Norwegian University of Life Sciences

Master's Thesis 2020 60 ECTS
Faculty for Environmental Sciences and Natural Resource Management

Migrations and utilization of the fjord habitat by anadromous brown trout (*Salmo trutta*) from three watercourses in Hardangerfjord, Norway

Marte Lise Lægreid
Biology

Preface

This thesis is a part of the project Salmon Tracking 2020 which aims to obtain concrete knowledge about the salmonid stock, and thereby secure a better platform to evaluate measures to preserve the wild stocks of salmonids in the Hardangerfjord and Bjørnafjord. The project was funded by PO3 Kunnskapsinkubator and the Ministry of Education and Research. This thesis completes my MSc in Biology and my time at the Norwegian University of Life Sciences (NMBU).

First and foremost, I would like to thank my main supervisor Thrond Oddvar Haugen for the help and support during the entire process. It has been both educational and fun to explore the world of statistics and modelling, and I could not have managed to navigate through it all without your help and encouragement! Secondly, I would like to thank my co-supervisor Henning Andre Urke at INAQ for the knowledge you shared during the fieldwork and the feedback during the writing process. I would like to thank you both for the opportunity to participate in the project studying the brown trout population in the village Eidfjord, in which I grew up and discovered my interest in biology.

I would also like to thank Torstein Kristensen, John Birger Ulvund, Kristin Bøe, Eskil Bendiksen, Ove Kambestad, Geir Ove Henden, Aksel Fiske, Sigurd Domaas, Aksel Røste and Sigmund Skår for invaluable help and high spirits during the fieldwork.

Thanks to my significant other and friends for your continuous help, understanding and encouragement during this process. Lastly, I want to dedicate this thesis to my mom. Thank you for all the nature experiences you gave me during my childhood, and every summer we spent in Hellehalsen, Hardangervidda. I would not have discovered my passion for biology without it.

Ås, June 2020

Marte Lise Lægreid

Abstract

The marine survival of the brown trout (*Salmo trutta*) seems to be reduced in western and middle regions of Norway, likely as a consequence of an excess abundance of the ectoparasite salmon lice (*Lepeophtheirus salmonis*), climate change and reduced abundance of food. The Norwegian traffic light system for capacity adjustments of fish farming came into force in October 2017, and the work of including the anadromous brown trout into the same system started in 2019. However, several knowledge gaps exist; life history, population status, migratory route and behavior, and general knowledge about how the salmon lice affects the populations of brown trout. The aim of my thesis was to compare the use of the Hardangerfjord by 125 brown trout from the Rivers Eio, Granvinselva and Oselva (located from inner-to-outer fjord in this order), by using acoustic telemetry. The results showed that the estimated biweekly survival in fresh water was generally high for tagged brown trout from all three populations. The estimated bi-weekly likelihood of migrating from fresh water to the near fjord-zone was higher for the Os brown trout compared to the Eio and Granvin brown trout. Fewer of the Granvin brown trout individuals were migratory (55%), but those who were, migrated early and far. The time of migration to the respective river mouths happened within the same time span for all three populations, with the Eio population portraying the broadest time period of migration from April 14th to June 29th. Os had the narrowest migration time span in the study (April 12th to May 26th), and the migration seemed to be more coordinated among the individuals compared to the Eio and Granvin individuals. Water flow and day of year were favored additive predictors by model selection for the estimated migration to the river mouth in Eio and Granvin, while temperature and daily change in water level was favored in Os. The arrival time in the different areas of the Hardangerfjord was observed to vary among the three populations. The maximum distance travelled (on average 11.3 km) was not size dependent and did not vary among the three populations. In general, the residence time in the middle parts of the Hardangerfjord was observed to be short (< 12 days on average) for all three populations. The Eio brown trout utilized the inner middle zones of the Hardangerfjord the most (on average approximately 56 days), while the Granvin brown trout used on average approximately 30 days in the inner part of Bjørnafjord. Brown trout from Os spent the least amount of time in fresh water in this study (on average approximately 44 days). Migratory brown trout from Os had the highest fraction of time spent in the estuary (approximately 34.7%), compared to the migratory brown trout from Eio that spent the least percentage of time in their respective estuary (approx. 31.2%). It was estimated

that the largest individuals by length (> 24 cm) from Os and Eio spent more time in their respective estuary compared to smaller individuals (< 19 cm). However, the smallest individuals from Granvin spent more time in their respective estuary compared to larger individuals, and compared to time spent in the estuary by smaller fish from Eio and Os.
In conclusion the results provided in this study indicate that there is a difference in fjord use among the three studied populations, and that the brown trout population in Os seems to be the most affected study area by salmon lice. However, further research over several years is needed to gather concrete knowledge about the wild anadromous brown trout stock in order to better evaluate preservative measures in the Hardangerfjord and Bjørnafjord system.

Table of contents

1. Introduction

The brown trout (*Salmo trutta*) exploit different habitats and populations are often partially migratory, the anadromous – living in both salt- and fresh water, and resident individuals – occurring only in fresh water (Jonsson & Jonsson, 2011; Jonsson & Finstad, 1995; Klemetsen et al., 2003). Before migrating from fresh water to coastal waters the parr goes through the smoltification process, which leads to changes in physiology, morphology and behavior, adapting it to a life in saltwater (Jonsson & Jonsson, 2011). Smolting and timing of sea migration is influenced by photoperiod, water temperature and water flow (Jonsson & Finstad, 1995; McCormick et al., 1998; Wedemeyer et al., 1980). After migrating the brown trout gradually spreads from the river mouth and out into the fjord and inshore waters (Middlemas et al., 2009), where they are most abundant near the surface and often draw close to land to feed on insects, crustaceans, polychaetes and small fish (Jonsson & Finstad, 1995; Klemetsen et al., 2003; Knutsen et al., 2001; Rikardsen et al., 2006). Individuals that migrate into the sea returns to their home rivers or estuaries in the autumn to spawn and or to pass the winter (Jonsson & Jonsson, 2011; Jonsson & Finstad, 1995), but Jensen et al. (2015) observed several individuals that passed the winter in other river systems before eventually returning to their home rivers to spawn in later years.

