and depth use. One main advantage of acoustic telemetry is that it can be utilized in both freshwater and saltwater (Cooke et al. 2004). It has proven an efficient tool in Norway in later years with good results when it comes to documenting Arctic charr and brown trout migrations in marine areas (e.g. Davidsen et al. 2014; Finstad & Heggberget 1993; Jensen & Rikardsen 2008; Jensen 2013; Jensen et al. 2014). Several of these studies have contributed with new knowledge about the species, amongst others information about the fishes use of marine areas through the whole year, the use of different temperatures and depths, and the effect size and size at smoltification (smolt length) has on the migration behavior.

Information from the current study about the migratory behavior of Arctic charr and brown trout will act as a baseline survey and aid the decision making process around the planned harbor areas. In addition, the general findings may aid managers in deciding how the species will be managed in the future.

Based on the background described, the main aim of the current study was to i) investigate the fjord area use of Arctic charr and brown trout in the Neiden and Bøk fjord system by use of acoustic telemetry. More specifically, the aim was to ii) spot differences in fjord area use between the two species and the factors contributing to these variations and iii) find the effect smolt length has on how far from the river outlet the brown trout migrates. In addition, the analyses aimed to iiii) calculate the probability for the fish to interact with the areas with planned and established human developments. Finally, this thesis discusses management implications of Arctic charr and brown trout in areas with anthropogenic impacts.

2 Material and methods

2.1 Study area

The Neiden and Bøk fjord system is located in eastern Finnmark county in northern Norway at 69°45'N and 29°52'E. The fjord system mouths in the large Varanger fjord, which is the easternmost fjord in Norway before the Russian border. The fjord system also includes the Kjø, Lang and Kors fjords (Figure 1). The depth in this fjord system are below 200 meters in the outer parts of the Kjø fjord and Bøk fjord, while the depth in Neiden and Kors and Lang fjords are between 20 and 60 meters. Thresholds are found in the inner part of the Neiden fjord, the middle part of the Kors fjord, at the Høybukt bay and approximately one kilometer north of Kirkenes in the Bøk fjord. The Lang fjord is a narrow fjord (between 200 and 600 m wide) located further inland from the Bøk fjord. The strait Storstraumen is a shallow choking point for the water, which somewhat separates the Lang fjord from the remaining fjord area. Due to the strait, there is little inflow of cold oceanic water, which makes the water in the Lang fjord warmer than the remaining fjord system during summer. The study area is approximately 25x30km.

There are six known anadromous watercourses in the fjord system, and fish from three of these rivers where tagged and included in this study; the Neiden, Sandnes and Bras River (Figure 1) (Christensen et al. 2014). In addition, fish were tagged in the bay of Høybukt, where the Nos River enters the sea (Figure 1). The Neiden River (Figure 2) is the largest of the rivers in the fjord system. It originates in the Finnish Lake Iijärvi, has a total length of 79 km and supports annual in-river catches between 5000 and 15000 kg Atlantic salmon *Salmo salar* L. and 200 - 1500 kg brown trout (Statistisk Sentralbyrå 2015). The Bras watercourse (Figure 2) mouths approximately 6.5 km north of the Neiden River. The watercourse has a short river stem which is connected to the Braselv and Lille Braselv Lakes. Both rivers mouths in the Neiden Fjord. The Sandnes River is a small river that mouths in the Lang fjord.

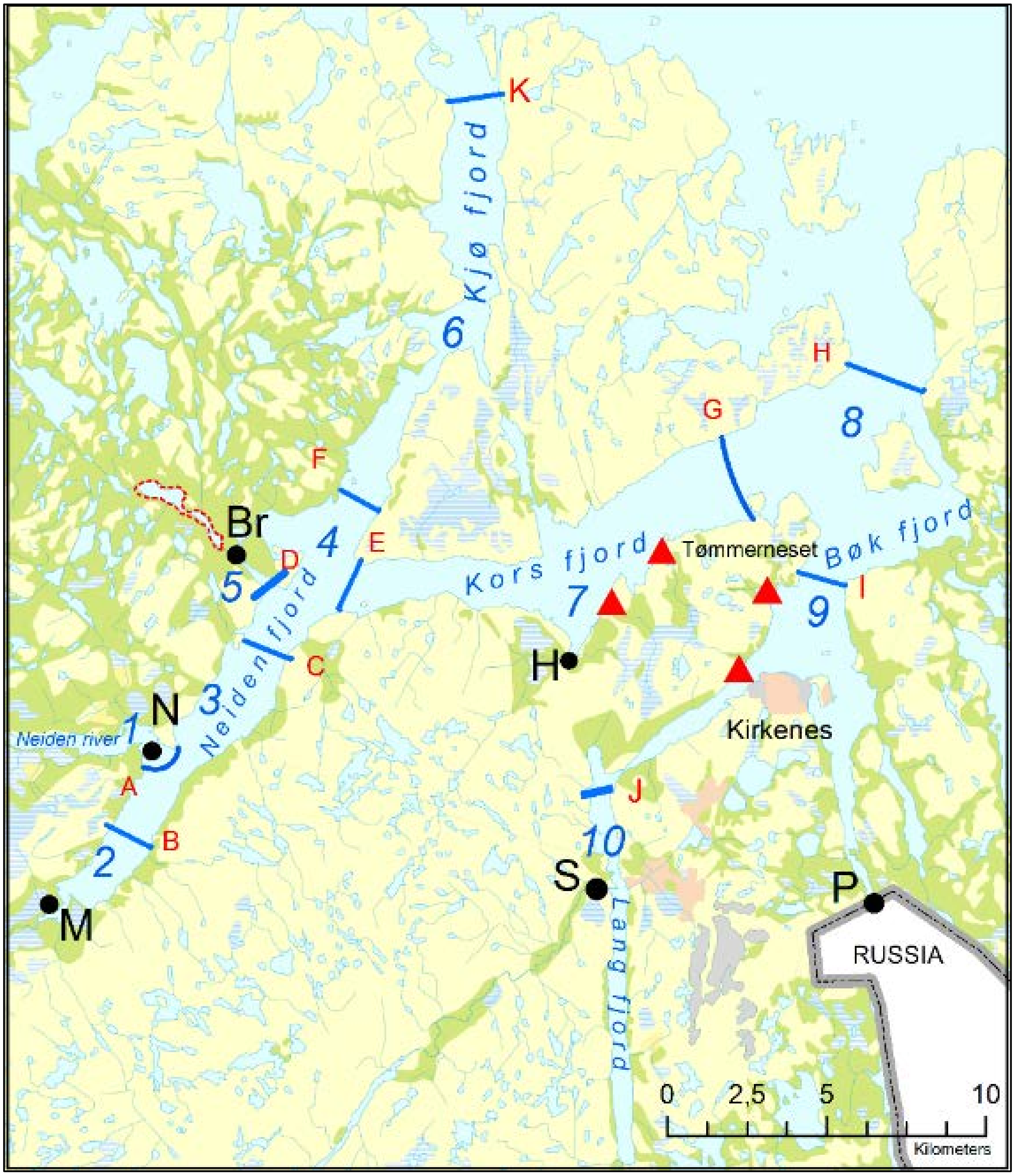


Figure 1: Map of the Neiden and Bøk fjord system. The blue lines indicate the arrangement of the acoustic receivers in transects (corresponds to red letters A-K) across the fjord system. For data analyses the fjord system was divided into different zones, shown in blue numbers 1-10. Black dots indicate outlets of rivers documented to hold populations of anadromous salmonids. N = Neiden River, Br = Bras River, S = Sandnes River, H = Nos River and Høybukt bay, M = Munk River, P = Pasvik River. The red dotted line indicates the Braselv Lake, and the red triangles groups of receivers in the planned harbor areas around the Tømmerneset.

Figure 2: Top picture: The Neiden River in June 2015. The water body to the far right is the river outlet and the Neiden fjord. Bottom picture: The Bras River with the river outlet and the Braselv bay in June 2015. The Neiden fjord is at the far right. Photo: Odin Lagerborg Kirkemoen.

2.1.1 Fish capture and tagging

Different methods were used to capture fish for tagging; traps, ice fishing, rod and reel and attended nets. Traps are the gentlest method, as it causes no or little harm to the fish. Of the other methods, capture by rod and reel is preferred as this has less effect on anadromous fish behavior than netting (Mäkinen et al. 2000). There is to our knowledge no known documentation of the effects of ice fishing on anadromous fish behavior. Rod and reel and nets were used to capture brown trout, while traps, ice fishing (one individual) and nets (two individuals) were used to capture Arctic charr.

During May and June 2014, 28 brown trout were caught and tagged in the Neiden River, 19 brown trout in the Sandnes River mouth, 21 Arctic charr in the Bras River and one Arctic charr in the Sandnes River mouth (Table 1). In 2015, the corresponding numbers were 12 brown trout in the Neiden River, six brown trout in the Sandnes River mouth and 10 Arctic charr in the Bras River. In addition, 21 brown trout and one Arctic charr was tagged in the Høybukt bay in 2015 (Table 1). The fish were tagged between April and June in 2015. The brown trout varied in length from 31 to 71 cm and 0.3 to 3.3 kg, and the Arctic charr size ranged from 23 to 53 cm and 0.1 to 1.9 kg (Table 1).

Table 1. Overview of Arctic charr (AC) and brown trout (BT) tagged with acoustic transmitters in the Neiden and Bøk fjord system during spring 2014 and 2015. The table shows number of tagged individuals and average size (LF in cm and mass in kg, range in parenthesis). Note that some transmitter batteries lasted for three years, therefore fish tagged in 2014 could be detected also in 2015. The number of fish annually that were documented on receivers in the fjord and estuaries are also shown in the table.

Place	**Sp.**	**# tagged**		**# retrieved data**		**Length L_F**		**Mass**	
		2014	**2015**	**2014**	**2015**	**2014**	**2015**	**2014**	**2015**
Bras River	AC	21	10	20	10	30 (23-46)	33,5 (23.5-44)	0,23 (0.1-1.0)	0,33 (0,1-0.68)
Sandnes River	AC	1		1	1	53		1,9	
Høybukt Bay	AC		1		1		46,5		0,94
Neiden River	BT	28	12	26	12	47 (37-65)	60,5 (51-71)	1,1 (0.5-3.3)	2,1 (1.34-2.78)
Sandnes River	BT	19	6	16	13	41 (31-52)	41,5 (38-44)	0,8 (0.3-1.4)	0,85 (0.63-1.01)
Høybukt Bay	BT		21		21		45 (36-58.5)		0,93 (0.56-1.74)

The fishes from the different places are hereafter referred to by a combination of species and place: The Arctic charr tagged in the Bras River is hereafter referred to as “Braselv Arctic charr”, the Arctic charr tagged in the Sandnes River mouth (estuary) as “Sandnes Arctic charr”, the Arctic charr tagged in the Høybukt Bay as “Høybukt brown trout”, the brown trout tagged in the

Neiden River/estuary as “Neiden brown trout”, the brown trout tagged in the Sandnes river estuary as «Sandnes brown trout», and the brown trout tagged in the Høybukt Bay as “Høybukt brown trout”.

The trap in the Bras River (Figure 3) consisted of a v-shaped leading net and a fyke net, and was checked every one - two days. Of the Arctic charr captured in 2014 with this trap, 16 were kept in a cage in the river for up to 14 days. These individuals were kept in captivity because of their small size, and larger individuals were expected to get captured. In lack of larger fish, these 16 individuals were tagged with smaller transmitters than planned (see below for description).

Figure 3 The trap in the Bras River in 2015, with the v-shaped net and the fyke net to the right. The cage can be seen in the background. Photo: Odin Lagerborg Kirkemoen.

All Høybukt brown trout were caught by using attended nets (mesh sizes 45-55mm). The nets were attended in order to detect captured fish as early as possible. Caught fish was carefully untangled and put in a 100 L water filled tub. Some of the Neiden brown trout were also caught using this method in the river mouth (18 in 2014 and nine in 2015). Two of the Arctic charr were caught by nets.

2.1.2 Tagging procedure

The fish were tagged with acoustic tags from Vemco (Vemco Inc., Canada, www.vemco.com) or Thelma Biotel (Thelma Biotel AS, Norway, www.thelmabiotel.com). The tags transmitted individually coded acoustic signals through the water. With the exception of the smallest Arctic charr (16 individuals), data about temperature and pressure were also transmitted. The pressure measurements were used to calculate the depth in meters. The Vemco tags were mainly of the model V13TP-1L (13x48 mm cylindrical, 13 g in air, signal interval; 30/90 s, 180 days on/off period, estimated battery life time 1339 days). The tags from Thelma Biotel were of the model ADT-9-LONG (9x39 mm cylindrical, 6.8 g in air, signal interval 30/90 s, estimated battery life time 210 days). In 2014, the smallest Arctic charr (n=16) were tagged with Vemco V7-2L (7x20 mm cylindrical, 1.6 g in air, signal interval 30/90 s, estimated battery lifetime 132 days) to avoid unwanted behavior due to too large transmitters (Moore et al. 1990; Thorstad et al. 2009). The V13TP-1L transmitters were programmed to turn off during winter (on/off period) to maximize their battery life time.

In accordance with regulations regarding animal experiments, a qualified scientist with proper training performed the surgical implantation of the transmitters. The fish was anesthetized prior to tagging by use of 2-phenoxy-ethanol (0.5 ml per L of saltwater or freshwater, depending on where the fish was caught). When the fish was unresponsive, it was placed in a tagging tube (Figure 4) with the ventral side facing up and the head and gills submerged in clean water. On the ventral side posterior to the pelvic girdle, a 1 - 2 centimeter long incision was made with a scalpel (Rikardsen, Audun H. et al. 2007). The tag was thereafter inserted into the abdominal captivity. After the insertion, the incision was stitched with one to three silk sutures (3-0, Ethicon, Dilbeek, Belgium). All equipment in contact with fish was sterilized prior to tagging with 96% ethanol. After tagging, fork length (L_F) and mass were registered, and five to seven scales were collected from the brown trout. The samples were taken above the lateral line, posterior to the dorsal fin (Fjørtoft et al. 2014). Fish larger than 30 cm were tagged with an Floy T-bar anchor tag for recognition upon recapture (Olsen et al. 2012). Genetic material was sampled from the adipose fin. After tagging, the fish was released back to the water where it recovered from the anesthetic while being observed. The whole tagging procedure including anesthesia took less than six minutes, and the fish recovered to seemingly normal behavior (i.e. keeping a vertical position and swimming away) within 5-10 minutes.

Figure 4: Top picture: an acoustic-tagged Arctic charr being sutured by scientist Jenny Jensen. Photo: Odin Lagerborg Kirkemoen. Bottom picture: an acoustic-tagged Arctic charr released back to the Braselv watercourse. Photo: Jenny Jensen, Akvaplan-niva.

2.1.3 Tracking

When a fish with an acoustic tag is within the detection range of a receiver, a hydrophone detects the signals and the logging function in the receiver saves the information together with date and time (Cooke et al. 2004). The receivers were submerged five meters under the sea surface, attached to an anchored rope on a buoy. In the Braselv Bay, in the Neiden River outlet and in the Lang fjord the receivers were positioned at three meter depth. On the most used seaways in the study area, a pole with a flag, radar reflector and light was mounted on the buoy. The Norwegian Coastal Administration and the port administration in Kirkenes were informed about the positions of the receivers. All receiver positions were saved on a GPS.

In 2014, 63 receivers were used, while the number was increased to 72 in 2015. The receivers were arranged in transects (letters A-K, Figure 1) across the fjords, to detect tagged fish passing the transects. A new transect (letter K, Figure 1) was added in 2015 in order to detect how far past transect F the fish migrated. These transects divided the study area into a total of 10 zones (numbers 1-10, Figure 1) where the fish could be at any given time. In 2015, one additional receiver was added to the Neiden River, the Bras River and the Lang fjord, while three receivers were added to the north side of Tømmerneset (Figure 1).

Depending on environmental conditions such as waves, haloclines and tidal currents (Mathies et al. 2014), the detection range of the transmitters varied between 200 – 1000 m. The receivers arranged in transects were placed 200-400 m apart to avoid fish passing the transects without being detected. Some receivers were lost during the study. Lost receivers were replaced when discovered. Data was retrieved from the receivers once during summer and in early- to mid-October in both study years.

The public was informed of the project through local papers, the web pages of the local fishing associations and by information posters along the rivers and shoreline.

Scale readings

The growth of the scale and the length of the fish is considered an approximately 1:1 relationship, which means that the scale can be used to back-calculate the length of a fish at different stages of its life (Dahl 1907; Jonsson 1976). The scale samples were used to determine the smolt age and smolt length of the tagged brown trouts in this study. The scales were cleaned and scanned into a computer program (IM50, Leica Microsystems AG, Germany) through a magnifier (Leica S8APO, Leica Microsystems AG, Germany) with a digital camera (Leica DFC320, Leica Camera AG, Germany). Each scale was analyzed and measured by using a program called “Image pro express 6.3” (Media Cybernetics Inc., The total length from the center of the scale, the focus, to the outer edge of the scale was measured. The end of all annual growth rings (annulus) (Figure 5) and the year when the fish smoltified was marked. The latter was done by finding the annulus where the fish drastically increased its growth rate, *i.e.* where the growth rings’ wideness increased. According to Klumb et al. (1999), the smolt length was calculated by using the Dahl-Lea model (Dahl 1907; Lea 1910) .

$$L_S = L_F \left(\frac{R_S}{R_T}\right);$$

L_S = back-calculated length at smoltification

L_F = length at capture,

R_S= scale radius to annulus where fish smoltified

R_T= total scale radius

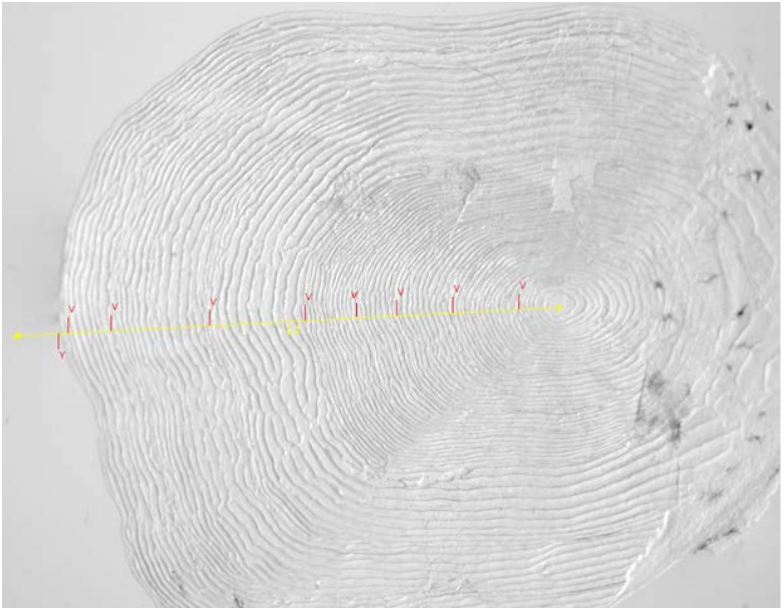


Figure 5: A scale from the brown trout "5HT16". Red "V"s mark each annuli. The scale shows that the fish smoltified at age five and that the fish was eight years when caught. After smoltification (year five), there is a substantial increase in annual growth. Photo: Odin Lagerborg Kirkemoen.

For eight brown trout the smolt age could not be determined due to missing annuli from the first living years. These scales are called replacement scales (Lund & Hansel 1991). For most of these replacement scales it was possible to calculate a smolt length because the distance from the focus to the annuli when the fish smoltified would be close to the same as a normal scale (pers. comm. Thrond Oddvar Haugen, NMBU). Two brown trout got assigned an average smolt length based on smolt lengths of all the brown trout because it was not possible to calculate smolt length for these individuals based on the scales.

The mean smolt length for the tagged brown trout (2014 and 2015 grouped) was 18.44 ± 3.0 (SD) cm, 17.56 ± 2.68 (SD) cm and 19.64 ± 3.32 (SD) cm for fish tagged in Neiden, Sandnes and Høybukt, respectively. The mean smolt age for the tagged brown trout (2014 and 2015 grouped) was 3.96±0.45 (SD) years, 3.94±0.78 (SD) years, 3.95±0.59 (SD) for Neiden, Sandnes and Høybukt trout, respectively.

Fish tagged in 2014 were not recaptured or remeasured in 2015. In order to establish a reasonable fork length for the analysis of these individuals detected in 2015, average annual sea growth for all brown trout measured in 2014, except the first year after smoltification, was added to these individuals' fork length. The first year after smoltification was not included because the growth is usually higher the first year after a fish enters the sea (de Leeuw et al. 2007; Jonsson & Jonsson 2007). An average annual sea growth of 8.7cm was added to these brown trout's fork lengths for the 2015 analysis.

2.2 Data handling and analysis

Fish were removed from further analyses after it was last detected at sea, either due to up-river migrations or that the tag was not registered any more for other reasons. The fish that ceased to be registered may have died or lost its tag in areas not covered by the receiver arrays, the tag may have malfunctioned, or the fish may have migrated up another watercourse than the study rivers for spawning and/or overwintering. As there is uncertainty of the fate of fish that ceased to be registered, all survival estimates presented are to be considered minimum estimates.