The benefit of migrating can be access to better feeding opportunities (Gross et al., 1988), leading to increased growth, gonadal production and reproductive success (Jonsson & Jonsson, 2011) as egg size, and therefore early offspring growth and viability, increases with the size of the parent (Einum & Fleming, 1999). Flaten et al. (2016) found that the post-smolts of brown trout in Hemnfjord and Snillfjord, Trøndelag, often utilized near shore habitats in the innermost parts, and spent less time in pelagic areas in the outer areas of the two fjords. Individuals utilizing the outer fjord areas were larger and had a higher return rate to fresh water, indicating that the distribution and survival in the fjord was size dependent (Eldøy et al., 2015; Flaten et al., 2016). (Eldøy et al., 2015) suggested that earlier returns to fresh water by long-distance migrants was due to them finding more energy-rich prey in the outer parts of the fjord, thus gaining mass quicker short-distance migrants. On the other hand, brown trout in the Romsdalsfjord has been observed to utilize the inner fjord system and did not seem to migrate towards the open sea (Finstad et al., 2005). This could imply that the brown trout often tends to remain in the inner parts of the fjord systems utilizing near shore habitats for grazing, while the long-distance migrants, that possibly feed on prey of higher energy-richness in pelagic areas, seems to be larger individuals with a higher return rate to fresh water.

Migration also has costs, such as increased mortality because of the energy cost and risk of predation or disease (Jonsson & Jonsson, 2011). There's a strong predation pressure in the open sea from gulls and fast-swimming pelagic predators (Lyse et al., 1998), as well as the strong negative impacts by the ectoparasite salmon lice (*Lepeophtheirus salmonis*) (Thorstad et al., 2019), impacting both individual fish (reduced marine growth, tissue damage, and physiological stress) and entire populations (premature migratory return to fresh water and changes in population structure arising from mortality) (Thorstad et al., 2014). Hence, the gain in fitness from accessing areas with better feeding opportunities must exceed the fitness obtained from living only in fresh water, despite of the predation risk and energy costs of migrating (Gross et al., 1988; Jonsson & Jonsson, 2011). Anadromy must maximize the lifetime product of reproductive success and survivorship in order to spread in populations (Jonsson & Jonsson, 2011), but this adaptation is under threat due to aquaculture activity and salmon lice reducing the benefit of a marine phase to the life cycle (Thorstad et al., 2014).

The brown trout in the western and middle regions of Norway seems to have experienced reduced marine survival, likely because of an excess abundance of the salmon lice, climate change and reduced abundance of food (Bjørn et al., 2009; Direktoratet for naturforvaltning, 2009; Thorstad et al., 2019). The farming of Atlantic salmon (*Salmo salar*) started in the late 1960s and have increased enormously, with 1,1 million tonnes of salmon and 46 400 tonnes of trout exported in 2018 (Norges Sjømatråd, 2019). Due to the increase in production volume of farmed salmon, the salmon lice population in the fjords and along the coast has increased and caused problems for the wild populations of brown trout (Havforskningsinstituttet, 2018b). Brown trout infected by salmon lice might experience weakened health, increased mortality and reduced growth, also making it more vulnerable to other influences like for example predation or acidification (Direktoratet for naturforvaltning, 2009; Halttunen et al., 2018; Havforskningsinstituttet, 2018a). This implies that the salmon lice can act as a significant stock regulating factor for the brown trout in the Hardangerfjord system, with the outer areas of the fjord showing the highest infection pressure, and observations of individuals returning earlier to fresh water with partly significant infections of salmon lice (Bjørn et al., 2009; Direktoratet for naturforvaltning, 2009; Heuch et al., 2009).

Halttunen et al. (2018) found that brown trout in the Etnefjord, a small side-fjord in the outer part of the Hardangerfjord, spent more time in the outer areas of the fjord during years of low infestation pressure, and remained closer to the river outlet during years of high infestation pressure. The brown trout returned earlier to the rivers in years of high infestation pressure compared to the low years, and would spend longer periods in fresh water (Halttunen et al., 2018). By choosing fresh water refuges it was suggested by Halttunen et al. (2018) that the brown trout had adapted their migration behavior to escape from immediate mortality risks due to salmon lice infections, which could lead to reduced growth and fecundity, increased long-term mortality, and a reduced likelihood of seaward migration. Bjørn et al. (2009) found that the sustainability regarding the interaction between salmon lice stemming from salmon farms and wild stocks of salmon seemed to be exceeded in the Hardangerfjord. In order to lower the infestation pressure by salmon lice, their numbers need to be kept as low as possible to prevent them from being released into the water where they can later infect wild salmonids in surrounding areas (Heuch et al., 2009).

The Norwegian traffic light system for capacity adjustments of fish farming came into force in October 2017, but focused only on assessing the risk of mortality on wild salmon by salmon lice (Nærings- og fiskeridepartementet, 2017). In 2019 the work of including the anadromous brown trout into the same system started, but several knowledge gaps exists; life history, population status, migratory route and behavior, and general knowledge about how the salmon lice affects the populations of brown trout (Havforskningsinstituttet, 2019; Nilsen, F. et al., 2019). The aim of my thesis was to compare the use of the Hardangerfjord and Bjørnafjord, hereby referred to as the Hardangerfjord, by three populations of brown trout from the Rivers Eio, Granvinselva and Oselva by using acoustic telemetry.

More specifically my study questions and hypotheses were;

i) What factors influence migration in spring?
H1: The brown trout migrates from fresh water and enters the river mouth with increasing water discharge and water temperature.

ii) When does the brown trout arrive in different areas of the fjord, and how far do they migrate?
H2: Maximum distance travelled from their respective rivers increases with fish size.

iii) Does the amount of time spent in delousing areas by migratory individuals vary?
H3: Individuals that migrate to the outer fjord areas with high salmon lice densities spend a higher fraction of time in their respective estuaries than those that only use inner and mid parts of the fjord.
H4: Large individuals have a higher rate of return to their respective estuaries than smaller individuals.

iv) What are the most important factors affecting fjord survival for all three populations?
H5: Survival probabilities are lowest in the outer Hardangerfjord (salmon lice-induced).
H6: Survival probabilities are at their lowest right after migration from fresh water to the fjord (predation-induced).

2. Materials and methods

2.1 Study area

The Hardangerfjord is the second-longest fjord in Norway, located in Vestland county (Figure 2.1). The relatively short river Eio flows into the fjord in Eidfjord and consists of two main rivers, Bjoreia and Veig that flows into the lake Eidfjordvatnet, with upstream parts of Bjoreia being a part of the hydro-electric power station in Simadalen, Sy-Sima power plant (Figure 2.2). In Granvin, the River Storelvi flows through agricultural land and into the lake Granvinsvatnet, which leads to the River Granvinselva and fjord (Figure 2.3). The River Oselva flows from the lake Samdalsvatnet, through several small lakes and empties into the fjord at Osøyro (Figure 2.4). Arctic charr (*Salvelinus alpinus*) is present in both Eio and Granvin, while pike (*Esox lucius*) is present in Os (Miljødirektoratet, 2013).

According to the salmon register (www.lakseregisteret.no), the condition of the brown trout in 2013 was considered «demanding» for all three locations (Miljødirektoratet, 2013). Thorstad et al. (2019) studied the state of 430 Norwegian brown trout populations in 2017, including the three populations in this study. The Eio brown trout population was classified to good, the Granvin population to moderate, and the Os population to poor. The biggest impacting factor for all three populations was salmon lice, and potentially in addition to hydropower production for the Eio population. Spawning counts were conducted in the Hardangerfjord from 2004 to 2018, indicating that the Eio river system seems to have the largest increase among the brown trout populations in the Hardangerfjord (Skoglund et al., 2019). The brown trout population in Granvin was observed to increase from 2012 to 2014 but decreased again after 2014.

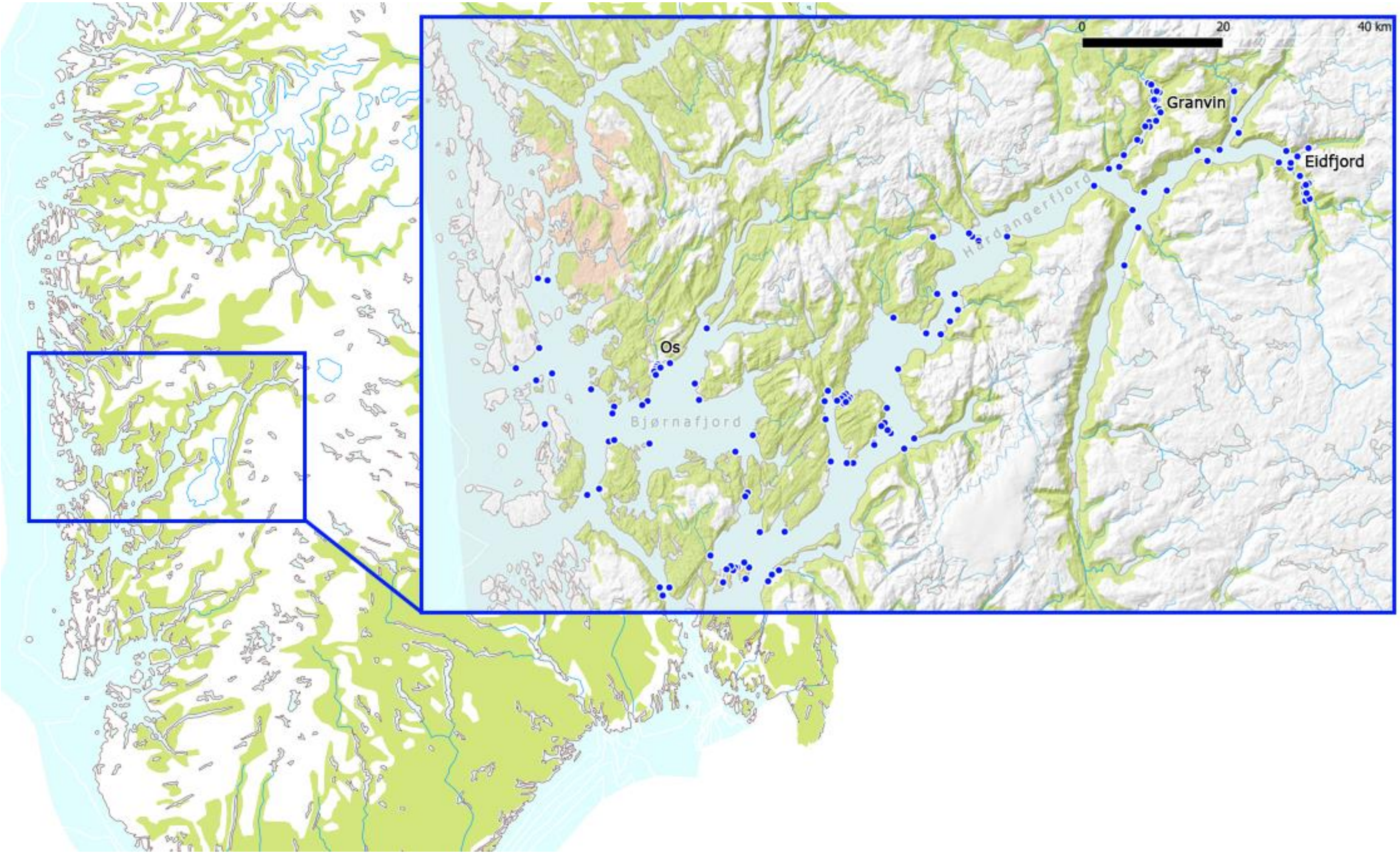

Figure 2.1: Map of the study area with GPS locations of all TBR receivers (blue dots).