Some transmitters generated data from the same depth for a prolonged time, and these were removed from further analysis after the last movement. Of the brown trout tagged in 2014, four individuals died or got their transmitter rejected and seven in 2015 (Table 3, Results). Refer to the Appendix (Table S1) for individuals that have been taken out of the analysis due to death or tag rejection. Clear examples of death/loss of transmitters are brown trout number NT8 and 5HT13 in the 2015 depth data (Figure 17, Results). The former clearly shows that the individual or its transmitter has sunk to the bottom of the fjord and has been there since the start of the study period. The latter clearly died/lost its transmitter on study day 70, where the depth data increased suddenly until it was laying on the bottom.

The only Sandnes Arctic charr included in the study was tagged in 2014, and was recorded through the 2015 season as well. This individual, as well as the one Høybukt Arctic tagged in 2015, has been taken out of statistical analysis because of the very small sample size. Instead, the migration of these individuals is presented in Figure S1-S4.

Of the Arctic charr used in the statistical analyses, one individual tagged in 2014 was re-detected in 2015. During analysis including this individual, five cm was added to its fork length for 2015. This was done based on a study by Berg and Berg (1989) which looked at the sea growth rates for an Arctic charr population in northern Norway.

During data analysis, each fish got assigned as being in one of the zones at every given time. The Høybukt brown trout was an exception, as the location of the fish prior to tagging was unknown. Initial zone was always set to be the tagging and release site. For fish that were last detected near a river, the fish were assigned to be in the same zone for the remaining timeslots (see next chapter for definition of timeslots). Fish that were detected for the last time in the Neiden River or estuary was assigned to zone1 for the remaining timeslots, and similarly Arctic charr last detected in zone 5 was assigned to zone 5 and fish last detected in zone 10 were assigned to zone 10 for the rest of the timeslots. If an Arctic charr was lastly detected at transect F followed by no detections over the next 72 hours, it was assigned to zone 6 due to the sheer size of this zone and distance between the different transects. If a fish was detected at transect F multiple times under 72 hours in-between, after a detection at transect F was set to zone 4.

In order to see the bigger picture of the migration behavior and get good enough estimates for the statistical analyses, the zones were grouped into new areas. Table 2 and Figure 6 shows merged areas (refer to the study area map in Figure 1 for original zones, numbered 1-10). The new areas were named "Close", "Middle" and "Far". These areas are defined according to distance from the spot where the fish were captured and tagged. This means that the "Close", "Middle" and "Far" areas include different zones for fish captured and tagged in the Bras, Neiden and Sandnes Rivers and the Høybukt bay.

The "Close" area is located in the sea for all fish except the Neiden brown trout, where this zone was defined as the Neiden River mouth. The "Close" area for Braselv Arctic charr is the Braselv bay, the "Close" area for Sandnes brown trout is the Lang fjord and the Kors fjord is the "Close" area for the Høybukt brown trout.

Table 2: Overview of which zones (blue numbers 1-10, Figure 1) that were merged into the new areas "Close", "Middle" and "Far". These new areas are based on the distance from where the fish was captured and tagged.

	Close	Middle	Far
Braselv Arctic charr	5	4	1-3 & 6-10
Neiden brown trout	1	2-5	6-10
Sandnes brown trout	10	9	1-8
Høybukt Brown trout	7	4	1-3 & 5-6 & 8-10

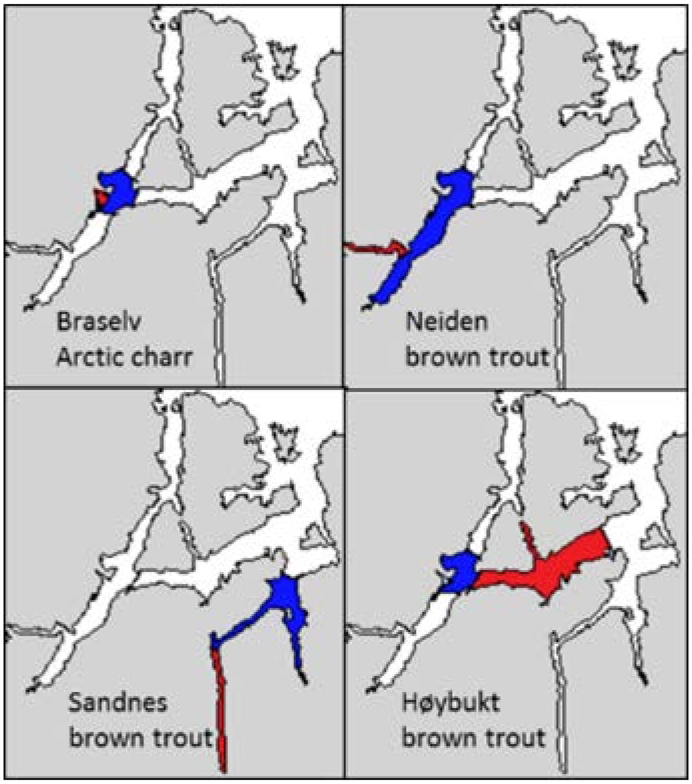


Figure 6: Map of the study area divided into the areas "Close" (red), "Middle" (blue) or "Far" (white) for the groups Braselv Arctic charr, Neiden brown trout, Sandnes brown trout and Høybukt brown trout.

2.2.1

2.2.2 Statistics

All statistical analyses and plotting was undertaken using the program R (R-core team 2012). This thesis order to estimate large-scale fjord area use probabilities, *i.e*. the probability of utilizing either the "Close", "Middle" of "Far" areas, a multinomial modeling approach was undertaken. In particular, it was aimed to estimate these probabilities at any given point in time during the study period, which was not likely to change in a linear fashion over the entire time span. This was achieved by using a vector-generalized additive model approach (VGAM, Yee & Wild 1996). This modeling approach allows for non-linear and non-parallel response-trajectories among the response categories. The response trajectories were fitted as spline functions constrained to produce total fjord area allocation probabilities = 1 on a probability scale. The probabilities were fitted on logit-scale so as to secure fulfillment of this constraint. The models were fitted using the VGAM-package in R (Yee, Thomas W 2010), and model selection (*i.e*.

optimal number of spline knots, k) was conducted using the built-in generalized cross validation procedure (Gu & Wahba 1991). In addition to the time effect, this method fitted candidate models exploring the support for alternative internal drivers for area use, such as fork length at tagging and, in brown trout, the effect of smolt size (retrieved from back calculation). Model selection was conducted using AICc as criterion (Burnham & Anderson 1998).

When exploring drivers behind depth and temperature use, a linear mixed effects modeling (LME) approach was used (Pinheiro & Bates 2000). Candidate models with day of study (DoS) as *a priori* fixed effect and ID as *a priori* random effect were constructed and subjected to model selection procedures described in Zuur et al. (2009). The candidate models included group effects (species and origin) as well as individual covariates (fork length at tagging and smolt size). The ID random effect was fitted as individual intercepts to correct for repeated measurements and fulfill major assumptions of independency among fitted model residuals (Pinheiro & Bates 2000)The models were fitted using the lmer-procedure embedded in the R library lme4 (Bates et al 2015).

The same R-package was used for fitting models quantifying probabilities of using areas planned for harbor constructions (Figure 1) as function of species, origin and individual covariates. The same modeling approach as for the depth and temperature use was undertaken, apart from using a logit link to secure predicted probabilities to attain values between zero and one. The response was coded as “1” when an individual, at a given day, was registered at receivers located within the vicinity of the development area (Figure 7) and “0” when not. Candidate models were fitted using the glmer-procedure in the lme4 library. Note the added receivers in 2015: one in Høybukt bay and two in the east side of the Kors fjord, which might increase the predictions for harbor area use in 2015 compared to 2014. The total number of receivers used in this analysis was 14 in 2014 and 17 in 2015.

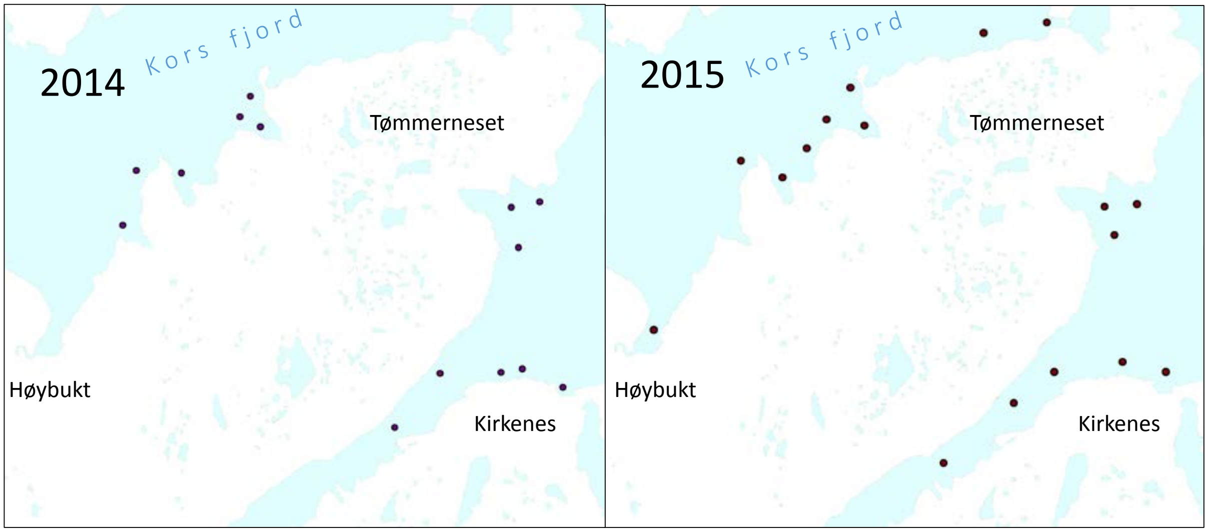


Figure 7. Map of the receivers included in the prediction of harbor area use for 2014 (left) and 2015 (right). Note the added receivers in 2015: one in Høybukt bay and two in the east side of the Kors fjord, which might increase the predictions for harbor area use in 2014 compared to 2015.

3 Results

3.1 General aspects of the data

In 2014, a total of 22 Arctic charr and 47 brown trout were tagged (Table 1), and data was retrieved from 21 (95%) Arctic charr and 42 (89%) brown trout. In 2015, 11 Arctic charr and 39 brown trout were tagged, and data was retrieved from 10 (90%) Arctic charr and 29 (74%) brown trout.

Of the 12 Arctic charr detected in 2015, two were tagged in 2014. Of the brown trout detected in 2015, nine Neiden brown trout and seven Sandnes brown trout were tagged in 2014. During the two-year study period, a total of 11 brown trout were documented to have tag rejections or died. No Arctic charr had deviation from the data recording.

In 2014, the first detection was recorded on the 23rd of May, and the last on the 9th of October, both records by Neiden brown trout (Table 3). In 2015, the first detection was recorded on the 14th of May by the Sandnes Arctic charr. The last detection in 2015 was from a Høybukt brown trout on the 4th of October. Accordingly, the first study day during data analysis was set to the 23rd of May in 2014 and the 14th of May in 2015. In total, the study period lasted 141 days in 2014 and 144 days in 2015.

Both first and last detections were recorded earlier in 2015 for all groups, except for Neiden brown trout that had its first detection on the 23rd of May in both years. In contrast to individuals tagged in the estuary, none of the brown trout tagged in the main Neiden River in 2015 were documented to migrate to sea.

The number of detections varied greatly among fish from the different tagging locations. The Sandnes brown trout were on average recorded most frequently, with an average of 13 518 and 25 960 detections per individual in 2014 and 2015, respectively (Table 2). In comparison, the Neiden brown trout had an average of 8 253 and 5 760 detections per individual in 2014 and 2015, respectively, and the Høybukt brown trout 3 331 detections in 2015. The Braselv Arctic charr had an average of 3 828 and 4 756 detections per individual in 2014 and 2015, respectively.

3.2 General migratory behavior

The results showed large variation in migratory behavior between and within the two study species. Brown trout individuals differed much among the groups. The Arctic charr from Braselv and Sandnes (SC1) used the areas in the outer fjord more frequently than the brown trout. The Sandnes brown trout was by far the most homogenous of all the groups, as they mostly stayed within the Lang fjord. Both the Neiden and the Høybukt brown trout mainly used the areas close to the Neiden River and the inner Neiden fjord. However, there was large individual variation in migratory behavior within groups of tagged fish.

Individual fish movement is shown in Appendix (Arctic charr S1-S2, brown trout S3-S4). There were also individual differences in both migratory distance from tagging location and the length of the sea residency.

During the study period, no fish migrated from the Neiden River to the Lang fjord, or vice versa. There were no indications that any fish in this study swam directly from zone 6 to 8 (Figure 1) or the other way around, *i.e.* the fish that went past the outer transects in either the Kjø fjord or the Bøk fjord returned on the same route as they went out of the fjord.

The average duration of the sea residency of Arctic charr was 32 days in 2014 and 43 days in 2015, whereas the average brown trout sea residency (all groups) duration was 60 days in 2014 and 54 days in 2015.

Table 3: The dates of first and last detections for Arctic charr and brown trout tagged with acoustic transmitters in the Neiden and Bøk fjord system in 2014 and 2015, and the average number of detections per individual (standard deviation in parenthesis) and number of tag rejections/mortality per group of tagged fish. Numbers in the table are based on fish/transmitters that generated data.

Group	2014				2015			
	First	Last	Detections	Reject/ death	First	Last	Detections	Reject/ dead
Braselv Arctic Charr	4.6	21.7	3 828(6363)		24.5	5.8	4 756(3 768)	
Sandnes Arctic charr	23.6	7.7	1 435		14.5	17.7	37971	
Høybukt Arctic charr					29.6	29.6	46	
Neiden brown trout	23.5	9.10	8253(4367)	3	23.5	29.9	5 760(5 484)	4
Sandnes brown trout	20.6	13.9	13518(16867)	1	17.5	19.9	25 960(22 723)	2
Høybukt brown trout					6.6	4.10	3 331(4 223)	1

3.2.1 Arctic charr

Of the tagged Braselv Arctic charr, 13 individuals (65 %) returned to the Braselv River in 2014 and seven individuals (63%) in 2015. In 2014, one Braselv Arctic charr was last detected in the outlet of the Neiden River, and two were last detected upstream in the Neiden River. No Arctic charr were last detected in the Neiden River the following year. Only one Arctic charr was detected at the K-transect in 2015, *i.e.* in the outermost part of the Kjø fjord. This Arctic charr was tagged in the Braselv River. Two of the Braselv Arctic charr were detected in the outer Bøk fjord (transect H) in 2014, and none in 2015.

The Sandnes Arctic charr migrated to the outer Bøk fjord (transect H) during both study years. It was last detected in 2015 at transect I. The Sandnes Arctic charr was the largest Arctic charr tagged (L_F =53 cm, mass = 1.9 kg in 2014, Table 1), and it migrated further away from the tagging location than most of the Braselv Arctic charr. The Høybukt Arctic charr was only detected a few times after tagging in Høybukt before disappearing.

3.2.2 Neiden brown trout

Of the tagged Neiden brown trout, 22 individuals (88%) returned to the Neiden River in 2014 and 8 (72%) in 2015. In 2014, five Neiden brown trout were detected in the outer Bøk fjord. Examples are NT16 and NT17 (Figure S3, Appendix). None of the Neiden brown trout were detected in the same area in 2015. Only one brown trout was detected at the K-transect in 2015, and this individual was tagged in the Neiden River.

3.2.3 Sandnes brown trout

Of the tagged Sandnes brown trout, 14 individuals (73%) returned to the Sandnes River in 2014 and 12 (100%) in 2015. In general, the tagged Sandnes brown trout was quite stationary and homogenous in their migratory behavior. Three individuals migrated out of the Lang fjord in 2014, and one in 2015. Examples are ST9 and ST13 shown in the Appendix (Figure S3), which both used parts of the Bøk fjord in 2014. Of the Sandnes brown trout, 87% returned to the Sandnes River in 2014 and 100% in 2015 (Figure S4).

3.2.4 Høybukt brown trout

Of the tagged Høybukt brown trout, five individuals (14%) returned to the Høybukt bay in 2015, while 71 % were last recorded in the Neiden River or inner Neiden fjord. They used the Neiden fjord to a great extent, especially after mid-July 2015. Two Høybukt brown trout were detected east of the Kors fjord. The rest of the detections were in the Kors and Neiden fjords.

3.3 Fjord area use

All groups of tagged fish used the area close to the tagging location to a much greater extent than the other parts of the study area during both years (Figure 8 and 9), except the Høybukt brown trout which used the “Far” area more than the other areas. The ”Middle” area was only used more than the “Far” area in Høybukt brown trout and Sandnes brown trout in 2015. All other groups used the “Middle” more than the “Far” area. One Braselv Arctic charr individual was detected in the “Far” area in 2014, and none in 2015.

The dates of least use of the “Close” area was approximately the same in both years for all groups. The Braselv Arctic charr had its lowest use of the “Close” area around the 20th of June in both years, while the Neiden brown trout used the “Close” area the least on the 1st of July and Sandnes on the 1st of August.

The following graphs (Figure 8-9) show predictions of fjord area use of Arctic charr and brown trout that were detected in the sea. The predictions are given as a function of time.

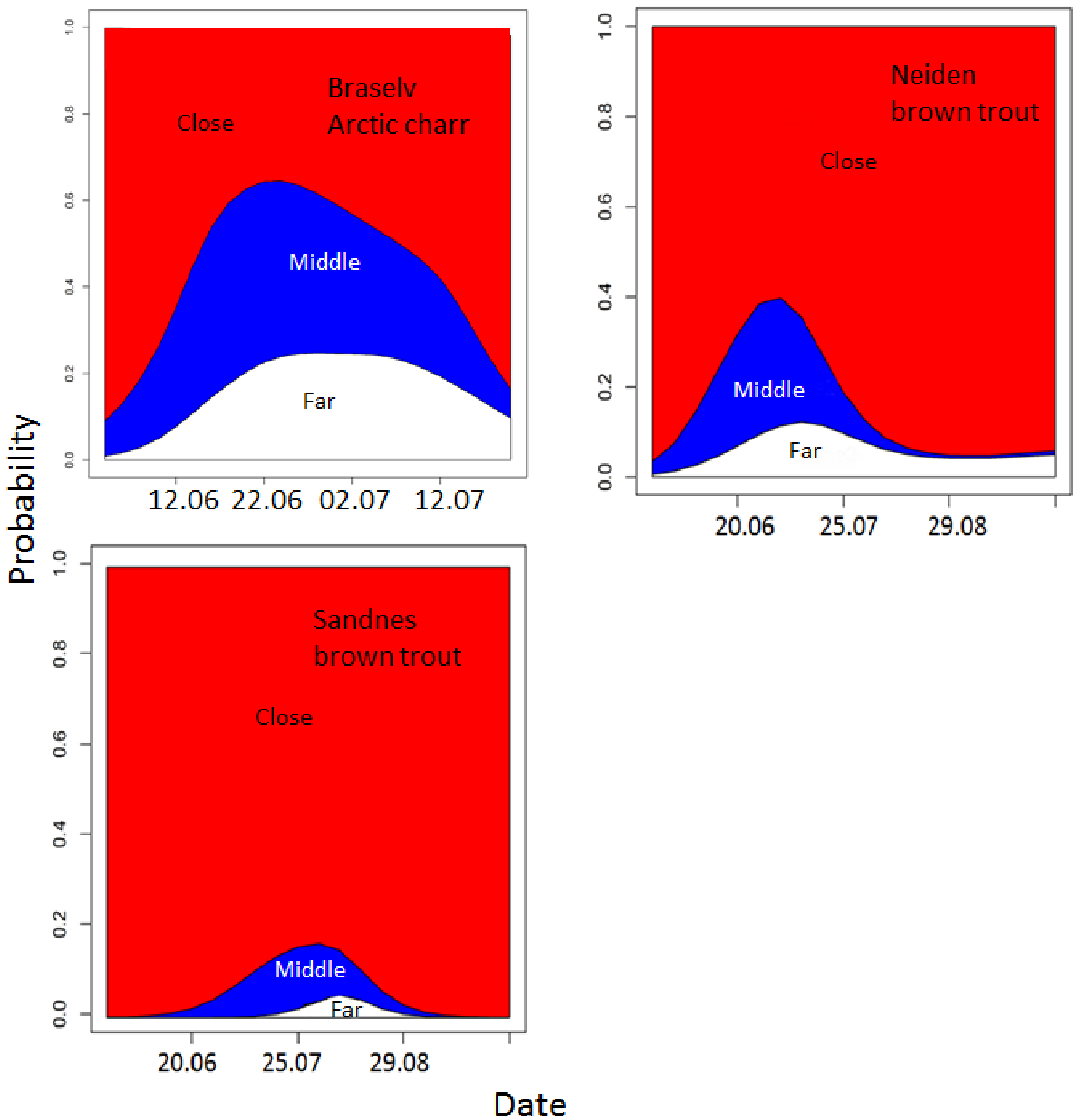


Figure 8. The probability of finding acoustically tagged Braselv Arctic charr, Neiden brown trout and Sandnes brown trout in areas "Close" (red), "Middle" (blue) or "Far" (white) away from the tagging location in the Neiden and Bøk fjord system during spring – autumn 2014. For definition of the areas, see Table 2 and Figure 6. Note the x-axis scale differences between Arctic charr and brown trout, as the Arctic charr resided at sea shorter than brown trout.