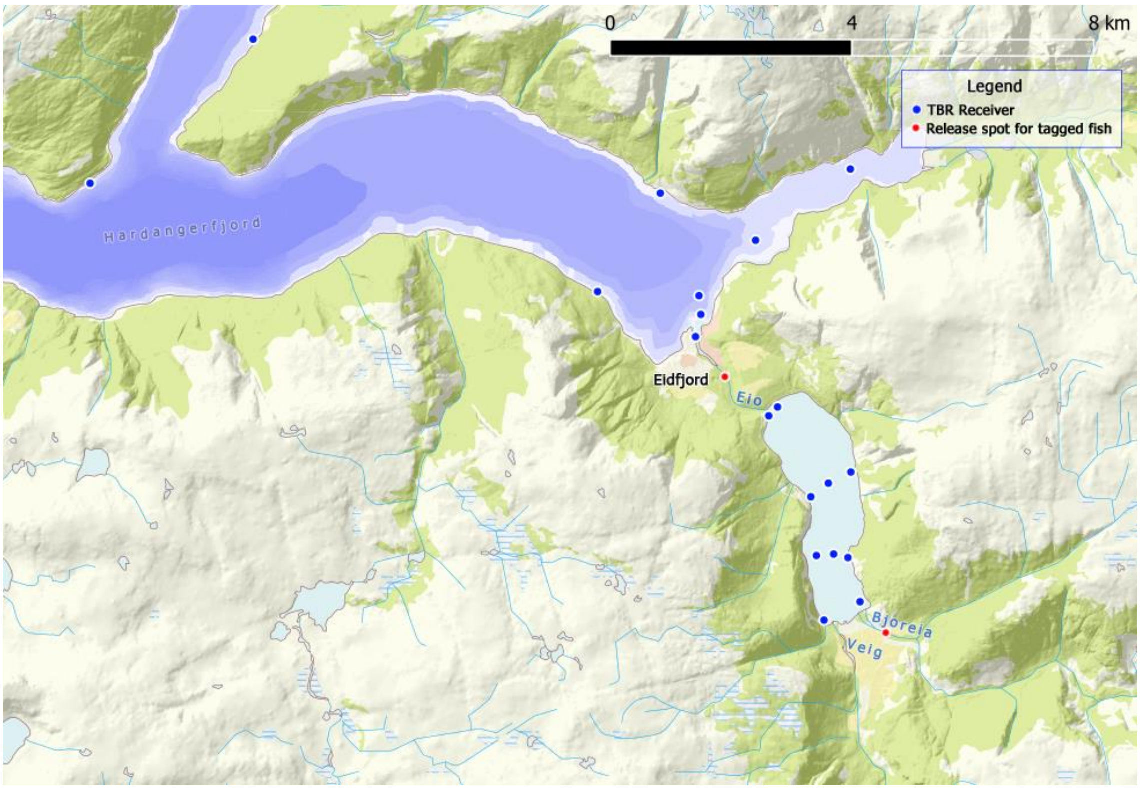

Figure 2.2: Enlarged map of the Eio river system with location of receivers and release sites of tagged fish.

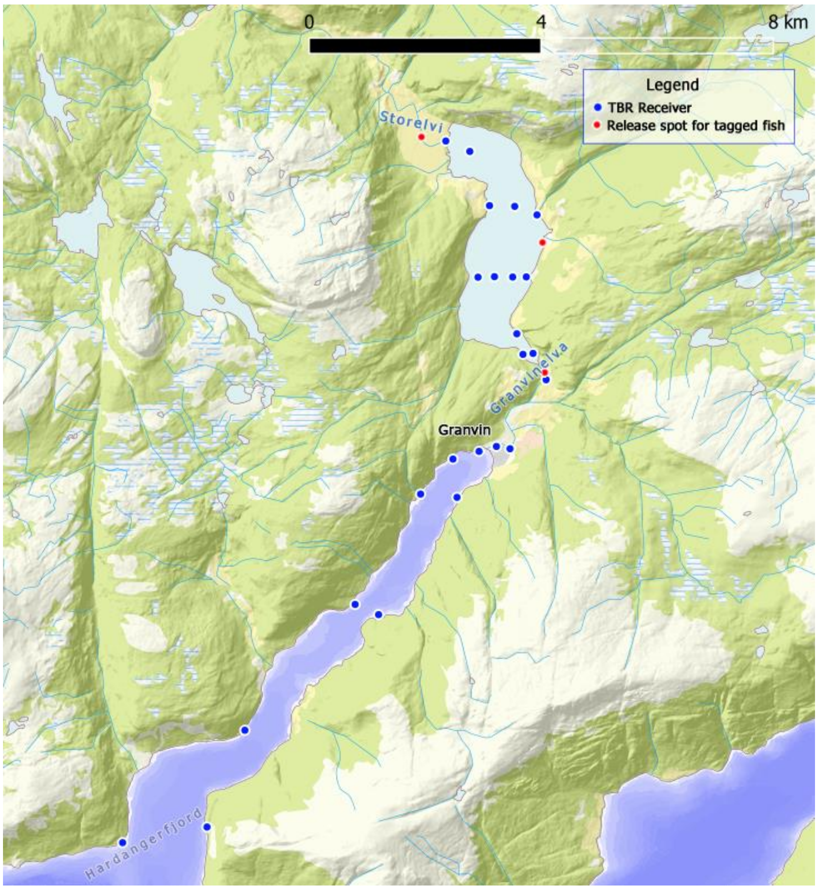

Figure 2.3: Enlarged map of the Granvin river system and inner fjord with location of receivers and release sites of tagged fish.

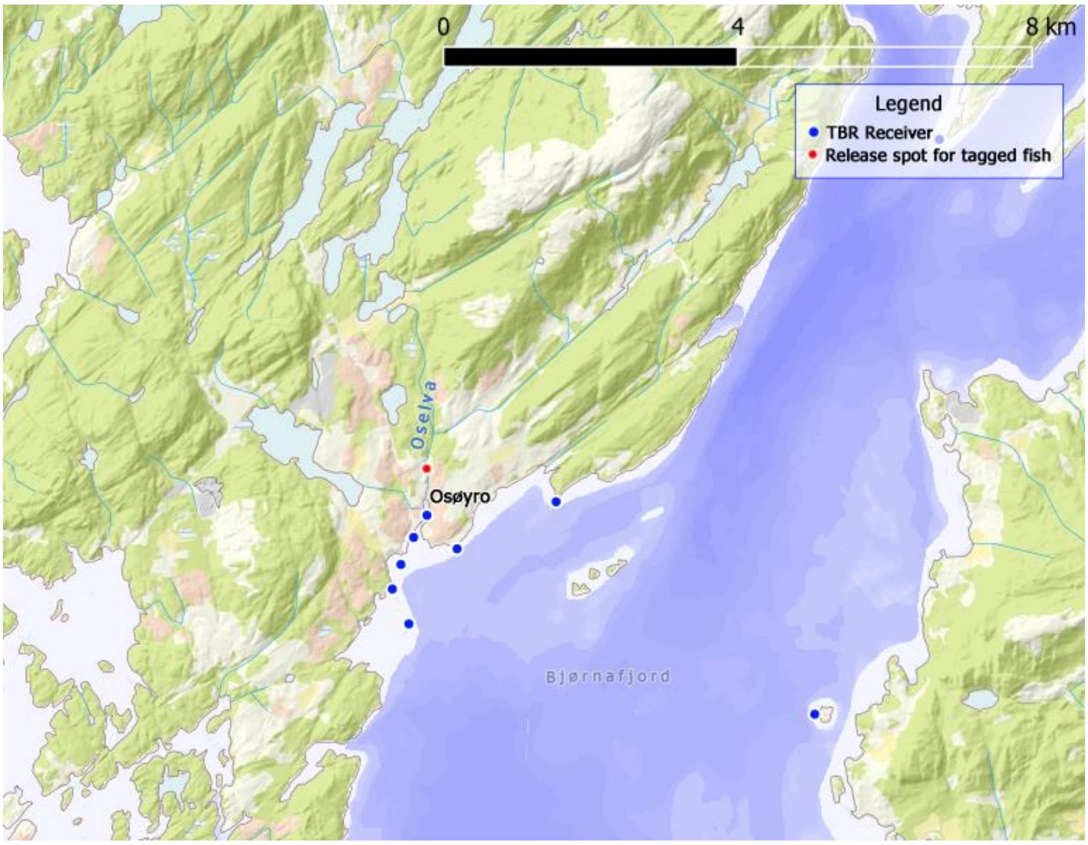

Figure 2.4: Enlarged map of the Os river system with location of receivers and release sites of tagged fish.

2.2 Data collection

2.2.1 Acoustic telemetry

Transmitters, hereby called tags, transmits a coded acoustic signal that gets detected by receivers located within the detection range and stores the data from the tags (Figure 2.5). Three tags of different sizes from ThelmaBiotel AS (www.thelmabiotel.com) were used for the brown trout smolts, all transmitting depth in addition to the tag ID (Table 2.1). The receiver also registers time of signal arrival (at millisecond level) based on a built-in clock along with information on signal strength (dB) and

Figure 2.5: Tags with ID numbers to the left, and the TBR 700 receiver to the right.

the signal-to-noise ratio. The tags had a code repeat rate of 30-150 seconds to minimize the probability of a collision between two closely located tags transmitting signals at the same time. The TBR 700 receivers (n=147) were placed throughout the Eidfjord and Granvin lake, the Rivers Eio, Granvinselva and the outlet of Oselva, and finally in the Hardangerfjord and Bjørnafjord (Figure 2.1), attached to an anchored rope with a buoy. The GPS-location of every receiver was recorded, also giving us the position of the fish with every detection. The detection range of the receivers is about 200-400 m, but differs with noise levels caused by wind, rain, water stratification and so on (Urke et al., 2018). The battery-life of the TBR 700 receivers is 6-13 months. Data from the receivers was transferred to a computer by wireless Bluetooth and the computer software ComPort, during 18th to 20th of October 2019.

Table 2.1: Specification for tags used in the study.

	D-LP9L	**D-LP7**	**D-2LP7**
Diameter	9 mm	7.3 mm	7.3 mm
Length	27.5 mm	22.5 mm	27.7 mm
Weight water	2.5 g	1.2 g	1.8 g
Lifetime	26 months	5-7 months	14 months
Signal range	300-400 m	100-200 m	100-200 m
Signal intervals	90-150 sec	30-130 sec	90-150 sec
Number of tags used	46	35	44

Acoustic telemetry is an expensive and time-demanding method, but once all tags and receivers are placed in their planned positions it can provide vast amounts of data per individual over several months at a time. Because it is an expensive method that require fishes larger than 12.5 cm, relatively low numbers of fishes are tagged. Acoustic telemetry works in both fresh and salt water, making it highly relevant for anadromous fish studies.