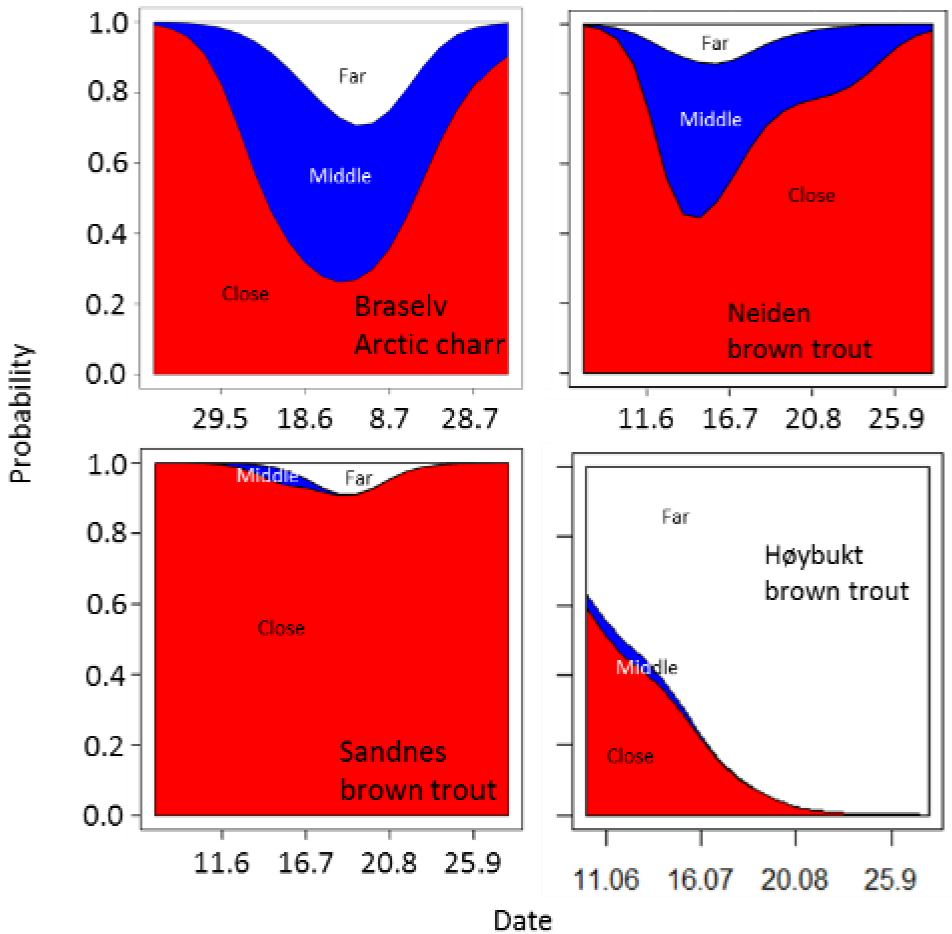


Figure 9. The probability of finding acoustically tagged Braselv Arctic charr, Neiden brown trout, Sandnes brown trout and Høybukt brown trout in areas "Close" (red), "Middle" (blue) or "Far" (white) away from the tagging location in the Neiden and Bøk fjord system during spring – autumn 2015. For definition of the areas, see Table 2 and Figure 6. Note that the scale on the x-axis differs, as Arctic charr resided at sea for a shorter period than brown trout and Høybukt brown trout was tagged later than other brown trouts in the study.

3.3.1 Intrinsic drivers of fjord area use

3.3.1.1 Braselv Arctic charr

Fish length influenced the Braselv Arctic charr fjord migration pattern. The VGAM model selection favored a model where fish length and time had an interaction effect on fjord area use (Figure 10). This model attained 89.1 (2014) and 5.4 units (2015) lower AICc values than the second-most supported model (Table S2-S5).

The prediction graph for Braselv Arctic charr showed the same pattern for both study years, but the 2014 graph show more diversity of migration between the different areas based on fork length. In general, fish length had little effect on the area use before mid-June and after early August in 2014, and before early June and after mid-July in 2015. However, length had a large effect on the fjord area use in the corresponding between-periods where large and small individuals had highest probabilities of using the most distant area and medium sized individuals had highest probabilities of using the "Middle" area. The "Far" area was more likely to be used by the smallest individuals and the ones that were about 40 cm in fork length.

In 2015, Braselv Arctic charr individuals with medium sized fork length (30-45cm) were most likely to be found in the "Middle" area. The probability for a large or small Arctic charr to be in the "Far" area was higher than for medium-sized individuals. Medium-sized Arctic charr stayed away from the "Close" area for the longest period.

The following prediction plots are the most supported models. Refer to Appendix for model selection though AICc and parameter estimate tables.

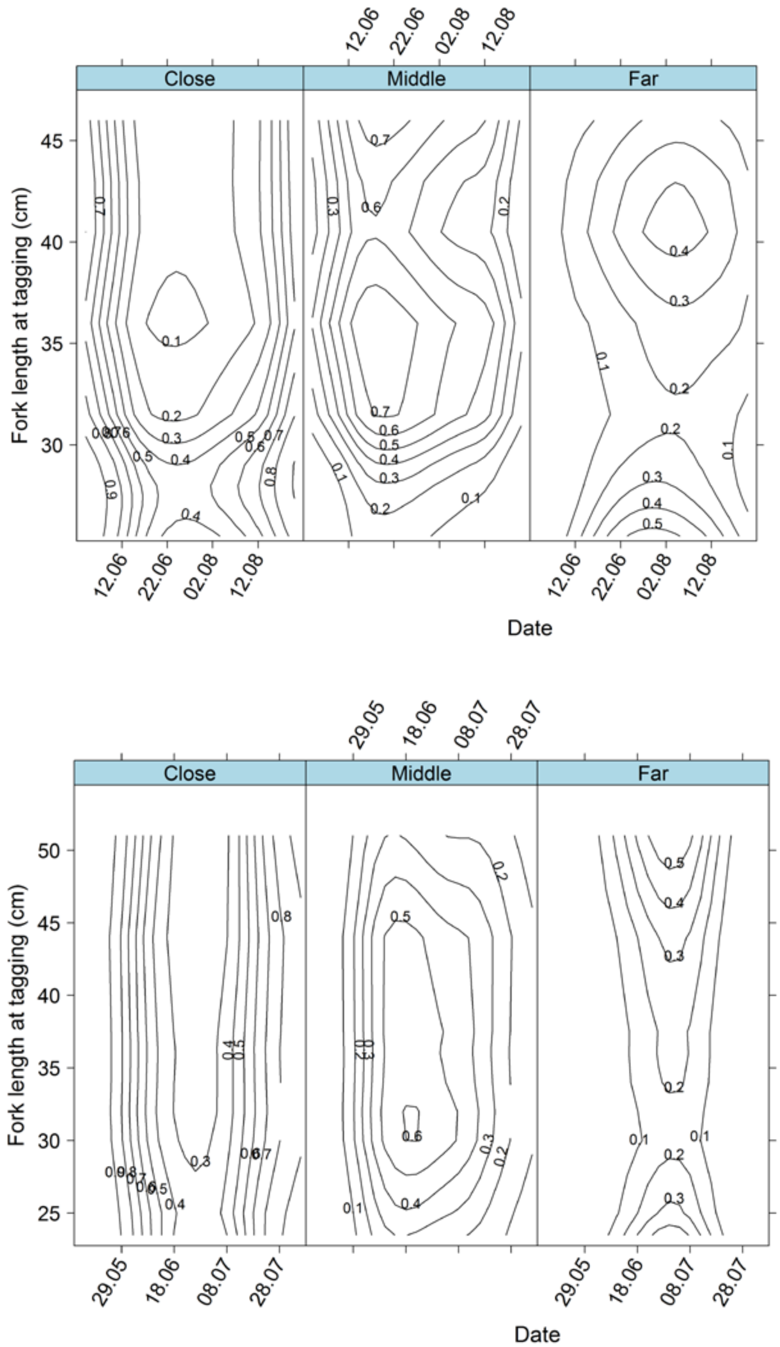


Figure 10. VGAM-based prediction plot of fjord area use for Braselv Arctic charr in 2014 (top) and 2015 (bottom) as a function of time and fork length (cm). The Neiden and Bøk fjord system was divided into the areas: "Close", "Medium" and "Far" as a function of distance from the tagging location (Figure 6 & Table 2). Contour lines represent probabilities over a four-day period for 2014 and a two-day period for 2015. Estimates were retrieved from the most supported model shown in Table S2 and S3 (2014) and in Table S4 and S5 (2015).

3.3.1.2 Neiden brown trout

In both 2014 and 2015, the model selection process favored a model where smolt length, fork length at tagging and time had interacting effects on the area use for Neiden brown trout. This model attained 11.5 (2014) and 24 units (2015) lower AICc values than the second-most supported model (Table S6-S9).

The largest individuals used the “Far” area the most in both years. The smallest individuals used the “Middle” area the most. Only one individual of the medium and small fish had smolt lengths over 20 cm.

In 2015, there were no Neiden brown trout detections from fish smaller than 47 cm fork length (Figure 11). All Neiden brown trout below 50 cm in fork length were between 17 and 20 cm in smolt length. Of the Neiden brown trout, the big individuals (L_F > 50cm) with smolt lengths between 16 and 20 cm were most likely to use the “Far” area. For both years the large individuals had the highest probability to use the “Far” area.

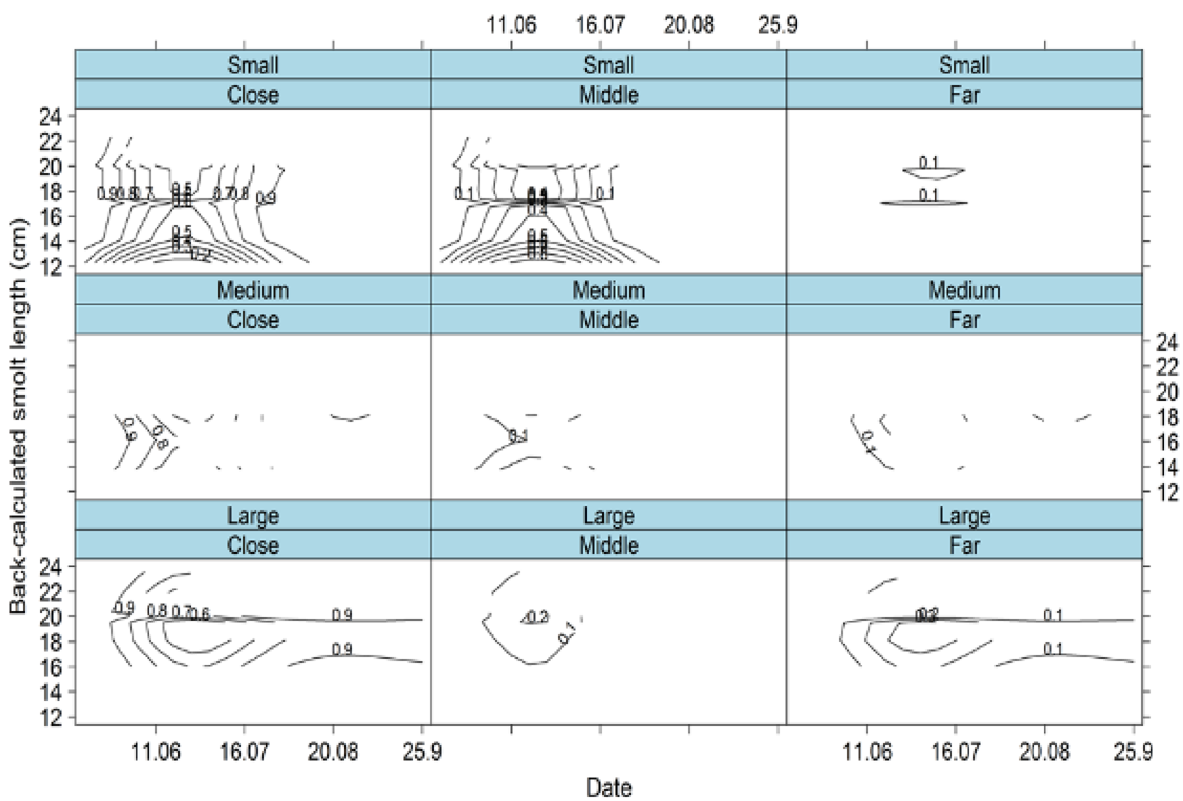


Figure 11. VGAM-based prediction plot of fjord area use for Neiden brown trout in 2014. The fjords are divided into the areas: “Close”,”Medium” and ”Far” as a function of distance from the tagging location (Figure 6 & Table 2). The fish are divided into groups according to fork lengths, where small represents fish <45 cm, medium fish between 45 and 50 cm and large fish >50 cm. The probabilities are given as a function of date and smolt length (cm). Contour lines represent weekly probabilities. Estimates were retrieved from the most supported model shown in Table S6 and S7.

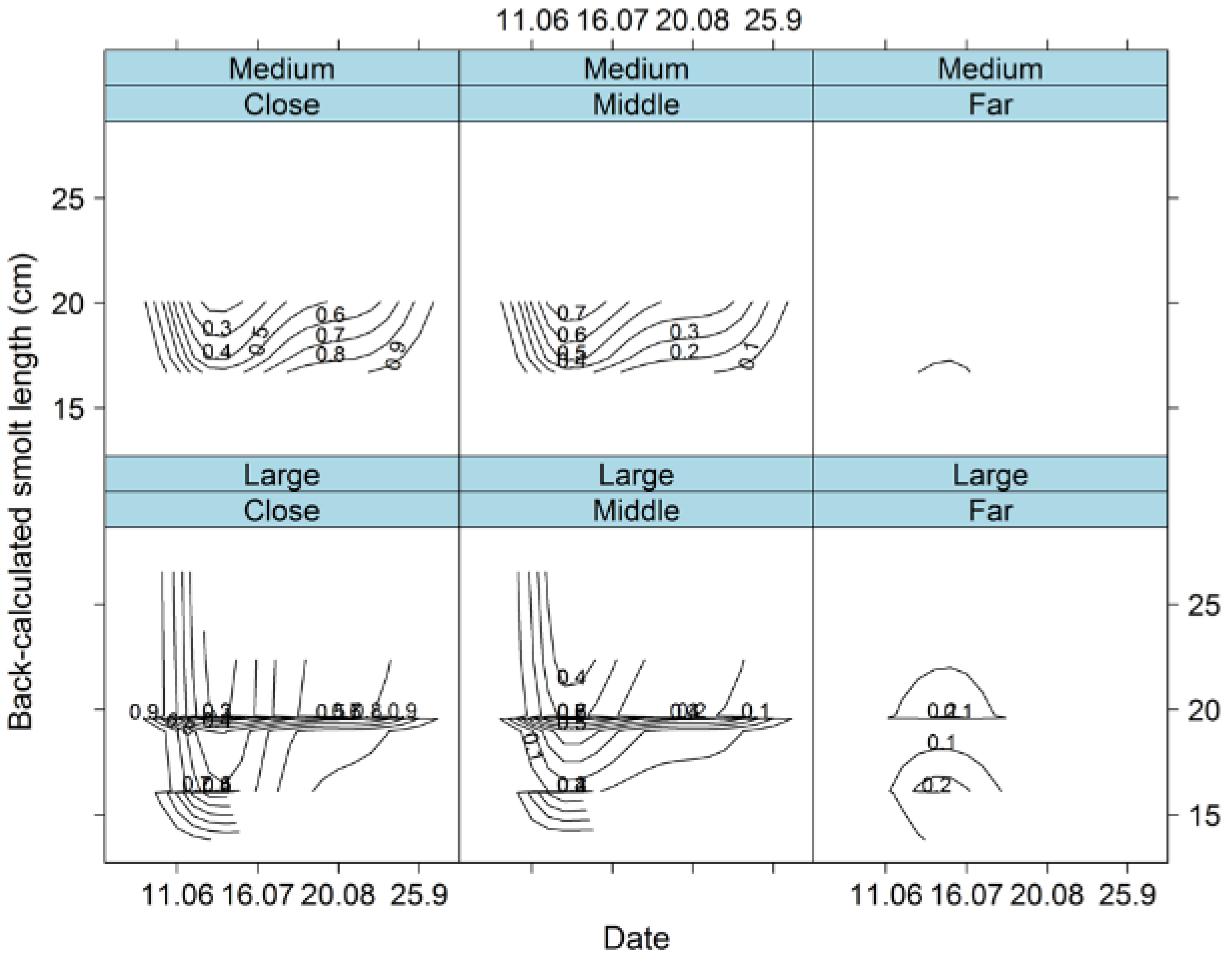


Figure 12. VGAM-based prediction plot of fjord area use for Neiden brown trout in 2015. The fjords are divided into the areas: "Close","Medium" and "Far" as a function of distance from the tagging location (Figure 6 & Table 2). The fish are divided according to fork lengths, where small represents fish <45 cm, medium fish between 45 and 50 cm and large fish >50 cm. The probabilities are given as a function of date and smolt length (cm). Contour lines represent weekly probabilities. Note that no detections were registered for small fish. Estimates were retrieved from the most supported model shown in Table S8 and S9.

3.3.1.3 Sandnes brown trout

In 2014, the model selection process favored a VGAM-model where smolt length, fork length at tagging and time had interacting effects on the fjord area use for Sandnes brown trout. This model attained 24 units lower AICc values than the second-most supported model (Table S10).

The Sandnes brown trout was most likely to be detected in the “Close” area (Figure 13). Only the simplest prediction plot (Figure 8) was made for the Sandnes brown trout in 2015 because only one individual migrated out of the “Close” area (individual ST6, Figure S4). In 2015, most fish were below 45 cm in fork length and had relatively short smolt lengths (L_S<20cm). There were no detections of large fish (L_F >50cm). The fish with short smolt lengths were more likely to be detected in the “Far” area.

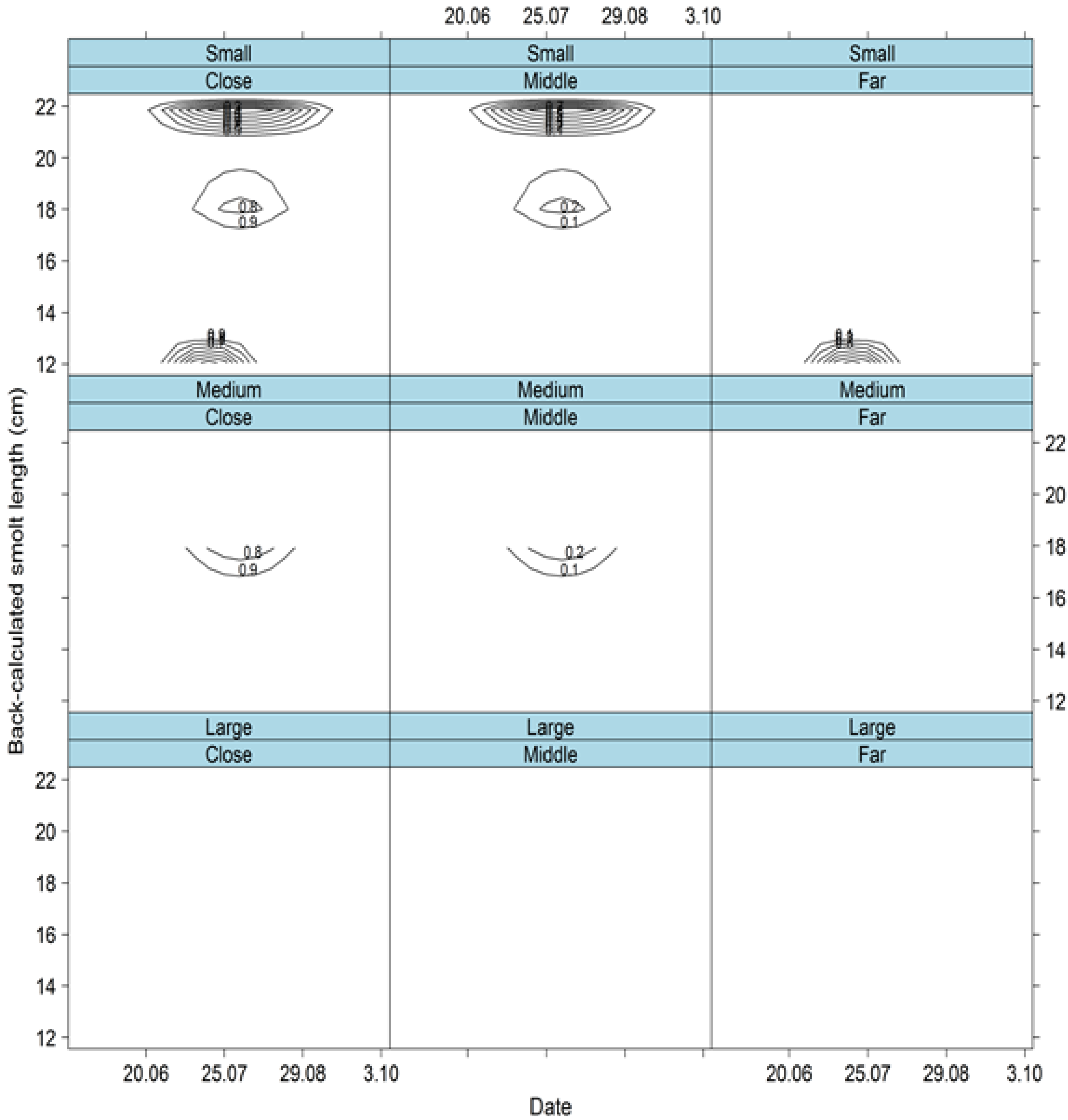


Figure 13. VGAM-based prediction plot of fjord area use for Sandnes brown trout in 2014. The fjords are divided into the areas: "Close","Medium" and "Far" as a function of distance from the tagging location (Figure 6 & Table 2). The fish are divided according to fork lengths, where small represents fish <45 cm, medium fish between 45 and 50 cm and large fish >50 cm. The probabilities are given as a function of date and smolt length (cm). Contour lines represent weekly probabilities. Note that there are no detections registered for large fish in this plot. Estimates were retrieved from the most supported model shown in Table S10 and S11.