2.2.2 Fish capture and tagging

A total of 125 brown trout were captured by electro-fishing and tagged in the Eio (n=60, length $\bar{x}$=18.73 cm, s=3.65 cm, weight $\bar{x}$=60.59 g, s=39.15 g), Granvin (n=31, length $\bar{x}$=19.07 cm, s=3.13 cm, weight $\bar{x}$=56.14 g, s=25.3 g) and Os (n=34, length $\bar{x}$=28.13 cm, s=6.95 cm, weight $\bar{x}$=225 g, s=190.17 g) rivers in the period between April 8th to 11th 2019 (Figure 2.6 and 2.7). Some of the larger individuals in Os were captured with angling tools.

Figure 2.6: Electro-fishing in the River Granvinselva.

The necessary permits for fish capture and tagging were gathered cf. Regulation on the use of animals in experiments (Forskrift om bruk av dyr i forsøk, 2015). The fish was collected from the main rivers in all three locations, in addition to the Granvin lake by using fishing nets. Several factors like conductivity, stream velocity, water temperature, water sight and so on were taken into consideration before collection of fish by electro fishing was initiated (Bohlin et al., 1989; Forseth & Forsgren, 2008). The fish was transported to a storing tub after collection, with constant water circulation to ensure optimal supply of oxygen. The fish spent about a day in the tubs with frequent supervision before the tagging procedure was initiated. The fish was first sedated using Finquel (60 mg/L) until it was unresponsive when being handled on the operation table. Length and weight were recorded before making a small incision into the abdomen, between the pectoral fins, where the tag then was inserted (Figure 2.7). All fish larger than 12.5 cm but smaller than 19.5 cm were tagged with the 7.3 mm tags, while fish larger than 19.5cm were tagged with the 9 mm tags. The incision was closed with three stitches using Resolon, 4/0 usp and the skin adhesive Histoacryl. All fishes had a constant flow of fresh water with half-concentration of aesthetic over the gills during the procedure. All individuals were tagged by an authorized professional apart from one individual that was tagged by me, under strict guidance by the professional (Figure 2.7). The fish was then observed during active recovery until it became capable of remaining upright and responsive to stimuli in the form of a weak water current. After ensuring that all tags were active and transmitting signals, the fishes were kept in transportation tubs with constant water circulation until they were released back into the locations they were originally captured from, 2-6 hours after the operation. All fish survived the operation and portrayed normal flight-responses when released back in their respective rivers.

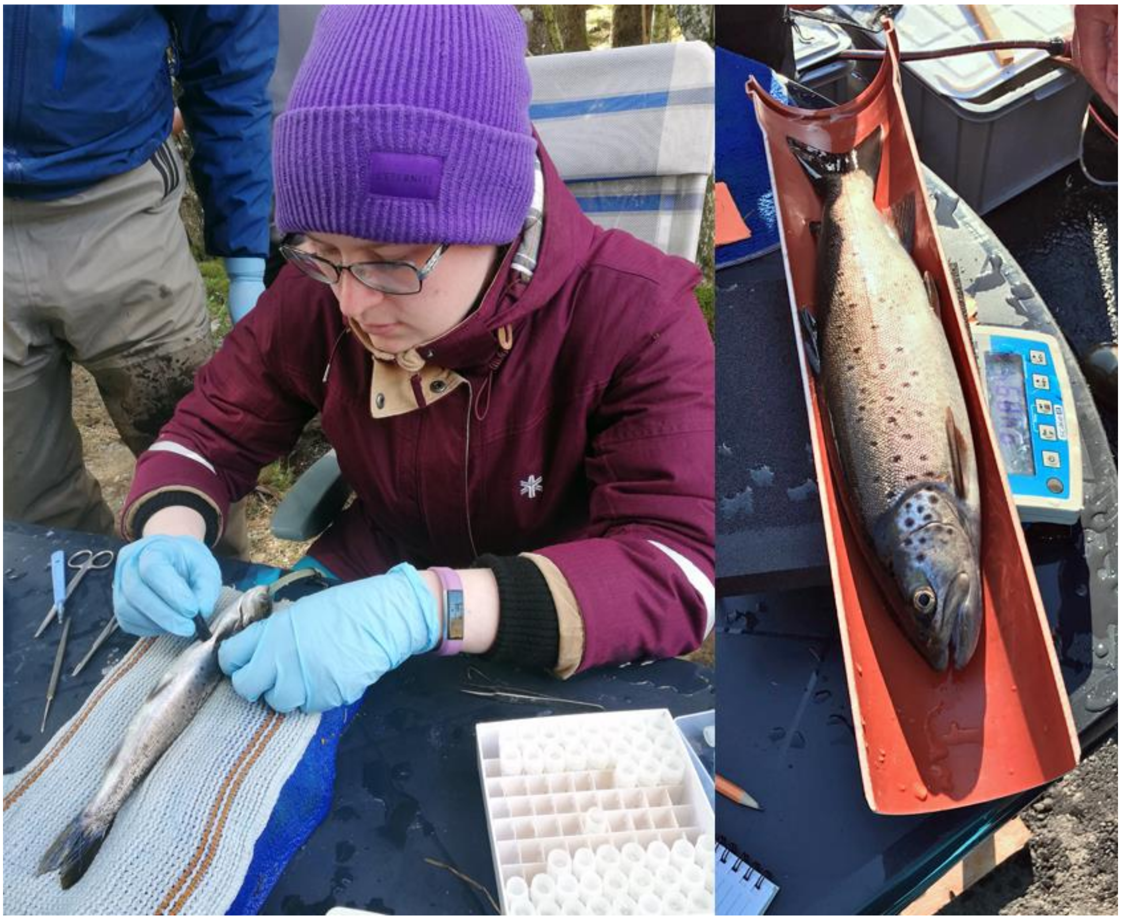

Figure 2.7: Tagging a brown trout (ID 152) with a 9mm tag to the left, measuring length and weight of a brown trout to the right.