3.3.1.4 Høybukt brown trout

The most supported model for Høybukt trout included fork length and time since tagging, but not smolt length. The second-most supported model attained AICc=1.18 units higher than the most supported model (Table S12). The likelihood of a Høybukt brown trout to be in the “Close” area after 16th of July was lowest for individuals with fork lengths between 42 and 50 cm. The model predicted a very low likelihood for Høybukt brown trout of any fork length to be detected in the “Middle” area, and it was very likely for individuals of all fork lengths to be detected in the “Far” area.

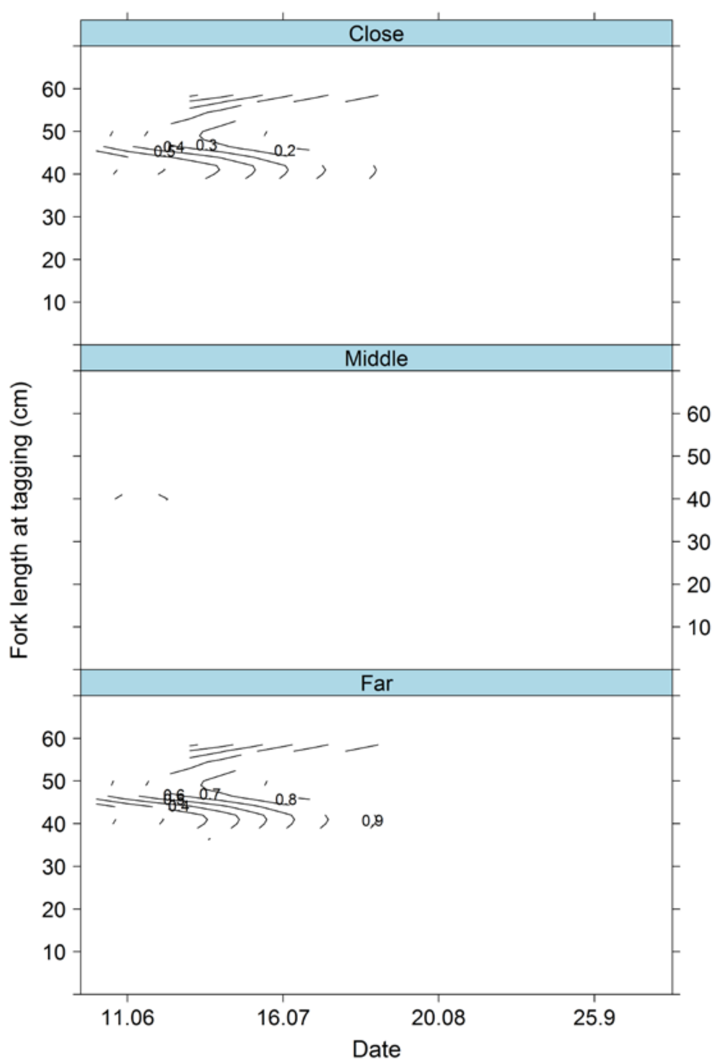


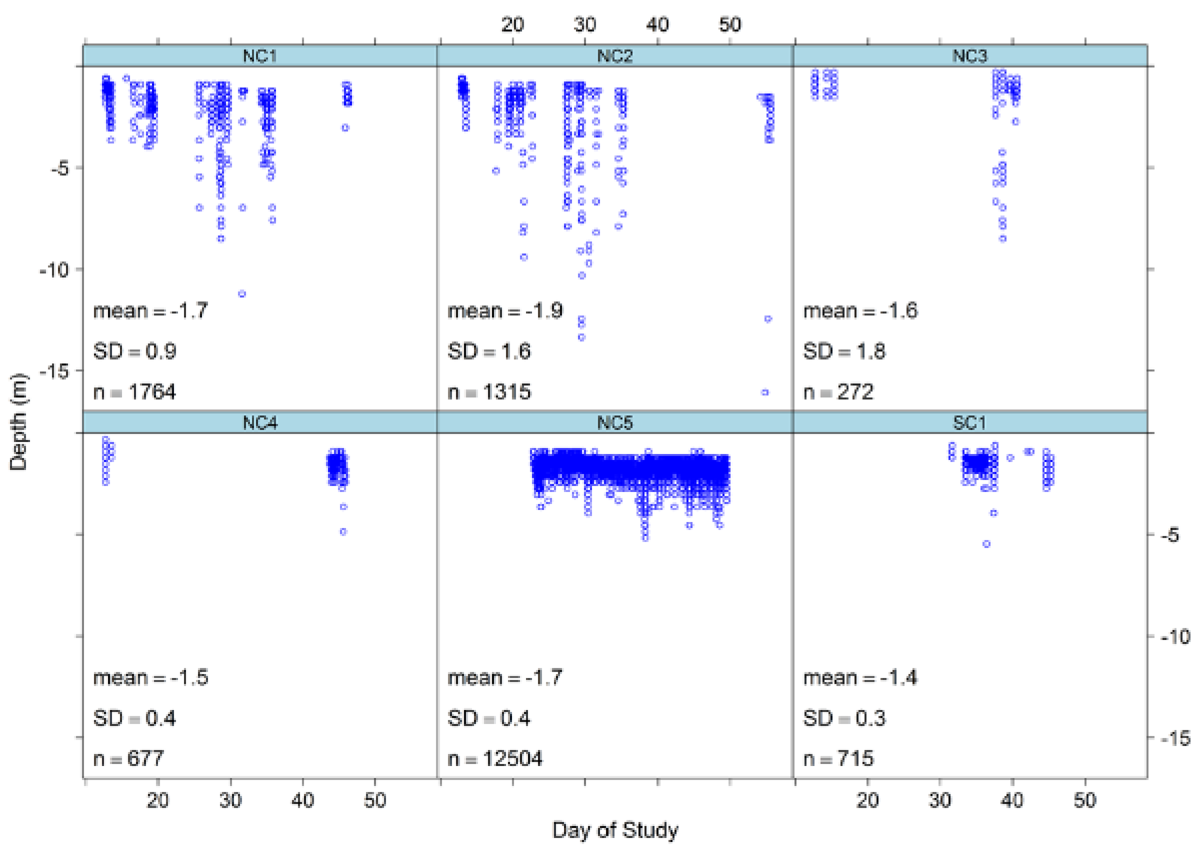
Figure 14. VGAM-based prediction plot of fjord area use for Høybukt brown trout in 2015. The fjords are divided into the areas: “Close”, ”Medium” and ”Far” as a function of distance from the tagging location (Figure 6 & Table 2). The probabilities are given as function of date and fork length at tagging (cm). Contour lines represent weekly probabilities. Estimates were retrieved from the most supported model shown in Table S12 and S13.

3.4 Depth use

The average depth uses of the different tagged groups in 2014 were 1.7±0.2 m (SE) for Braselv Arctic charr, 1.8±0.1 m for Neiden brown trout and 1.7±0.14 m Sandnes brown trout (Table S15). In 2015, the average depth use of Braselv Arctic charr was 0.8±0.2 meter, Neiden brown trout 2.1±0.2 m, Sandnes brown trout 1.9±0.2m and Høybukt brown trout 1.1±0.15 m (Table S17).

Some individuals of both species made occasional deep dives, and the deeper dives were mostly recorded during late periods of their marine migration (Figure 15). Both species used shallow depths (0-3m) during the first part of their marine residency. In 2015 the Artic charr deep dives were deeper, down to the double of the deepest dives in 2014 (max depth at 16m in 2014 and multiple dives at 25-32m in 2015). There is no noticeable difference between the deep dives in 2014 and 2015 for the brown trout.

A



B

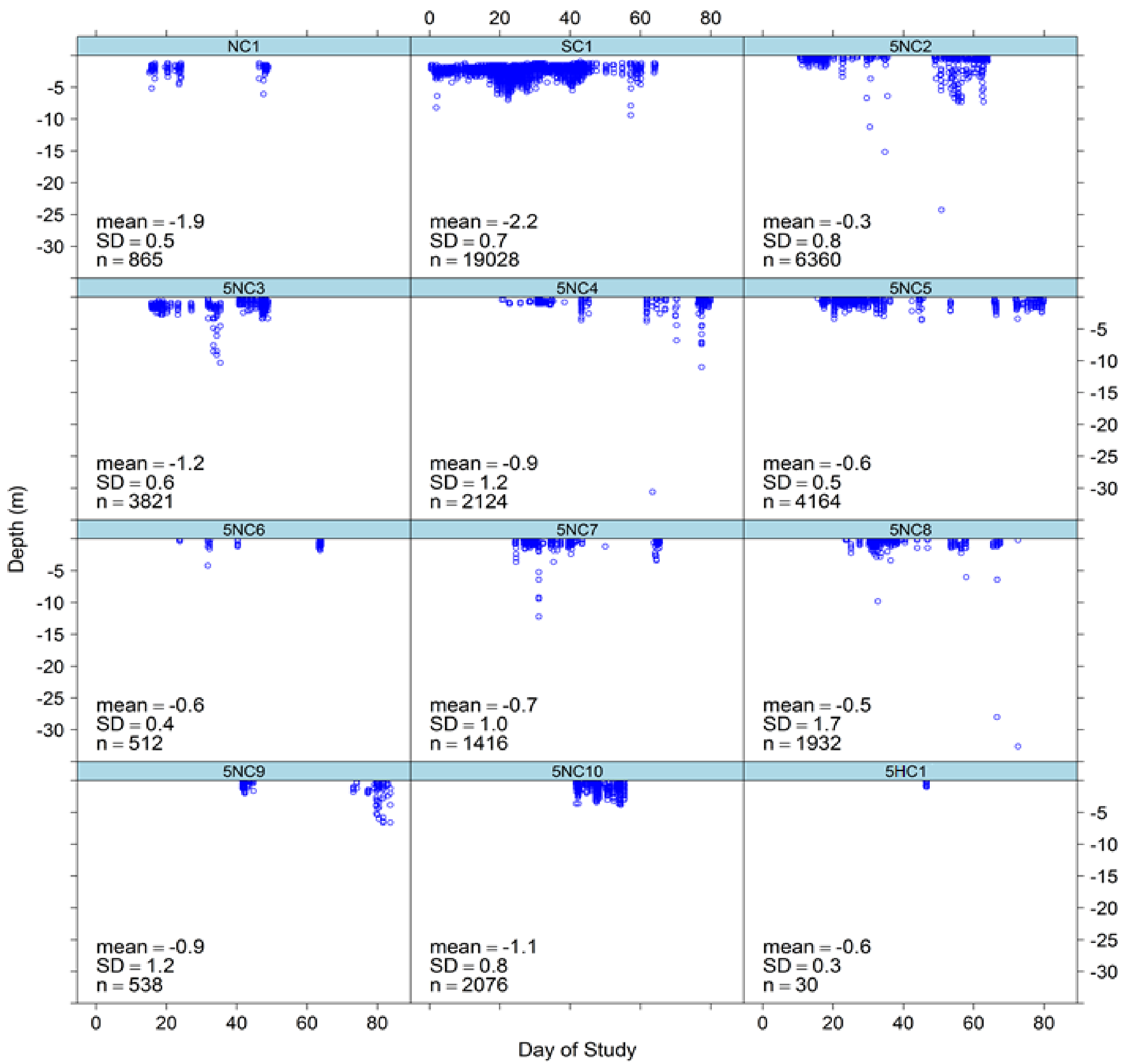


Figure 15: Individual depths recorded for acoustically tagged Arctic charr in the Neiden and Bøkfjord system in 2014 (A) and 2015 (B) as a function of time (day 1 = 23rd of May in 2014 and 14th of May in 2015). n = number of detections. NC = Arctic Charr caught and tagged in the Bras River in 2014, SC = Arctic Charr caught and tagged in the Sandnes River mouth in 2014, HC = Arctic Charr caught and tagged the Høybukt bay 2015, 5NC = Arctic Charr caught and tagged in the Bras River in 2015, 5HC = Arctic Charr caught and tagged in the Høybukt bay in 2015. Note different x- and y-axis scaling during the two years.

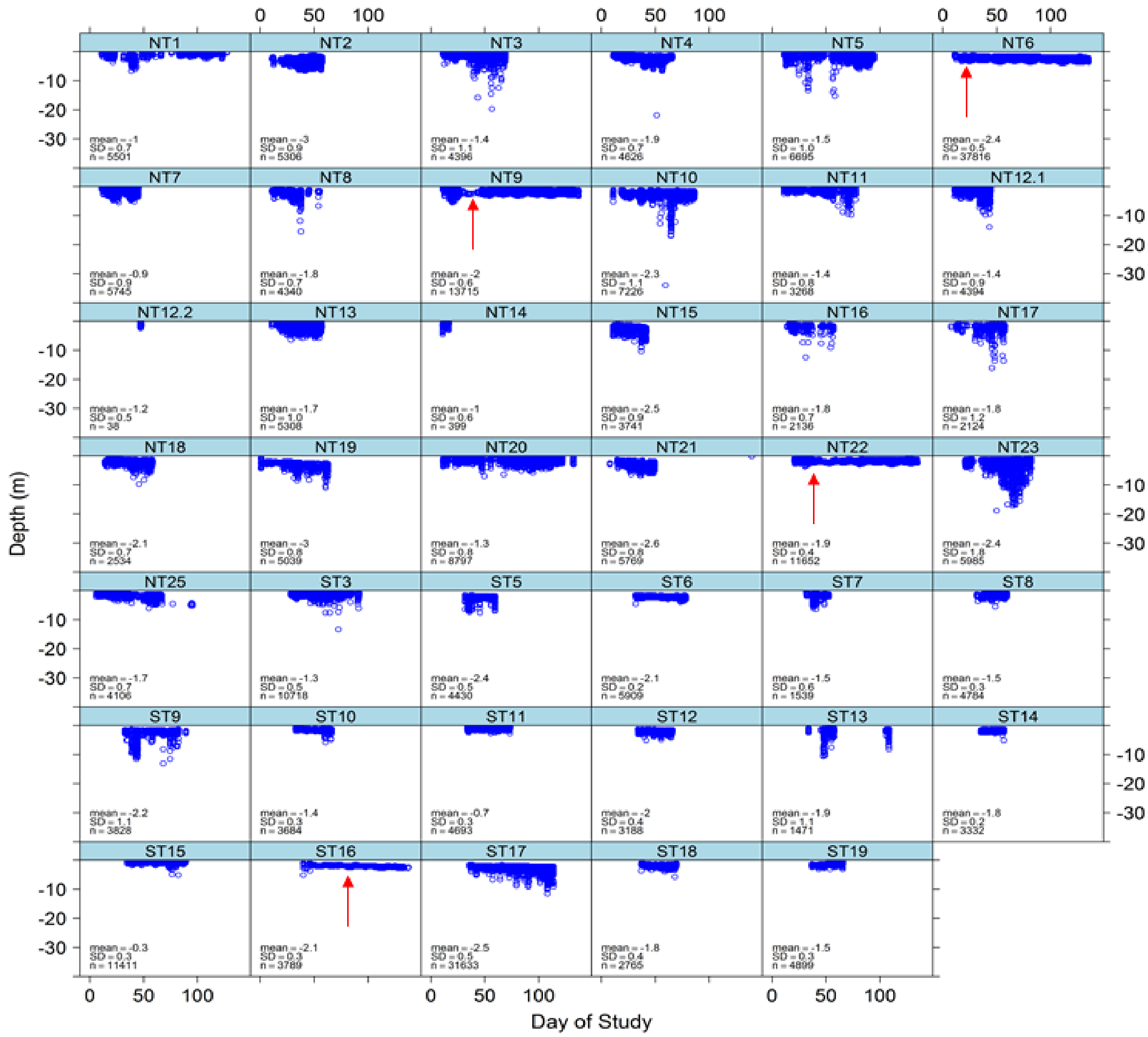


Figure 16: Individual depths recorded, in meters, for acoustically tagged brown trout in 2014 in the Neiden and Bøkfjord system as a function of time (day 1 = 23rd of May). Red arrows indicates death or tag rejection on ID=NT6, NT9, NT22 and ST16. Refer to Table S1 for date of death/tag rejection. n = number of detections. NT = brown trout caught and tagged in the Neiden River in 2014, ST = brown trout caught and tagged in the Sandnes River mouth in 2014.

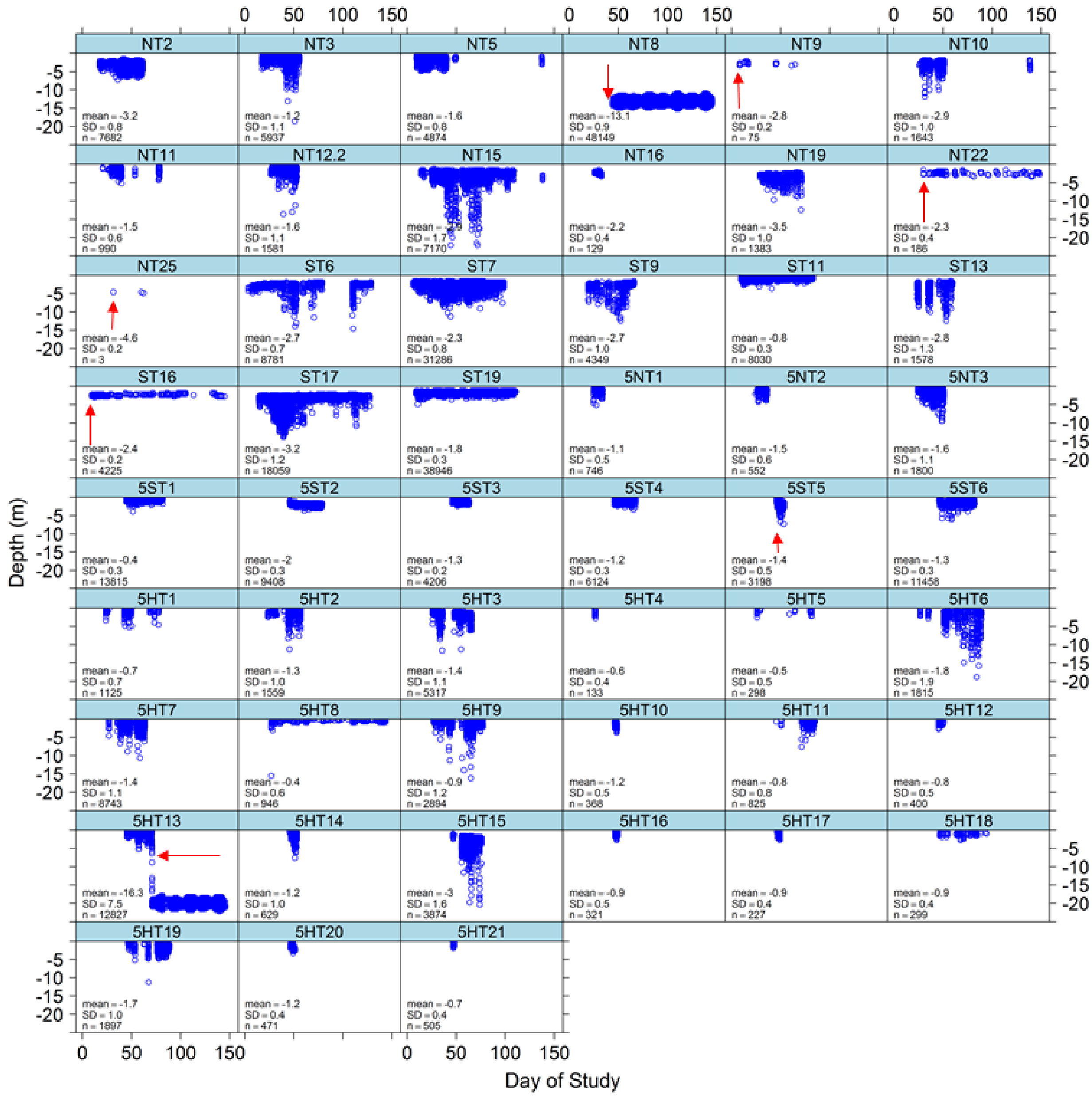


Figure 17: Individual depth detected, in meters, for acoustically tagged brown trout in 2015 in the Neiden and Bøk fjord system as a function of time (day 1 = 14th of May). Red arrow indicates death or tag rejection for ID=NT8, NT9, NT22 ,NT25, ST16, 5ST5 and 5HT13. Refer to Table S1 for date of death/tag rejection. n = number of detections. NT = brown trout caught and tagged in the Neiden River in 2014, ST = brown trout caught and tagged in the Sandnes River in 2014, 5NT = brown trout caught and tagged in the Neiden River in 2015, 5ST = brown trout caught and tagged in the Sandnes River mouth in 2015, 5HT = brown trout caught and tagged in the Høybukt bay in 2015. Note the different y-axis scaling compared to the previous figure.