2.3 Quantitative analyses

2.3.1 Data handling

The water level in Granvin and Os was recorded with a HOBO water logger, while the water discharge data for Eio was obtained from the Norwegian Water Resources and Energy Directorate (NVE). The maps were made using QGIS (QGIS Development Team, 2020) with layers from the Norwegian Mapping Authority (Kartverket).

There was a total of 17 178 075 detections of both salmon and brown trout before filtering the data using ComPort V3.0.0 (www.thelmabiotel.com). After filtering out the two frequencies (kHz) with five different protocols used for communication between the tags and receivers (listed below) 13 729 815 detections remained.

- R64K 71kHz
- R64K 73 kHz
- S256 73kHz
- S64K 71kHz
- S64K 73kHz

Max ID was set to 4259 (highest tag-ID in the study) resulting in 7 857 929 detections. Min ID was set to 10 (lowest tag-ID in the study) resulting in the final 7 856 982 detections, that were saved in a .csv file and imported to the statistics software R (R Development Core Team, 2019) for further filtering. After merging the detections with the receiver- and brown trout tag ID's in R 1 992 929 detections remained. Lastly, 505 detections considered to be ghost detections were removed, leaving a total of 1 992 424 detections for further analyses. Ghost detections were considered so based on them showing impossible movement distances, like individuals appearing in both Granvin and Eio the same day, or individuals that appeared to have migrated from Eio to Os but had no detections along their migratory route throughout the Hardangerfjord.

The R libraries "ggplot2", "lubridate", "directlabels", "AICcmodavg", "maptools", "ggmap", "sp", and "rgdal" were installed for handling the data and creating the plots used in this study.

The receivers were classified into zones to analyze and compare the migration and survival among them (Figure 2.8).

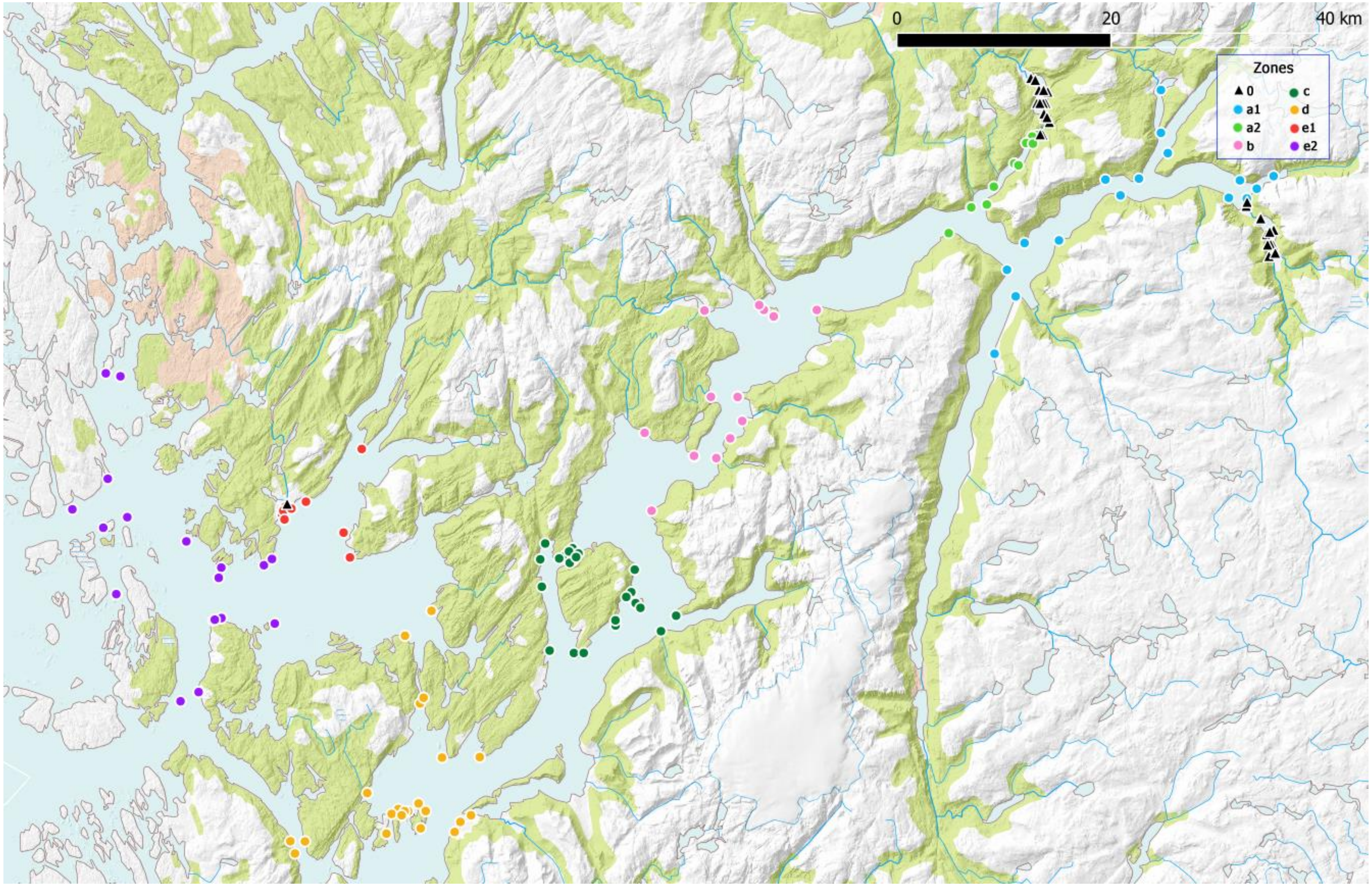

Figure 2.8: Zone classification for all TBR receivers in the Hardangerfjord. Each color marks a zone. 0 = fresh water.