3.4.1 Drivers of depth use

The most supported LME-model for depth use included both time and fork length for all fish groups during both study years. The most supported model attained AICc=403 units lower than the second-most supported model for 2014 (Table S14) and AICc=641 units lower for 2015 (Table S16).

Large individuals of all groups used larger depths than smaller individuals during both years, with the exception of Høybukt brown trout. Høybukt brown trout had the same depth use pattern early in the season, but had a negative relationship between depth use and fork length later in the season (Figure 18-19).

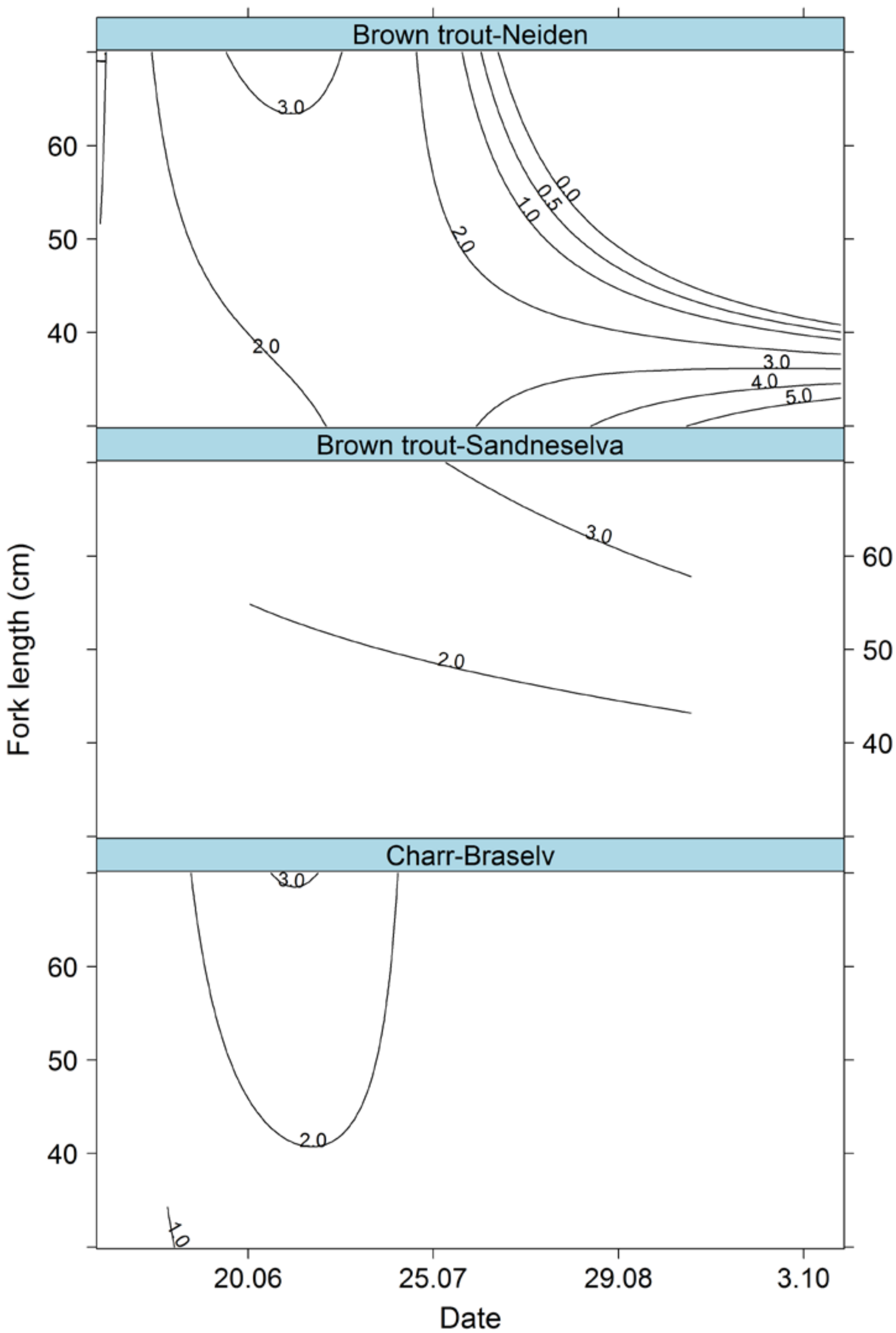


Figure 18. LME-based prediction plots of depth use (m) for Neiden brown trout (top), Sandnes brown trout (middle) and Braselv Arctic charr (bottom) in 2014. The predictions are given as a function of date and fork length at tagging (cm). Contour lines represent daily predicted depth in meters. Estimates were retrieved from the most supported model shown in Table S14 and S15. The prediction plots are cut where there is lack of data, to avoid misleading extrapolations.

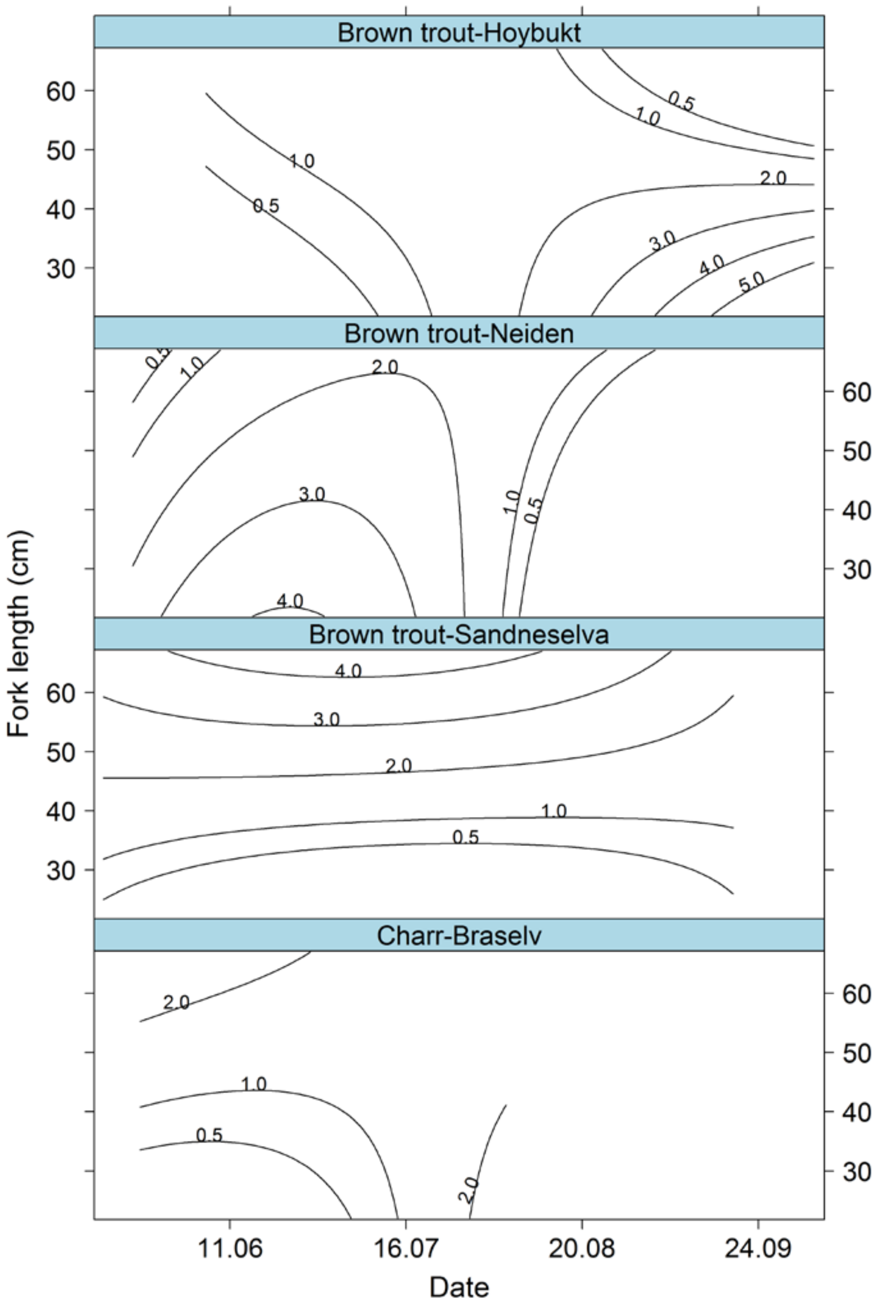


Figure 19: LME-based prediction plot of depth use (m) for Høybukt brown trout (top), Neiden brown trout (2nd from top), Sandnes brown trout (3rd from top) and Braselv Arctic charr (bottom) in 2015. The predictions are given as a function of date and fork length at tagging (cm). Contour lines represent daily predicted depth in meters. Estimates were retrieved from the most supported model shown in Table S16 and S17. The prediction plots are cut where there is lack of data, to avoid misleading extrapolations.

3.5 Temperature

The average temperatures used by the different fish groups in 2014 were 10.9±0.47°C (SE) for Braselv Arctic charr, 11.7±0.21°C for Neiden brown trout and 13.8±0.26°C for Sandnes brown trout (Table S19). In 2015, the average temperatures was 9.7±0.37°C for Braselv Arctic charr, 10.6±0.35°C for Neiden brown trout, 11.6±0.35°C for Sandnes brown trout and 11.3±0.27°C for Høybukt brown trout (Table S21).

3.5.1.1 Drivers of temperature use

The most supported LME-model for temperature use included both time and fork length for all groups and both years. The second-most supported model attained AICc=13 853 units lower than the best model for 2014 (Table S18) and 3 724 units lower for 2015 (Table S20).

There was a negative relationship between fork length and water temperatures amongst tagged Braselv Arctic charr, *i.e*. smaller individuals were registered more frequently at higher water temperatures (Figure 20). In general, the largest Neiden brown trout (L_F>50cm) were predicted to use warmer water than smaller individuals. In 2014, the Neiden brown trout used higher temperatures early in the season, while later the smaller individuals used warmer water. The largest Sandnes brown trout (L_F>50cm) were more likely to use warmer waters in 2014,while the relationship was reversed in 2015 (Figure 21). Høybukt brown trout used warmer waters at shorter fork lengths.

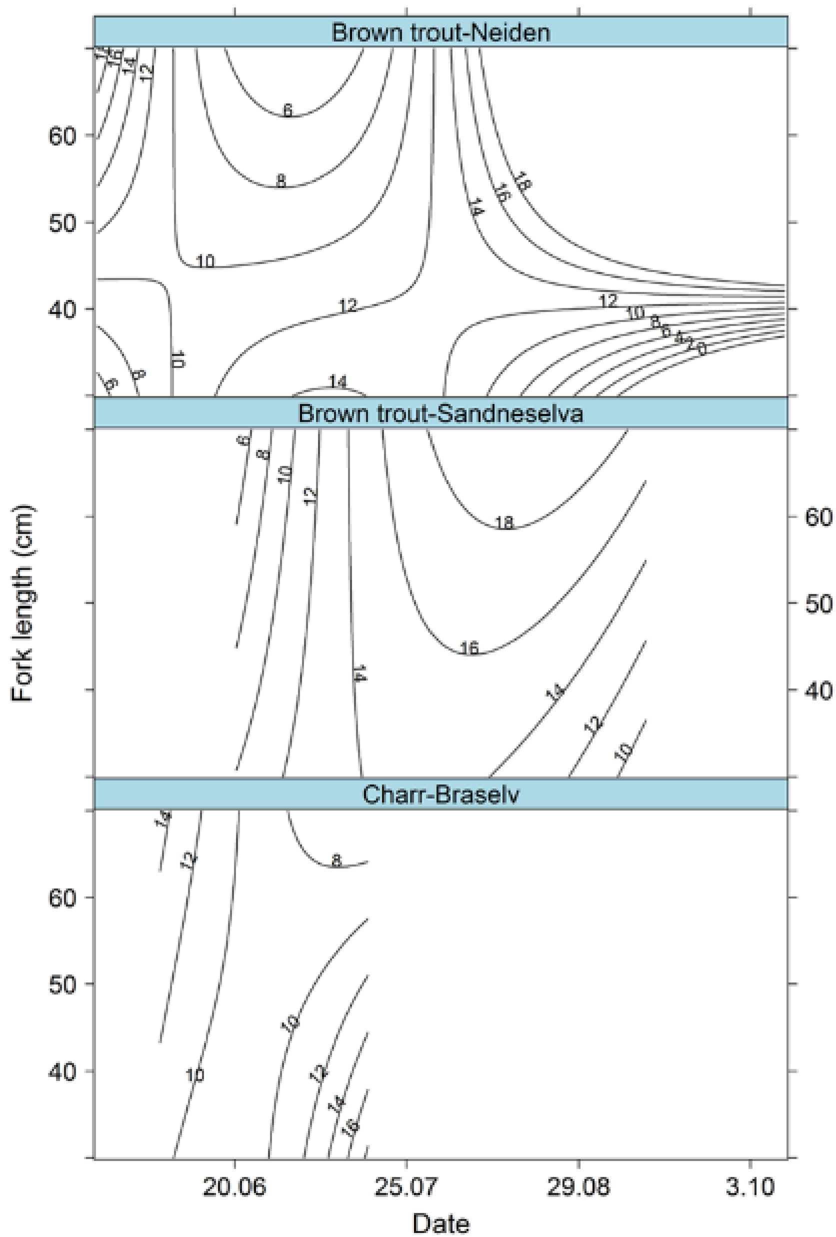


Figure 20: LME-based prediction plot of temperature use (°C) for Neiden brown trout (top), Sandnes brown trout (middle) and Braselv Arctic charr (bottom) in 2014. The predicted temperatures are given as a function of date and fork length at tagging (cm). Contour lines represent daily predicted temperatures in °C. Estimates were retrieved from the most supported model shown in Table S18 and S19. The prediction plots are cut a where there is lack of data, to avoid misleading extrapolations.

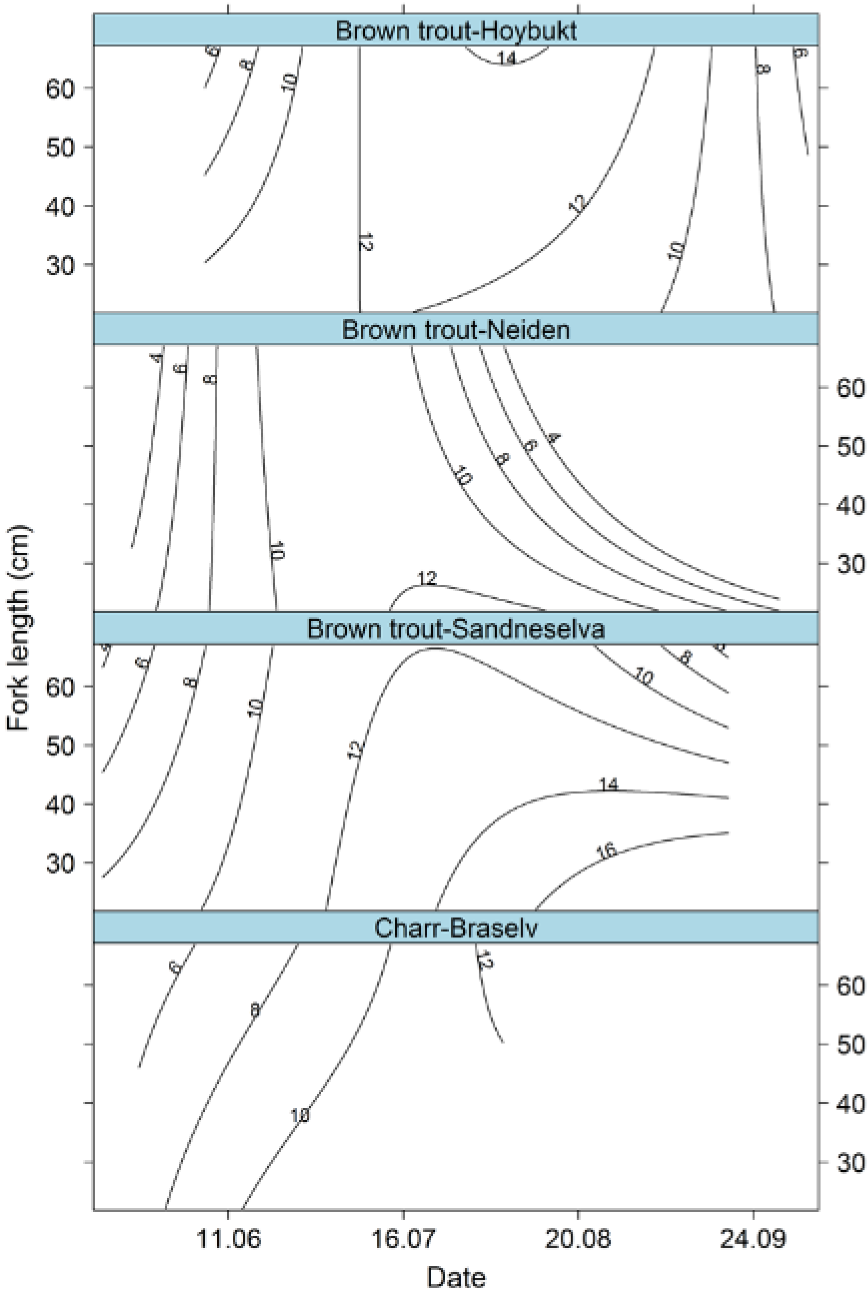


Figure 21. LME-based prediction plot of temperature use (°C) for Høybukt brown trout (top), Neiden brown trout (2nd from top), Sandnes brown trout (3rd from top) and Braselv Arctic charr (bottom) in 2015. The predicted temperatures are given as a function of date and fork length at tagging (cm). Contour lines represent daily predicted temperature in °C. Estimates were retrieved from the most supported model shown in Table S20 and S21. The prediction plots are cut where there are no data, to avoid misleading extrapolations.

3.6 Use of planned harbor areas

The different groups were merged as species during the analysis of the use of the planned harbor areas, *i.e.* the Braselv, Sandnes and Høybukt Arctic charr were merged. The same was done with brown trout. Høybukt brown trout were in addition analyzed alone.

Large individuals of all groups were more likely to be detected in the planned harbor areas. Of the two species, Arctic charr had a greater probability of being detected in these areas (Figures 22-25, Table 4). The Høybukt brown trout (Figure 26) had a much greater probability (probability of 0.999) of being detected in the planned harbor areas than Arctic charr or the merged brown trout. This is because there were detections of Høybukt brown trout during every timeslot through the Høybukt brown trout sea migration period.

The cumulated probability for an Arctic charr with a fork length of 51cm to use the planned harbor areas was estimated to be 0.0021 in 2014 and 2.931×10^{-04}in 2015, while the estimated probability for a brown trout to use these areas in 2014 was 7.647×10^{-07} and 2.465×10^{-06} in 2015 (Table 4).

Model predictions are provided as probabilities over four-day and two-day timeslots for Arctic charr in 2014 and 2015, respectively. The predictions for brown trout are provided as weekly probabilities. See Table S22 - S31 for model selection and parameter estimates.

Table 4. Cumulative probabilities for illustrative individuals at a given fork length (LF) to be detected in any of the planned harbor areas in 2014 and 2015. Refer to Table S22 - S31 for model selection and parameter estimates.

Example	2014	2015
Arctic charr L_F = 51cm	0.0021	2.931×10^{-04}
Brown trout L_F = 50cm	7.647×10^{-07}	2.465×10^{-06}
Høybukt brown trout L_F = 45cm		0.999

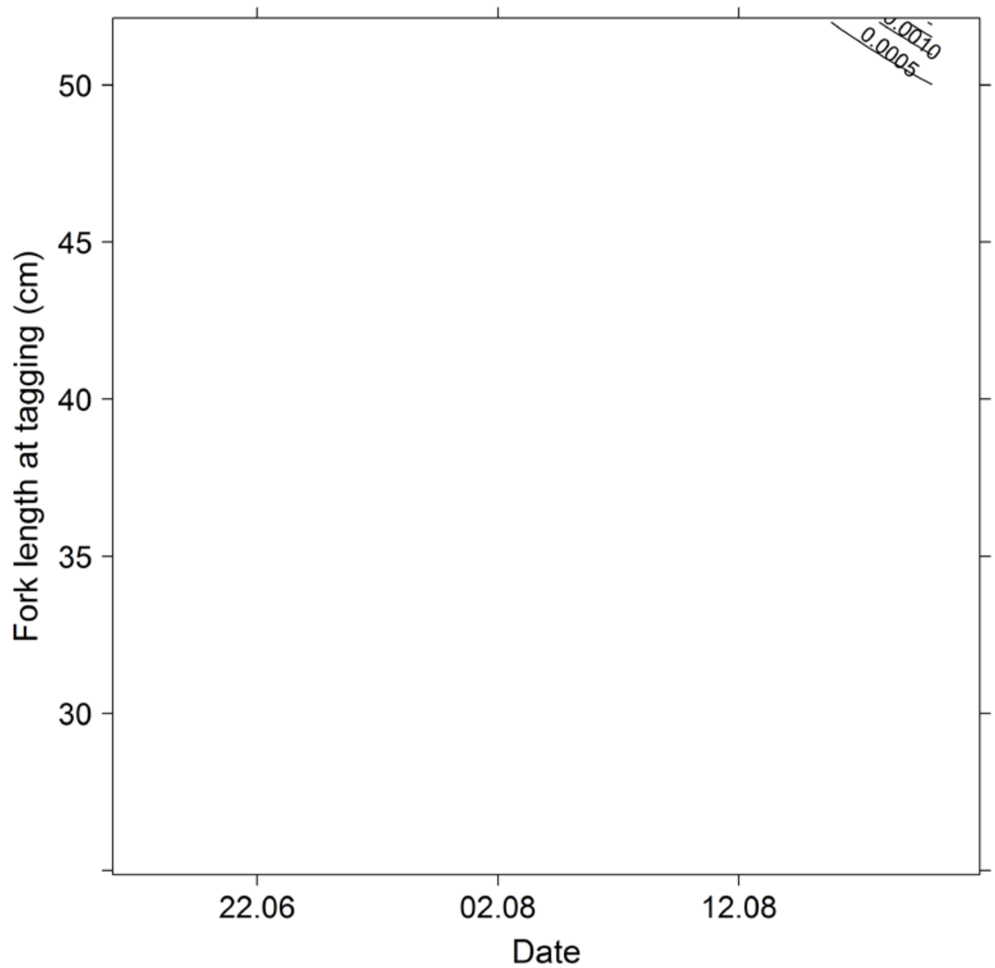


Figure 22. GLMM-based prediction plot of use of the planned harbor areas for Arctic charr in 2014. The probabilities are given as a function of date and fork length at tagging (cm). Contour lines represent four-day-probabilities. Estimates were retrieved from the most supported model shown in Table S22 and S23.

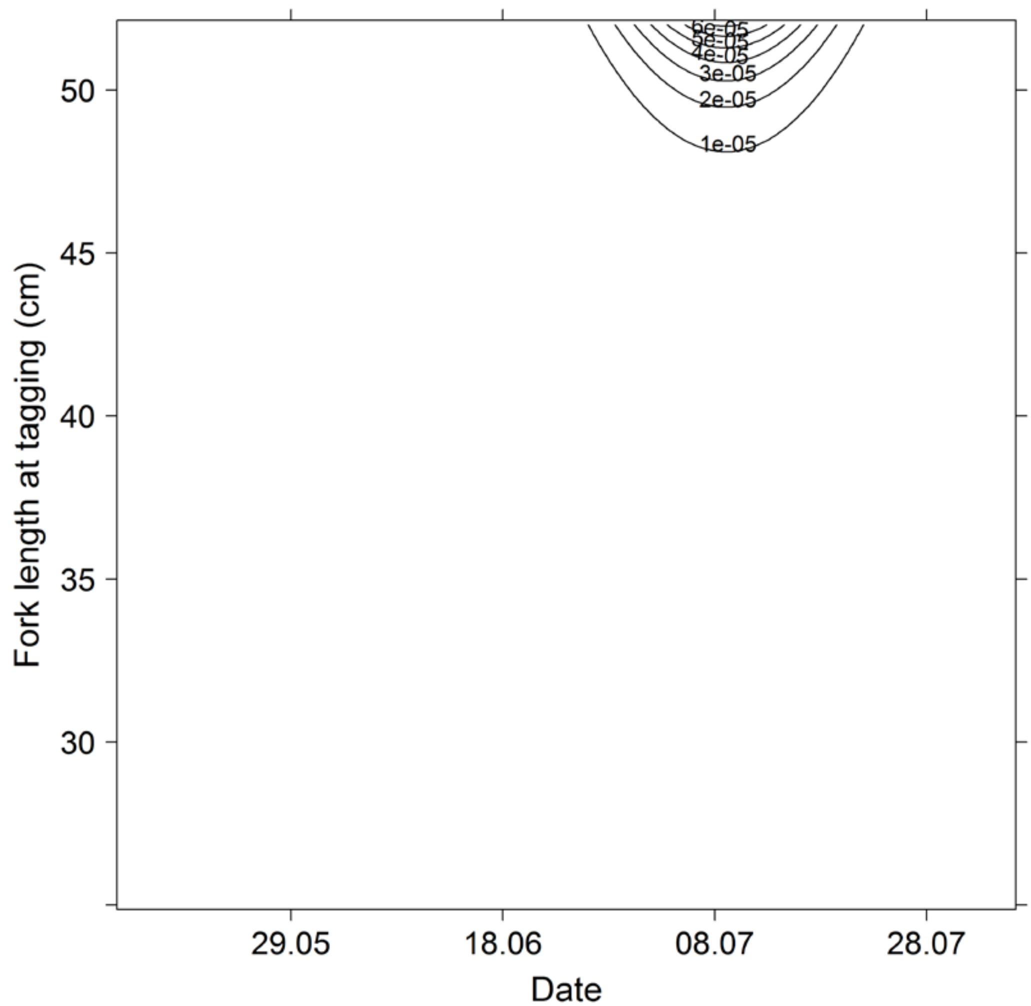


Figure 23. GLMM-based prediction plot of use of the planned harbor areas for Arctic charr in 2015. The probabilities are given as a function of date and fork length at tagging (cm). Contour lines represent two-day-probabilities. Estimates were retrieved from the most supported model shown in Table S24 and S25.

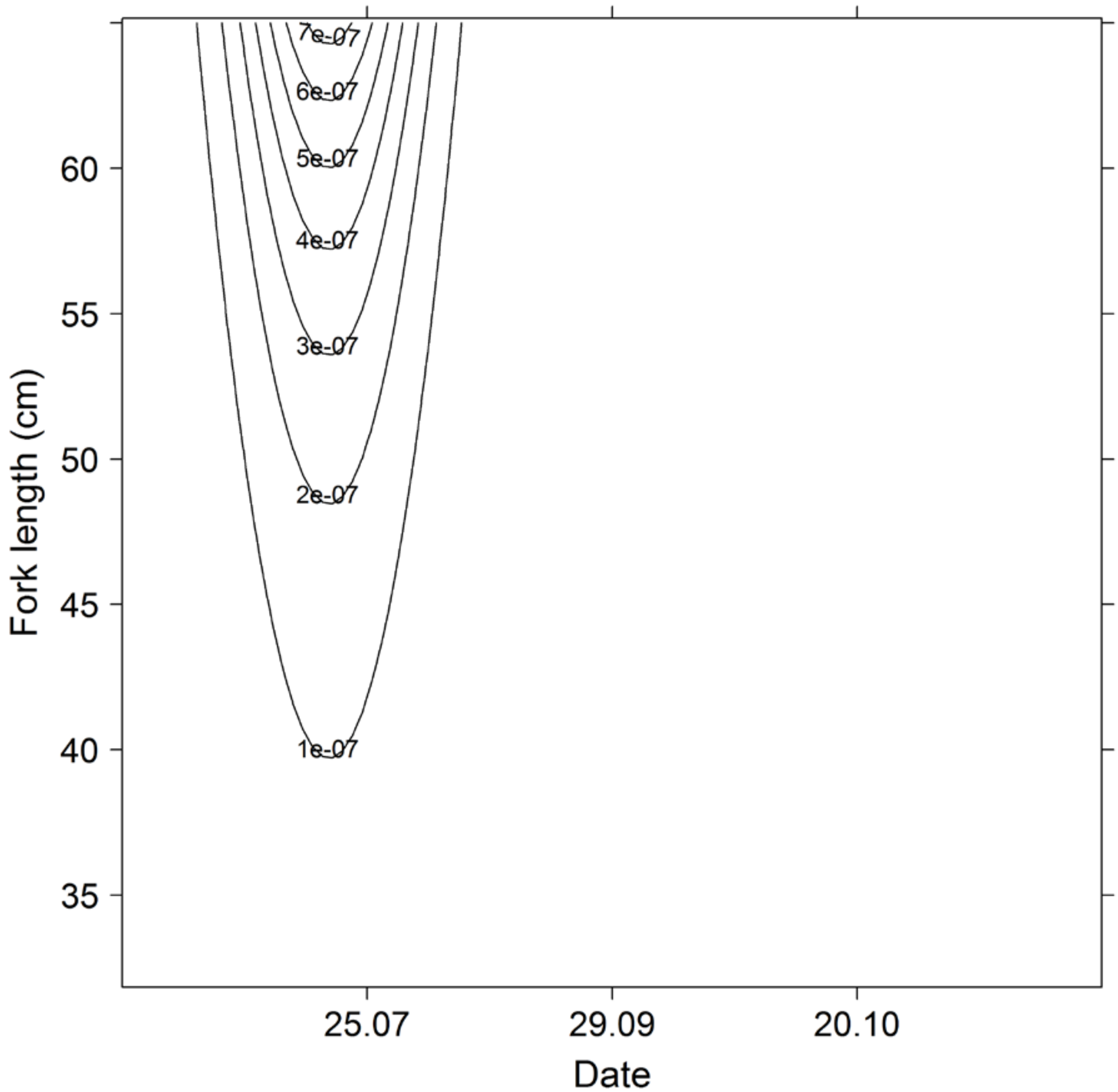


Figure 24. GLMM-based prediction plot of use of the planned harbor areas for brown trout in 2014. The probabilities are given as a function of date and fork length at tagging (cm). Contour lines represent weekly probabilities. Estimates were retrieved from the most supported model shown in Table S26 and S27.

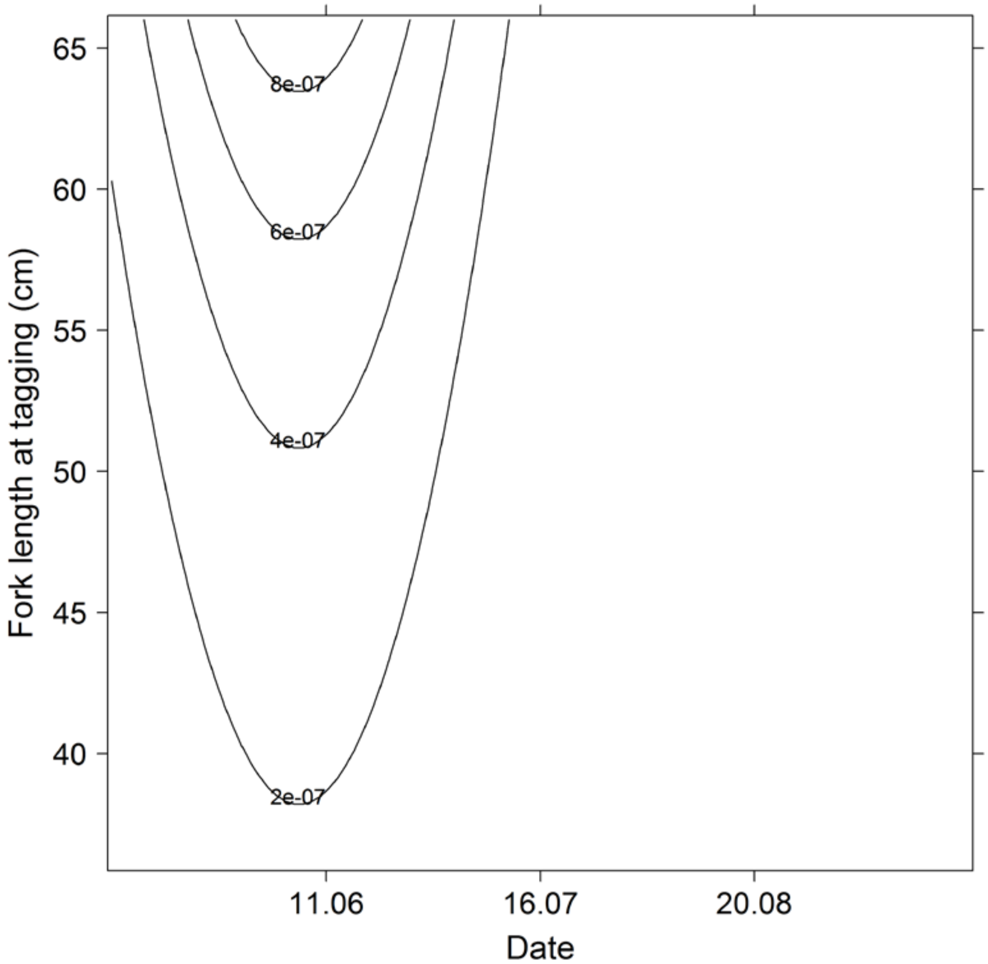


Figure 25. GLMM-based prediction plot of use of the planned harbor areas for brown trout in 2015. The probabilities are given as a function of date and fork length at tagging (cm). Contour lines represent weekly probabilities. Estimates were retrieved from the most supported model shown in Table S28 and S29.

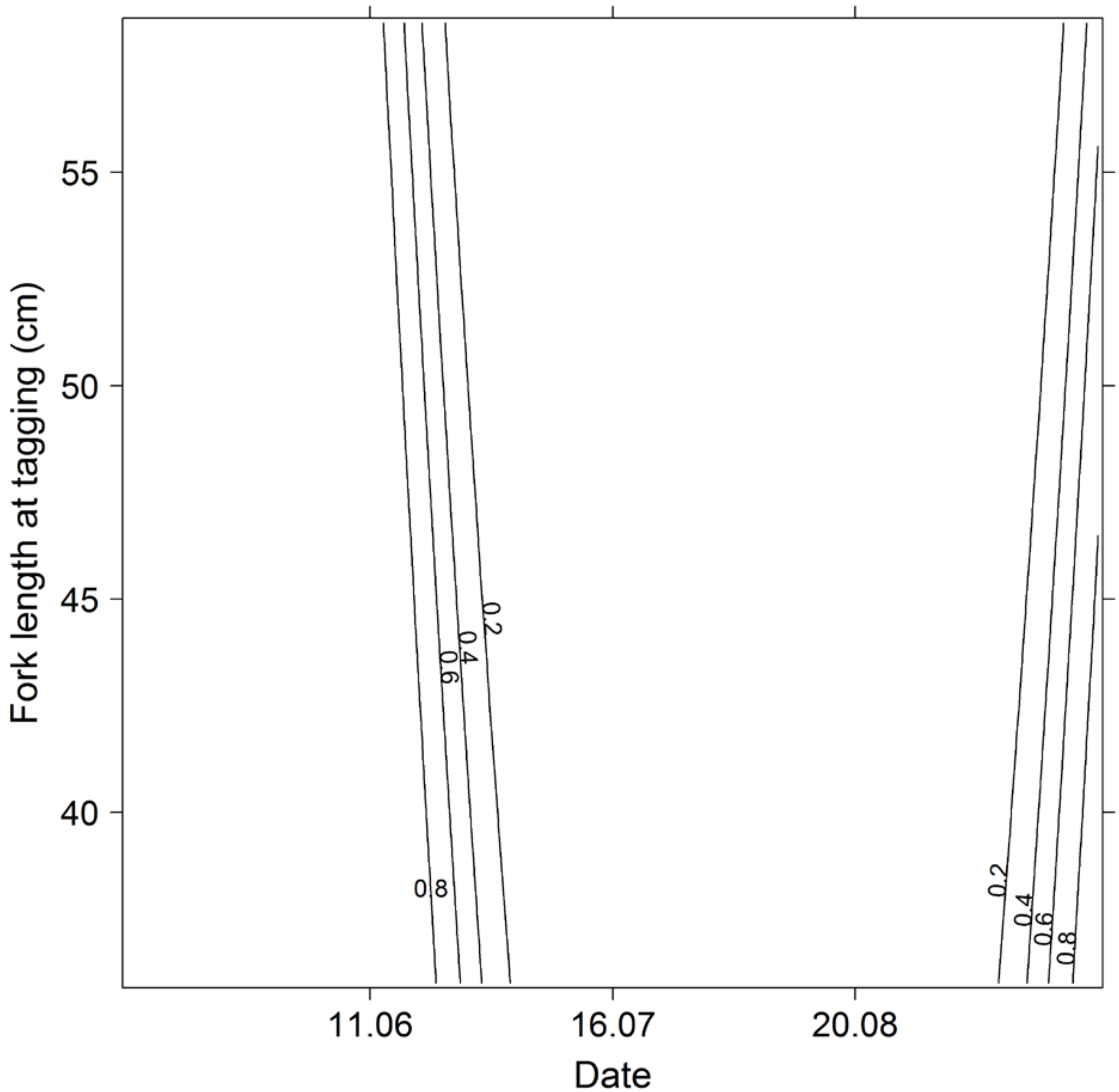


Figure 26. GLMM-based prediction plot of use of the planned harbor areas for Høybukt brown trout in 2015. The probabilities are given as a function of date and fork length at tagging (cm). Contour lines represent weekly probabilities. Estimates were retrieved from the most supported model shown in Table S30 and S31.

4 Discussion

4.1 Fjord area use and its intrinsic drivers

This study documented a difference in fjord area use between Arctic charr and brown trout. Both species used the areas closest to the river outlets more than any other parts of the fjord system. The Arctic charr used areas further out in the fjords to a greater extent than the brown trout, and large individual variation was found within both species.

The documented migratory behavior of Arctic charr, where both the outer fjord areas and the areas close to the tagging rivers were used to great extents, have previously been described in telemetry studies, both in Norway (Jensen et al. 2012; Jensen & Rikardsen 2008; Jensen 2013) and Canada (Morris & Green 2012; Spares et al. 2012). The fjord area use of the tagged Neiden brown trout was also similar to what other studies have found (Berg & Jonsson 1989; Eldøy et al. 2015; Jensen 2013). However, the behavior of the Sandnes brown trout was different, where the vast majority if the tagged fish resided very close to the Sandnes River outlet. Because the Lang fjord is very narrow and shallow and has limited water exchange with the Bøk fjord, the temperature in the Lang fjord is higher than in the rest of the study area. Water temperatures up to 16 °C were documented, which corresponds to brown trout's optimal growth temperature (Larson et al. 2005). When tagged, the Sandnes brown trout was in very good condition. The fjord seem to have easily available food sources and in general be a good habitat, as very few fish left the area.

Both internal and external variables effected the tagged fishes' fjord area use. Day of season and the tagged fish fork lengths were found to be the two most important drivers of the migratory behavior. By including smolt length into the models on brown trout area use, the predictions for this species area utilization were greatly improved. Temperature is also an important factor for which areas of the fjord the fish uses, which again may affect or be affected by the depth use.

The areas close to the river outlets were generally used more frequently in the beginning and in the late part of the fishes' sea residency. This temporal pattern in close-to-estuary area use was similar within-groups in both years. c. The brown trout used significantly larger depths during their marine migration than the Arctic charr, and when the fish resided in areas close to the river outlets the utilized depths were larger and temperatures lower than in other areas. The smallest and largest tagged Arctic charr individuals utilized the areas furthest away from the river mouth, while only the largest brown trout individuals used areas that are more distant. Many of the tagged brown trout individuals largely used the area close to the Neiden River outlet, which can indicate good food conditions in this area.

The Arctic charr used significantly larger depths in 2014 (mean=1.7m) than in 2015 (0.8m). The temperatures registered for 2014 were higher than in 2015. Arctic charr prefer colder water than brown trout (Rikardsen et al. 2007; Spares et al. 2012; Jensen et al. 2014). The depth use is most likely related to which areas the fish feed in. For example, fish residing in the river mouths may be feeding more on the bottom in the tidal zone than fish feeding in shallow bays further out along the coast (Rikardsenet al. 2007). The individuals equipped with tags that transmitted data on depth and temperature in 2015 were smaller than in 2014, which may explain the between-year difference in documented behavior. However, there were few individuals equipped with temperature and depth tags in 2014, which also might have influenced the results.

The fish length effect on migratory behavior has been documented before (Bendall et al. 2005; Davidsen et al. 2014; Jensen et al. 2014), where larger individuals used the areas further out in the fjord more frequently than smaller individuals. The areas the furthest away from the river outlet were used mostly by large individuals, which may be linked to e.g. availability of more suitable prey in these areas (Boel et al. 2014; Davidsen et al. 2014; Jonsson & Jonsson 2011a). Intraspecific competition in the river outlets may also be a reason why some individuals choose to migrate further (Eldøy et al. 2015).

Similar to the findings in this study, studies in southern Norway also found that smolt length was a driver of what parts of the fjords brown trout used (Dzadey 2014; Ruud 2015). This is interesting, as early life-history events can provide information about fish behavior later in life. The findings indicate that inherent traits controls which areas these fish use at sea. Determining the intrinsic reasons for these differences lies outside the scope of this study, but it seems likely that individual variation in factors such as appetite may control the fishes' behavior. In Atlantic salmon, it is known from stock-enhancement programs that smolt size can affect survival (Jonsson et al. 2003). It is also known from Arctic charr that growth and appetite is related to timing of the smoltification process (Rikardsen et al. 1997). A future deeper understanding how these factors affect anadromous fish behavior will increase our understanding of these species, and aid mangers in e.g. stock enhancement programs.

The average length of the sea residency of the Arctic charr documented in this study (on average 32 and 43 days for 2014 and 2015, respectively) was rather short for 2014 compared to the 45-55 days that has been found in earlier studies (Berg & Berg 1993; Jensen 2013; Rikardsen, A. H. et al. 2007). Many of the Braselv Arctic charr were kept in a submerged cage for up to 14 days in 2014 while awaiting captures of bigger fish. This might have led to an underestimation of the sea migration period in 2014. The marine residency time of brown trout (60 days in 2014 and 54 days in 2015) was also short compared to other studies in northern Norway (Berg & Berg 1989; Jensen & Rikardsen 2012; Klemetsen et al. 2003) (Jensen et al. 2014), where brown trout resided at sea for up to three months. Again, this may be due to the tagging and release time of the fish, as many were caught in the estuaries and sea and may have resided there for periods before tagging.

4.2 Reproducibility

The latitude of the study area, the inclusion of multiple rivers and the combination of two study species over two years make this study unique. The fjord system studied i is complex, with big differences in depth, width and length among the different fjords. Acoustic telemetry studies including both Arctic charr and brown trout in northern Norway have previously been performed (Jensen 2013; Jensen et al. 2014). The findings from these studies showed that the migratory behavior documented here resembles that in the Alta fjord further west in Finnmark county and the Lyngen fjord in Troms county. The inclusion of smolt length as an individual covariate greatly increased the statistical prediction precision, and should be considered to be included in future studies of migratory behavior of brown trout. Acoustic telemetry seems to be a good approach for studies of this kind, and thus have a high degree of reproducibility.

Understanding what controls the behavior of fish from different populations experiencing different environmental conditions is a key to understanding the species as a whole. Detangling the factors controlling the migratory behavior of brown trout in both northern and southern populations will greatly increase the understanding of this very plastic species (Jonsson & Jonsson 2011a; Klemetsen et al. 2003). The Sandnes brown trout might be the most suitable for comparing with southern populations, based on the higher temperatures the fish experience at sea. However, due to the special formation of the Lang fjord and the lower temperatures the fish experience in the rest of the fjord system, drawing direct parallels between the Sandnes brown trout and populations located further south should be avoided. However, comparing fjord use of brown trout living under such contrasting conditions may shed light on general drivers of this species' fjord behavior.

The models used in this study are fully validated methods to predict habitat use for fish (Knudby et al. 2010;, Thomas W. 2010, Bøe 2013, Freitas et al 2015), and can be utilized when studying migration behavior of different species in different habitats. Mixed effects modeling is an effective tool when analyzing data sampled over time or at different locations (Zuur et al. 2009).

4.3 Limitations and justifications

The VGAM-models used in this thesis work are not sensitive towards the amount of acoustic detections retrieved during the study, because only one zone is assigned for each timeslot (Zuur et al. 2009). An increasing amount of individual detections per zone and area will reduce the uncertainty of the zone assignment. By merging the zones into larger areas, the margin of error became even less prominent. When using the LME-models for temperature and depth use, individuals were modelled as a random effect which, at least largely, corrects for observation bias in number of detections per individual and also explicitly model intra-individual dependency in the error structure

All fishing equipment is selective in one way or another (Hard et al. 2008; Jurvelius et al. 2011). The selectivity might be based on individual body size, life stage, activity level and/or species. Both active and passive gear was used in this project to capture a wide specter of individuals, but parts of the different groups may not have been captured due to the described selectiveness. There was no sign of death or tag rejections in the Artic charr, which was captured using a trap. The use of rod and reel and gill-net capture can theoretically have influenced the results of this study by adding an increased mortality rate in the tagged brown trout. However, most fish migrated from the tagging location and were documented to be alive for days and weeks after tagging, wherefore mortality caused by capture seems unlikely. Gill-net capture and possibly rod and reel capture have been documented to have an impact on fish migration behavior in rivers (Mäkinen et al. 2000). It is therefore a possibility that the fishes migratory behavior may have been affected on a short time scale. Tag rejection rates have been documented to differ between Arctic charr and brown trout (Jensen 2013), and may explain the higher rates of tags from brown trout remaining stationary at the bottom than tags from Arctic charr.

An upstream migration trap was used in the Bras River during the summer 2014 in relation to another scientific project. The individuals captured using the trap was longer than the ones captured during river descent and tagged in this study. This indicate that the length of the Arctic charr used in this study was probably not representative of the whole population spawning in the Braselv Lake. The larger individuals may have entered the sea before the trap was deployed, or during very high tides in 2014 when the trap was fully submerged. The trap was also out of operation for one week in 2015 due to very high water levels and ice drifting down the river which destroyed the trap.

Because there were no receivers in the outermost part of the Kjø fjord in 2014, there is no way of knowing how far out in the Kjø fjord the fish resided during this study year. When there was receiver coverage in this area in 2015, only one individual of each species was detected in this area. It therefore seems like very few individuals migrate to the outermost parts of the Neiden and Bøk fjord system, but inclusion of this receiver transect in future study years is recommended. No previous acoustic studies in northern Norway have studied if the fish uses the outermost parts of the fjords close to more open oceans.

No brown trout tagged upstream in the Neiden River during spring 2015 were detected at sea, and few brown trout tagged in 2014 returned to the sea in 2015. This may be caused by fish not surviving spawning and/or overwintering, or it may indicate that the brown trout spend one year as immature individuals in the river before spawning. This type of behavior have been documented in brown trout in the Tana River located approximately 90 km north-west of the Neiden River (pers. comm. Narve Stubbraaten Johansen, Tanavassdragets fiskeforvaltning). The tags used on most of the Artcic charr in 2014 had short battery life times, and only one individual tagged during this study year was detected in 2015.

In future studies it will be important to study the smolt migration behavior of both Arctic charr and brown trout, as this is the most sensitive life stage of salmonids (Jonsson & Jonsson 2011a). Novel acoustic depth tags have recently been developed for smolt allowing for detailed fjord use studies in even these small individuals.

4.4 Management implications

River outlets are important feeding areas for both Arctic charr and brown trout (Jonsson & Jonsson 2011b; Klemetsen et al. 2003). These areas are especially important to protect from negative impact from humans. The areas around Tømmerneset and the planned harbor areas were sparsely used by both species. The shoreline on Tømmerneset with its planned harbor areas has a relatively low degree of human impact today. With an eventual building process, the marine environment could be affected and the quality as a habitat for anadromous fish reduced.

Fish are caught in the Høybukt bay and surrounding area with different passive and active equipment. Regulations state that it is not allowed to purposely fish for Arctic charr or brown trout in the sea with regular nets (Lakse- og innlandsfiskloven § 2 og § 33; Åpningsforskriften §1).

To reduce negative impact on the fish that uses the planned harbor areas, regulations like only allowing rod and reel could be implemented. To protect the important Arctic charr population in the Braselv watercourse, the same regulations could be used in the Braselv bay, as well as other bays surrounding watercourses harboring this species (Jensen 2013).

Today the minimum size limit of anadromous salmonids is 30 cm in northern Norway (Åpningsforskriften §3). Maximum size limit is an upcoming management tool to avoid the removal of the fish that contribute the most to the recruitment in the rivers. This study has shown that large fish used the planned harbor areas more than smaller ones. If there is concern about negative trends in recruitment in the Arctic charr and brown trout populations, a maximum size limit (Berkeley et al. 2004; Francis et al. 2007) (e.g. 45cm for Arctic charr and 50cm for brown trout) could be utilized as a management tool in the Neiden and Bøk national salmon fjord. Most of the tagged fish in this study was below this maximum size limit. If a management tool is needed, it should be easy to understand for the fishers and easy to enforce for management institutions.

As the global temperatures are increasing, knowledge on a cold-water-adapted species like Artic charr is becoming increasingly important (Lassalle & Rochard 2009; Winfield et al. 2010). Today there is not enough information about if and how this species will adapt to increasing water temperatures. Continued research on both brown trout and Arctic charr is needed to continue to build a strong knowledge base which managers can use to protect these potentially vulnerable species (Jensen 2013).

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6 Appendix

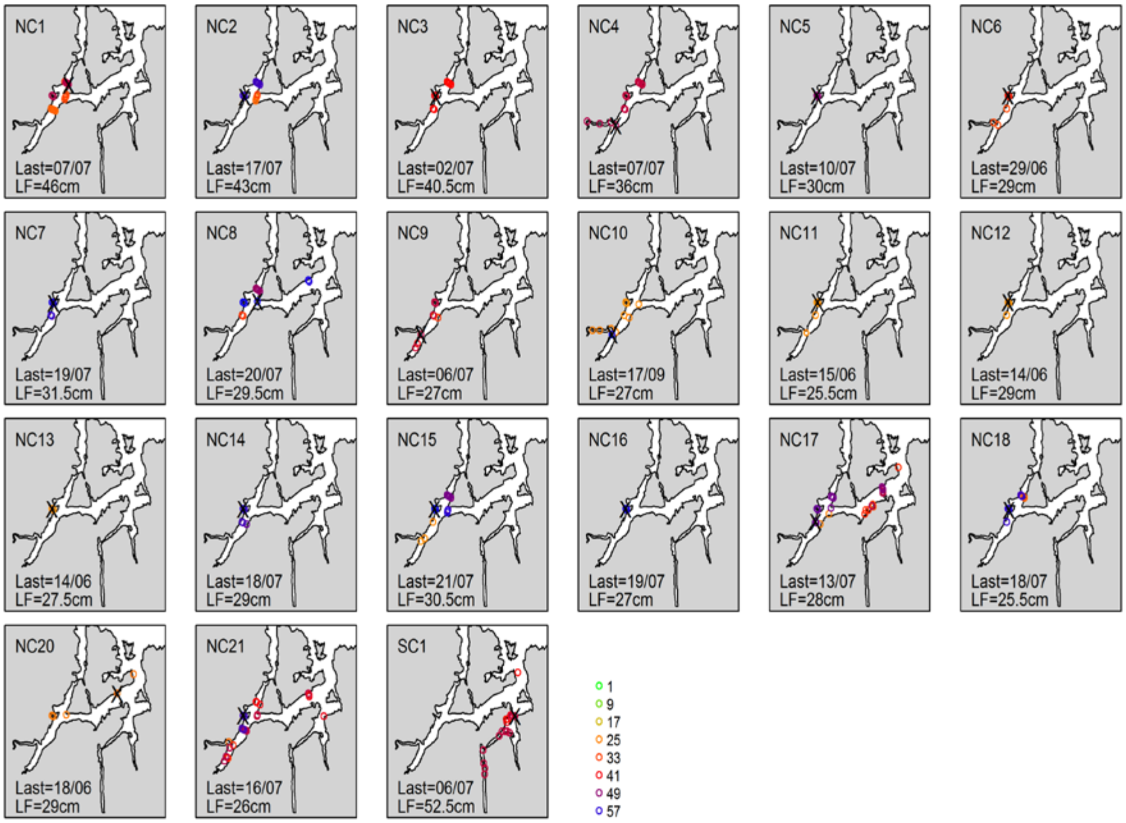

Figure S1. Maps with the individual detections of Arctic charr on receivers in the study area in 2014. X = last detection. LF = fork length. Color range represents day of study for 2014 (day 1 = 23rd of May). Green = early season, red = mid-season, blue = late season. NC = Arctic Charr caught and tagged in the Bras River in 2014, SC = Arctic Charr caught and tagged in the Sandnes River mouth in 2014. A later detection overwrites an earlier detection.

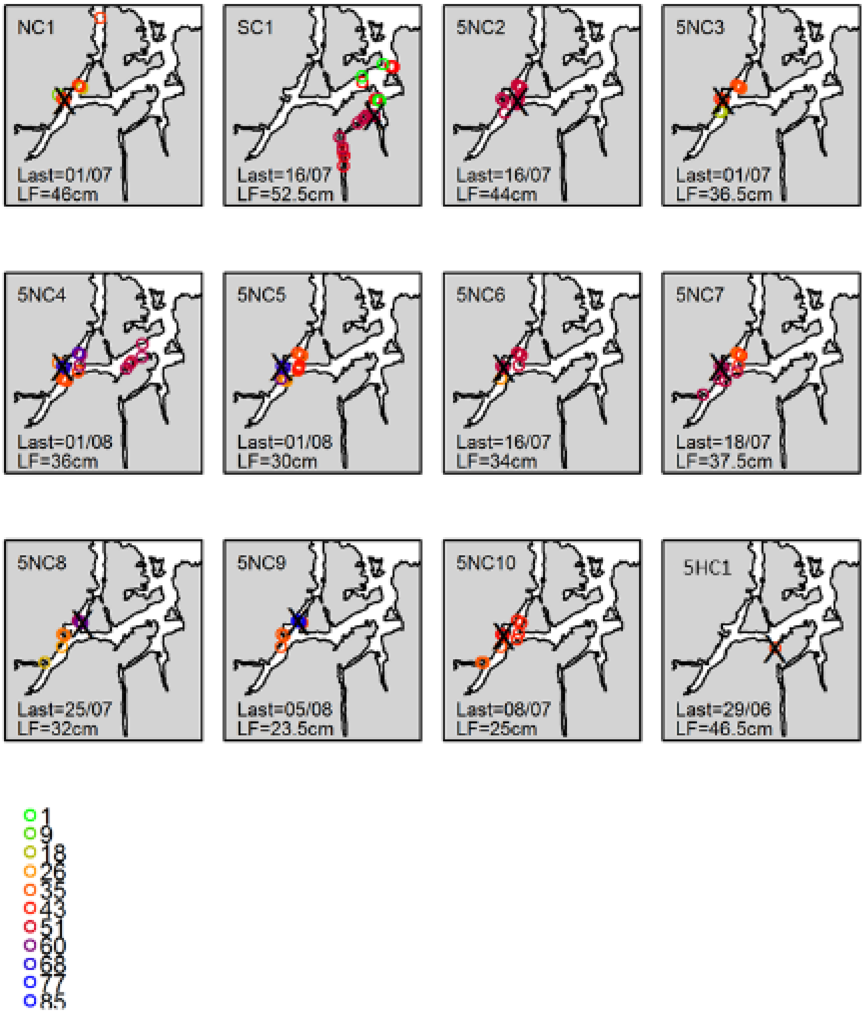

Figure S2. Maps with the individual detections of Arctic charr on receivers in the study area in 2015. X = last detection. LF = fork length. Color range represents day of study for 2015 (day 1 = 14th of May). Green = early season, red = mid-season, blue = late season. NC = Arctic Charr caught and tagged in the Bras River in 2014, SC = Arctic Charr caught and tagged in the Sandnes river mouth in 2014, 5NC = Arctic Charr caught and tagged in the Bras River in 2015, 5SC = Arctic Charr caught and tagged in the Sandnes River mouth in 2015, 5HC = Arctic Charr caught in the Høybukt bay in 2015. A later detection overwrites an earlier detection

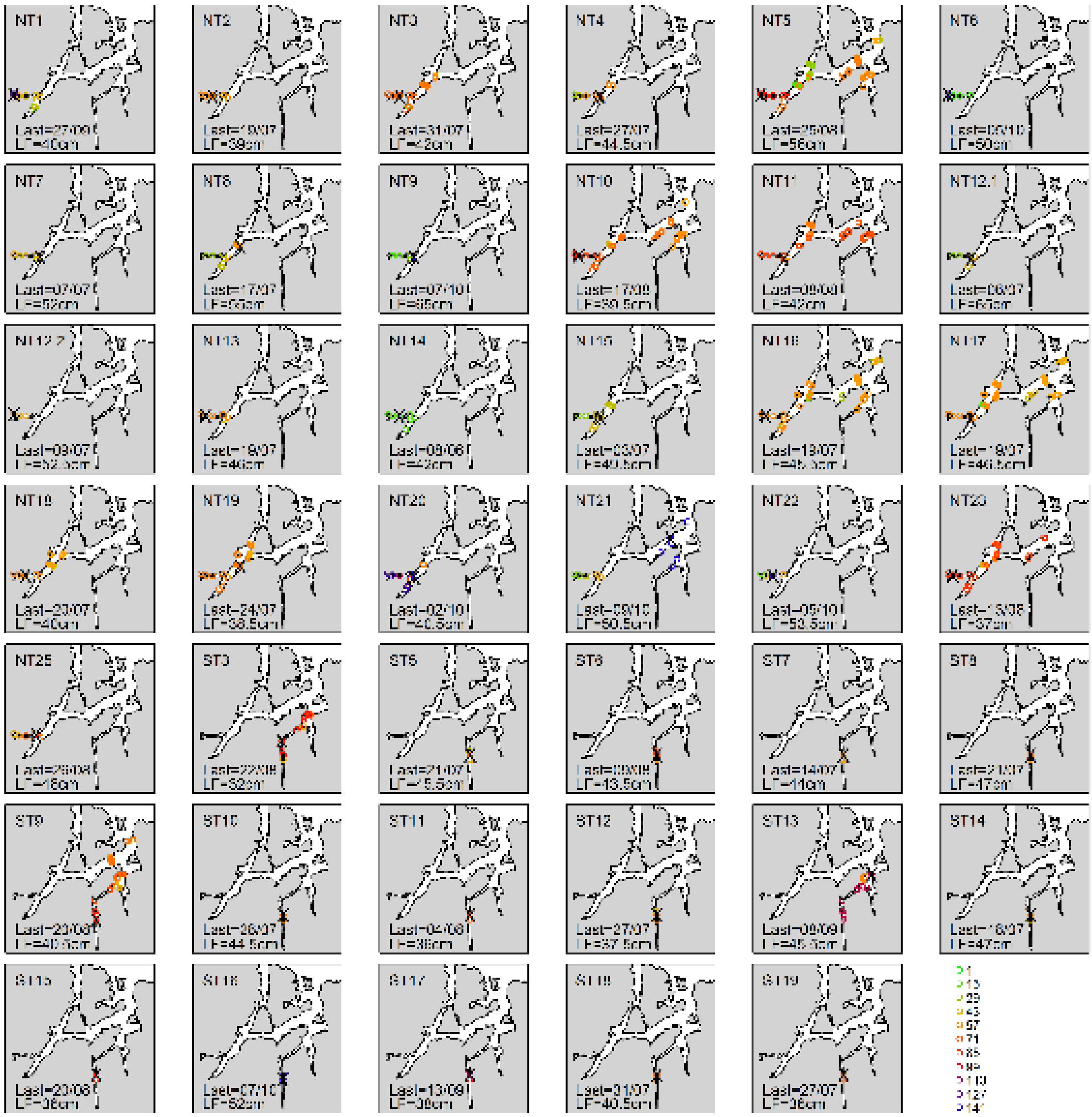

Figure S3. Maps with the individual detections of brown trout on receivers in the study area in 2014. X = last detection. LF = fork length. Color range represents day of study for 2014 (day 1 = 23rd of May). Green = early season, red = mid-season, blue = late season. NT = brown trout caught and tagged in the Neiden River in 2014, ST = brown trout caught and tagged in the Sandnes River mouth in 2014. A later detection overwrites an earlier detection.

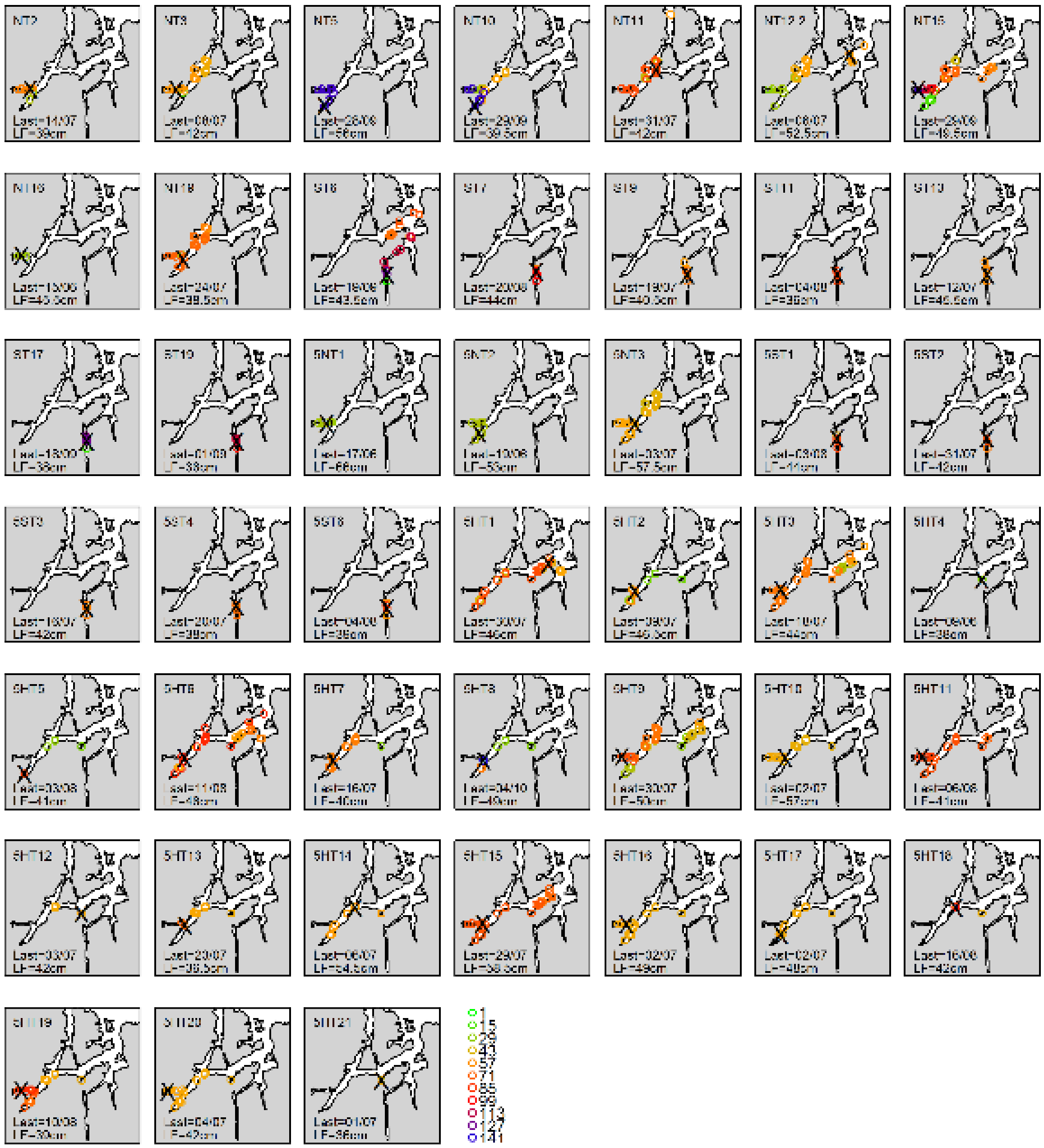

Figure S4. Maps with the individual detections of brown trout on receivers in the study area in 2015. X = last detection. LF = fork length. Color range represents day of study for 2015 (day 1=14th of May). Green = early season, red = mid-season, blue = late season. NT = brown trout caught and tagged in the Neiden River in 2014, ST = brown trout caught and tagged in the Sandnes River mouth in 2014, 5NT = brown trout caught and tagged in the Neiden River in 2015, 5ST = brown trout caught and tagged in the Sandnes River mouth in 2015, 5HT = brown trout caught and tagged in the Høybukt bay in 2015. A later detection overwrites an earlier detection.

Table S1: Overview of which individuals that have been removed from each of the study years 2014 and 2015, and from which date. "X" = the individual was removed from the whole study year. NT = brown trout caught and tagged in the Neiden River in 2014, ST = brown trout caught and tagged in the Sandnes River in 2014, 5ST = brown trout caught and tagged in the Sandnes River in 2015, 5HT = brown trout caught and tagged in the Høybukt bay in 2015.

2014		2015	
ID	Date	ID	Date
NT6	11.6	NT8	X
NT9	5.7	NT22	X
NT22	30.6	NT25	X
ST16	15.8	ST16	X
		5ST5	X
		5HT13	23.7

Fjord area use-tables (VGAM-models)

Table S2: AICcc values for the top six supported VGAM-model structures fitted to predict area use for Braselv Arctic charr in 2014. The models were fitted using ID as a random factor. s(TS)= smoothed timeslot, s(LF)= smoothed fork length. N.par = degrees of freedom.

Model	N.par	AICc	ΔAICc
s(TS)+ s(LF)	6	667.446	
s(LF)	4	756.5642	89.1182
s(TS)	4	787.3578	119.9118
constant prob.	2	863.4075	195.9615

Table S3: Parameter (logit) estimates of the most supported (Table S2) VGAM-model for Braselv Arctic charr in 2014: "timeslot + fork length". Degrees of freedom for terms and Chi-squares for nonparametric effects. The table is also including intercepts (Coefficients). s(TS)= smoothed timeslot, s(LF)= smoothed fork length.

Parameter	Coefficients	N.par	Npar Chisq	P(Chi)
Intercept:1	3.47			
Intercept:2	-1.09			
s(TS):1	-0.04	2.7	75.752	0
s(TS):2	-0.05	2.6	3.583	0.250415
s(LF):1	-0.06	1.8	37.033	0
s(LF):2	0.07	1.9	62.951	0

Table S4: AICc values for the top four supported VGAM-model structures fitted to predict area use for Braselv Arctic charr in 2015. The models were fitted using group as a random factor. s(TS)= smoothed timeslot, s(LF)= smoothed fork length. N.par = degrees of freedom

Model	N.par	AICc	ΔAICc
s(TS)+ s(LF)	6	312.14	
s(TS)	4	317.539	5.399
s(LF)	4	388.3654	76.2254
constant prob.	2	392.2832	80.1432

Table S5: Parameter (logit) estimates of the most supported (Table S4) VGAM-model for Braselv Arctic charr in 2015: "timeslot + fork length". Degrees of freedom for terms and Chi-squares for nonparametric effects. The table is also including intercepts (Coefficients). s(TS)= smoothed timeslot, s(LF)= smoothed fork length.

Parameter	Coefficients	N.par	Npar Chisq	P(Chi)
Intercept:1	-2.78			
Intercept:2	-0.75			
s(TS):1	0.04	2	25.722	0.000003
s(TS):2	-0.01	2.5	36.171	0
s(LF):1	0.03	2.1	6.03	0.052458
s(LF):2	0.01	1.9	7.171	0.025249

Table S6: AICc values for the top six supported VGAM-model structures fitted to predict area use for Neiden brown trout in 2014. The models were fitted using group as a random factor. Most supported model is "timeslot + fork length + smolt length". s(TS)= smoothed timeslot, s(LF)= smoothed fork length, s(LS)= smoothed smolt length. N.par = degrees of freedom.

Model	N.par	AICc	ΔAICc
s(TS)+s(LF)+s(LS)	8	364.3987	
s(TS)+s(LF)	6	375.9709	11.5722
s(TS)+s(LS)	6	386.3347	21.936
s(TS)	4	406.6078	42.2091
s(LF)	4	448.7439	84.3452
constant prob.	2	472.8743	108.4756

Table S7: Parameter (logit) estimates of the most supported (Table S6) VGAM-model for Neiden brown trout in 2014: "timeslot + fork length + smolt length". Degrees of freedom for terms and Chi-squares for nonparametric effects. The table is also including intercepts (Coefficients). s(TS)= smoothed timeslot, s(LF)= smoothed fork length, s(LS)= smoothed smolt length.

Parameter	Coefficients	N.par	Npar Chisq	P(Chi)
Intercept:1	4.48			
Intercept:2	8.82			
s(TS):1	0.03	2.4	38.236	0
s(TS):2	-0.12	2.1	4.734	0.104226
s(LF):1	-0.05	1.7	23.682	0.000005
s(LF):2	-0.13	1.8	30.23	0
s(LS):1	-0.01	1.6	18.718	0.000048
s(LS):2	-0.08	1.8	8.991	0.008303

Table S8: AICc values for the top six supported VGAM-model structures fitted to predict area use for Neiden brown trout in 2015. The models were fitted using group as a random factor. Most supported model was "timeslot + fork length + smolt length". s(TS)= smoothed timeslot, s(LF)= smoothed fork length, s(LS)= smoothed smolt length. N.par = degrees of freedom.

Model	N.par	AICc	ΔAICc
s(TS)+s(LF)+s(LS)	8	191.8671	
s(TS)+s(LF)	6	215.9239	24.0568
s(TS)+s(LS)	6	229.2747	37.4076
s(TS)	4	245.8448	53.9777
s(LF)	4	278.197	86.3299
constant prob.	2	302.6756	110.8085

Table S9: Parameter (logit) estimates of the most supported (Table S8) VGAM-model for Neiden brown trout in 2015: "timeslot + fork length + smolt length". Degrees of freedom for terms and Chi-squares for nonparametric effects. The table is also including intercepts (Coefficients). s(TS)= smoothed timeslot, s(LF)= smoothed fork length, s(LS)= smoothed smolt length.

Parameter	Coefficients	N.par	Npar Chisq	P(Chi)
Intercept:1	3.17			
Intercept:2	-6.07			
s(TS):1	0.07	1.9	51.044	0
s(TS):2	-0.03	1.8	13.014	0.001199
s(LF):1	-0.01	1.6	18.98	0.000042
s(LF):2	0.00	1.7	40.049	0
s(LS):1	-0.06	1.3	7.314	0.011688
s(LS):2	0.41	1.1	2.257	0.14389

Table S10: AICc values for the top six supported VGAM-model structures fitted to predict area use for Sandnes brown trout in 2014. The models were fitted using group as a random factor. Most supported model is "timeslot + fork length + smolt length". s(TS)= smoothed timeslot, s(LF)= smoothed fork length, s(LS)= smoothed smolt length. N.par = degrees of freedom.

Model	N.par	AICc	ΔAICc
s(TS)+s(LF)+s(LS)	8	191.8671	
s(TS)+s(LF)	6	215.9239	24.0568
s(TS)+s(LS)	6	229.2747	37.4076
s(TS)	4	245.8448	53.9777
s(LF)	4	278.197	86.3299
constant prob.	2	302.6756	110.8085

Table S11: Parameter (logit) estimates of the most supported (Table S10) VGAM-model for Sandnes brown trout in 2014: "timeslot + fork length + smolt length". Degrees of freedom for terms and Chi-squares for nonparametric effects. The table is also including intercepts (Coefficients). s(TS)= smoothed timeslot, s(LF)= smoothed fork length, s(LS)= smoothed smolt length.

Parameter	Coefficients	N.par	Npar Chisq	P(Chi)
Intercept:1	-25.59			
Intercept:2	2.02			
s(TS):1	0.00	2.4	38.236	0
s(TS):2	0.00	2.1	4.734	0.104226
s(LF):1	3.65	1.7	23.682	0.000005
s(LF):2	-0.15	1.8	30.23	0
s(LS):1	-10.16	1.6	18.718	0.000048
s(LS):2	0.12	1.8	8.991	0.008303

Table S12: AICc values for the top six candidate VGAM-model structures fitted to predict area use for Høybukt brown trout in 2015. The models were fitted using ID as a random factor. s(TS)= smoothed timeslot, s(LF)= smoothed fork length, s(LS)= smoothed smolt length. N.par = degrees of freedom.

Model	N.par	AICc	ΔAIC
s(TS)+s(LF)	6	179.0334	
s(TS)+s(LF)+s(LS)	8	180.215	1.1816
s(TS)	4	190.4867	11.4533
s(TS)+s(LS)	6	190.5927	11.5593
s(LF)	4	238.5302	59.4968
constant prob.	2	243.3617	64.3283

Table S13: Parameter (logit) estimates for the most supported (Table S12) VGAM-model for Høybukt brown trout in 2015: "timeslot + fork length". Degrees of freedom for terms and Chi-squares for nonparametric effects. The table is also including linear intercepts (Coefficients). s(TS)= smoothed timeslot, s(LF)= smoothed fork length, s(LS)= smoothed smolt length.

Parameter	Coefficients	N.par	Npar Chisq	P(Chi)
Intercept:1	-4.62			
Intercept:2	5.66			
s(TS):1	0.42	1.9	1.4146	0.46937
s(TS):2	-0.08	1.1	0.6517	0.46862
s(LF):1	0.04	2.1	15.6521	0.00047
s(LF):2	-0.18	1	0.8789	0.35577

Depth-tables (LME-models)

Table S14: AICc values for the top eight candidate LME-model structures fitted to depth use for all groups in 2014. The models were fitted using ID as a random factor. N.par = number of paramterers. DOS=day of study. LF=fork length

Model	N.par	AICc	ΔAICc	AICcWt	Cum.Wt	LL
group×DOS^2×LF	20	302154.6	0	1	1	-151057.3
group×DOS^2	11	302557.8	403.21	0	1	-151267.9
group×DOS^2	11	302557.8	403.21	0	1	-151267.9
group×DOS^2+LF	12	302558.9	404.26	0	1	-151267.4
group+DOS^2	7	304337	2182.42	0	1	-152161.5
group×DOS	8	303725.3	1570.7	0	1	-151854.6
group×DOS	8	303725.3	1570.7	0	1	-151854.6
group×LF	8	306161	4006.42	0	1	-153072.5

Table S15. Fixed effects parameter estimates for the most supported (Table S14) LME-model fitted to predict depth for all groups in 2014. Random effects: ID=0.31 (0.55,SD); R2c=0.77; R2m=0.65.

Group	Estimate	Std. Error	t value
Neiden Brown trout	1.7806	0.1109	16.061
Sandnes Brown trout	1.6686	0.1384	12.052
Braselv Arctic Charr	1.6623	0.2479	6.706

Table S16: AICc values for the top eight candidate LME-model structures fitted to predict depth use for all groups in 2015. The models were fitted using ID as a random factor. N.par = number of paramterers. DOS=day of study. LF=fork length

Model	N.par	AICc	ΔAICc	AICcWt	Cum.Wt	LL
group×DOS^2×LF	26	469867.7	0	1	1	-234907.8
group×DOS^2+LF	15	470508.7	641.08	0	1	-235239.4
group×DOS^2	14	470511	643.39	0	1	-235241.5
group×DOS^2	14	470511	643.39	0	1	-235241.5
group+DOS^2	8	473107	3239.35	0	1	-236545.5
group×DOS	10	472169.4	2301.71	0	1	-236074.7
group×DOS	10	472169.4	2301.71	0	1	-236074.7
group×LF	10	476556.3	6688.64	0	1	-238268.1

Table S17. Fixed effects parameter estimates for the most supported (Table S16) LME-model fitted to pred ict depth for all groups in 2015. Random effects: ID=0.47 (0.69,SD); R^2_c=0.513; R^2_m=0.27.

Group	Estimate	Std. Error	t value
Braselv Arctic Charr	0.8463	0.208	4.069
Høybukt brown trout	1.1296	0.1503	7.515
Neiden brown trout	2.0568	0.1988	10.349
Sandnes brown trout	1.887	0.1986	9.502

Temperature-tables

Table S18: AICc values for the top eight candidate LME-model structures fitted to temperature use for all groups in 2014. The models were fitted using ID as a random factor. N.par = number of paramterers. DOS=day of study. LF=fork length

Model	N.par	AICc	ΔAICc	AICcWt	Cum.Wt	LL
group×DOS^2×LF	20	476932.5	0	1	1	-238446.2
group×DOS^2+LF	12	490786	13853.55	0	1	-245381
group+DOS^2	7	546125.4	69192.98	0	1	-273055.7
group×DOS	8	579250	102317.59	0	1	-289617
group×DOS^2	11	490784	13851.58	0	1	-245381
group×DOS^2	8	531684	54751.5	0	1	-265834
group×DOS	6	579526.7	102594.27	0	1	-289757.4
group×LF	6	592056.2	115123.69	0	1	-296022.1

Table S19. Fixed effects parameter estimates for the most supported (Table S18) LME-model fitted to predict temperature for all groups in 2014. Random effects: ID=1.12(1.06,SD); R^2_c=0.92; R^2_m=0.22.

Group	Estimate	Std. Error	t-value
Neiden brown trout	11.7277	0.2121	55.29
Sandnes brown trout	13.7604	0.2647	51.98
Braselv Arctic Charr	10.9645	0.4743	23.12

Table S20: AICc values for the top eight candidate LME-model structures fitted to predict temperature use for all groups in 2015. The models were fitted using ID as a random factor. N.par = number of paramterers. DOS=day of study. LF=fork length

Model	N.par	AICc	ΔAICc	AICcWt	cum.Wt	LL
group×DOS^2×LF	26	584973	0	1	1	-292460.5
group×DOS^2+LF	15	588697.4	3724.37	0	1	-294333.7
group+DOS^2	8	593462.7	8489.63	0	1	-296723.3
group×DOS	10	653523.6	68550.57	0	1	-326751.8
group×DOS^2	14	588696.2	3723.18	0	1	-294334.1
group×DOS^2	14	588696.2	3723.18	0	1	-294334.1
group×DOS	10	653523.6	68550.57	0	1	-326751.8
group×LF	10	793585.7	208612.64	0	1	-396782.8

Table S21. Fixed effects parameter estimates for the most supported (Table S20) LME-model fitted to pred ict temperature for all groups in 2015. Random effects: ID=1.50 (1.22,SD); R^2_c=0.77 ; R^2_m=0.65.

Group	Estimate	Std. Error	t value
Braselv Arctic Charr	9.7043	0.3711	26.15
Høybukt brown trout	11.3242	0.2674	42.35
Neiden brown trout	10.5544	0.3535	29.85
Sandnes brown trout	11.5594	0.3531	32.74

Harbor area use-tables (GLMM-models)

Table S22: AICc values for the top three candidate GLMM-model structures fitted to predict harbor area use for Arctic charr in 2014. The models were fitted using ID as a random factor. N.par = number of parameters. TS=timeslot of four days. LF=fork length.

Model	N.par	AICc	ΔAICc	AICcWt	cum.Wt	LL
(LF)×(TS)	5	1718.37	0	1	1	-854.19
(LF)+(TS^2)	5	1941.62	223.25	0	1	-965.81
(TS)	3	2051.09	332.71	0	1	-1022.54

Table S23. Fixed effects parameter estimates (logit) for the most supported (Table S22) GLMM-model fitte d to predict harbor area use for Arctic charr in 2014. Random effects: ID=178.2 (113.4,SD). TS=timeslot of four days, LF=fork length.

Parameter	Estimate	Std. Error	z value	P-value
(Intercept)	-45.7438	2.6321	-17.379	2×10^{-16}
(LF)	2.0157	1.0492	1.921	0.0547
(TS^2):1	24.6951	2.4068	10.26	2×10^{-16}
(TS^2):2	-6.7607	0.6125	-11.039	2×10^{-16}

Table S24: AICc values for the top three candidate GLMM-model structures fitted to predict harbor area use for Arctic charr in 2015. The models were fitted using ID as a random factor. N.par = number of para meters. TS=timeslot of two days. LF=fork length.

Model	N.par	AICc	ΔAICc	AICcWt	cum.Wt	LL
(LF)+(TS^2)	5	2561.11	0	1	1	-1275.55
(LF)×(TS)	5	3002.67	441.56	0	1	-1496.33
(TS)	3	3124.24	563.13	0	1	-1559.12

Table S25. Fixed effects parameter estimates (logit) for the most supported (Table S24) GLMM-model fitte d to predict harbor area use for Arctic charr in 2015. Random effects: ID=315.8 (17.77,SD). TS=timeslot of two days, LF=fork length.

Parameter	Estimate	Std. Error	z value	P-value
(Intercept)	-42.603	0.3744	-113.8	2×10^{-16}
(LF)	0.7925	0.2333	3.4	0.000683
(TS^2):1	50.6039	0.258	196.2	2×10^{-16}
(TS^2):2	-27.4313	0.148	-185.3	2×10^{-16}

Table S26: AICc values for the top three candidate GLMM-model structures fitted to predict harbor area use for brown trout in 2014. The models were fitted using ID as a random factor. N.par = number of parameters. TS=timeslot of seven days. LF=fork length.

Model	N.par	AICc	ΔAICc	AICcWt	cum.Wt	LL
(LF)+(TS^2)	5	50576.94	0	1	1	-25283.47
(TS)	3	65765.87	15188.93	0	1	-32879.94
(LF)×(TS)	5	62531.86	11954.91	0	1	-31260.93

Table S27. Fixed effects parameter estimates (logit) for the most supported (Table S26) GLMM-model fitte d to predict harbor area use for brown trout in 2014. Random effects: ID=204.3 (14.3,SD). TS=timeslot o f seven days, LF=fork length.

Parameter	Estimate	Std. Error	z value	P-value
(Intercept)	-42.603	0.3744	-113.8	2×10^{-16}
(LF)	0.7925	0.2333	3.4	0.000683
(TS^2):1	50.6039	0.258	196.2	2×10^{-16}
(TS^2):2	-27.4313	0.148	-185.3	2×10^{-16}

Table S28: AICc values for the top three candidate GLMM-model structures fitted to predict harbor area use for brown trout in 2015. The models were fitted using ID as a random factor. N.par = number of parameters. TS=timeslot of seven days. LF=fork length.

Model	N.par	AICc	ΔAICc	AICcWt	cum.Wt	LL
(LF)+(TS^2)	5	63295.73	0	1	1	-31642.87
(LF)×(TS)	5	63441.52	145.79	0	1	-31715.76
(TS)	3	64399.75	1104.02	0	1	-32196.87

Table S29. Fixed effects parameter estimates (logit) for the most supported (Table S28) GLMM-model fitte d to predict harbor area use for brown trout in 2015. Random effects: ID=220.5 (14.9,SD). TS=timeslot o f seven days, LF=fork length.

Parameter	Estimate	Std. Error	z value	P-value
(Intercept)	-18.7339	0.2654	-70.57	2×10^{-16}
(LF)	0.5489	0.2023	2.71	0.00665
(TS^2):1	5.5497	0.1646	33.73	2×10^{-16}
(TS^2):2	-6.3518	0.1165	-54.5	2×10^{-16}

Table S30: AICc values for the top three candidate GLMM-model structures fitted to predict harbor area use for Høybukt brown trout in 2015. The models were fitted using ID as a random factor. N.par = number of parameters. TS=timeslot of seven days, LF=fork length.

Model	N.par	AICc	ΔAICc	AICcWt	cum.Wt	LL
(LF)+(TS^2)	5	29784.47	zz0	1	1	-14887.23
(LF)×(TS)	5	30602.49	818.02	0	1	-15296.24
(TS)	3	31048.32	1263.86	0	1	-15521.16

Table S31. Fixed effects parameter estimates (logit) for the most supported (Table S30) GLMM-model fitted to predict harbor area use for Høybukt brown trout in 2015. Random effects: ID=17.3 (4.2,SD). TS=timeslot of seven days, LF=fork length.

Parameter	Estimate	Std. Error	z value	P-value
(Intercept)	24.7425	1.2689	19.5	2×10^{-16}
(LF)	-1.0754	0.359	-3	0.00274
(TS^2):1	-40.6122	0.465	-87.34	2×10^{-16}
(TS^2):2	15.717	0.2304	68.22	2×10^{-16}

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