Generalized linear models (McCullagh & Nelder, 1989) were fitted to estimate the time of migration from fresh water to fjord, with daily fraction of number of individuals migrating on number of individuals available for migration as response, and the day of year, water temperature and discharge as potential effects. Generalized linear models were also fitted to estimate the determinates of residence time in the respective estuaries among the migratory individuals, with residence time in the respective estuaries as response, and home river, fish length, weight and condition factor as potential effects. Linear mixed effects models (Zuur et al., 2009) were used to analyze the migration lapse ($Dist_{MAX}$), with the distance to the river mouth (corresponding to river in which the individual was tagged) as response, home river, fish length, weight and condition factor as potential effects, and fish ID as a random effect (to account for structural dependency in the data). Akaike Information Criterion (AIC) was used as model selection criteria amongst candidate models (Akaike, 1974).

Some of the predictor variables for the candidate models with daily fraction of number of individuals migrating on number of individuals available for migration as response were calculated using the following formulas;

The difference in temperature and water discharge/ level between two days;

$\Delta T_t = T_t - T_{t-1}$

$\Delta Q_t = Q_t - Q_{t-1}$

$\Delta T_t/\Delta Q_t$: Difference in temperature/ water discharge (Eio) or water level (Granvin and Os).

T_t/Q_t: Temperature/ water discharge (Eio) or water level (Granvin and Os) of the actual day.

T_{t-1}/Q_{t-1}: Temperature/ water discharge (Eio) or water level (Granvin and Os) of the day before the actual day.

The relative difference in temperature and water discharge/ level;

$rel\Delta T_t = \Delta T_t/T_t$

$rel\Delta Q_t = \Delta Q_t/Q_t$

$rel\Delta T_t/rel\Delta Q_t$: Relative difference in temperature/water discharge (Eio) or water level (Granvin and Os).

$\Delta T_t/\Delta Q_t$: Difference in temperature/ water discharge (Eio) or water level (Granvin and Os).

T_t/Q_t: Temperature/ water discharge (Eio) or water level (Granvin and Os) of the actual day.

The predictor variable K-factor for the candidate model with distance to the river mouth and residence time in the respective estuaries as response were calculated using the Fulton formula (Froese, 2006);

$K = 100 * W/L^3$

K: condition factor,

L: total length in cm,

W: weight in grams.

2.3.2 Mark-recapture analysis

The data was analyzed using Mark V6.2 (http://www.phidot.org/), with 14 occasions corresponding to bi-weekly periods over which survival and dispersal probabilities could be estimated. The 14 occasions were separated into three periods; and early period from April 8th to June 16th, a mid period from June 17th to August 11th, and a late period from August 12th to October 13th (Appendix Table A-7). The fjord system was divided into three zones; fresh water (FW), near fjord (NF) and distant fjord (DF) (Table 2.2.).

Table 2.2: Zone classification for CAS-analysis

Zones	CAS-zones		
	Eio	**Granvin**	**Os**
0	1 - Fresh water	1 - Fresh water	1 - Fresh water
a1	2 - Near fjord	2 - Near fjord	3 - Distant fjord
a2	2 - Near fjord	2 - Near fjord	3 - Distant fjord
b	2 - Near fjord	2 - Near fjord	3 - Distant fjord
c	3 - Distant fjord	3 - Distant fjord	3 - Distant fjord
d	3 - Distant fjord	3 - Distant fjord	2 - Near fjord
e1	3 - Distant fjord	3 - Distant fjord	2 - Near fjord
e2	3 - Distant fjord	3 - Distant fjord	2 - Near fjord

In order to analyze among-zone movements and zone-wise survival for the tagged brown trout, a multi-state modelling approach was used. Technically this was done by fitting a so-called Conditional Arnason-Schwarz model (CAS) (Neil Arnason, 1973; Schwarz et al., 1993). The brown trout was assigned individual encounter histories comprised of 14-digit arrays of either “0”, “1”, “2” or “3”, depending on whether the individual was encountered during an encounter occasion ("1", "2" or "3" if encountered, 1-3 being in which zone it was detected) or not ("0"). An encounter history like "121230211202" would mean that the individual was captured, tagged and released in zone 1 at the first occasion, predominantly detected in zone 2 during the second occasion, predominantly detected in zone 1 and zone 2 during the third and fourth occasion respectively, then predominately detected in zone 3 during occasion five, and so on (Figure 2.10). There is a lack of detections during occasions 6 and 11, but the detections on occasions 7 and 12 confirms that although the individual is still alive.

The parameterization of the multi-state mark-recapture model is visualized in a fate diagram (Figure 2.9). Using the fate diagram, we can follow individuals tagged at occasion *k* that are captured, tagged and released in zone 1. S_k^1 is the survival probability over the *k* to the *k*+1 period for individuals that stayed in zone 1 at occasion *k*, ψ_k^{11} is the probability of staying in zone 1, while ψ_k^{13} is the probability of migrating from zone 1 to 3 during the *k* to the *k*+1 period. p_k^1 is the probability of being captured in zone 1 at occasion *k*. Encounter histories for some example fates are provided in the curly brackets to the right in Figure 2.9 (each encounter history corresponds to the fates on the same line in the figure). 0 = not detected, 1 = detected in zone 1, 2 = detected in zone 2, 3 = detected in zone 3, -1 means assigned as caught (and killed) in zone 1 (i.e., right censored).

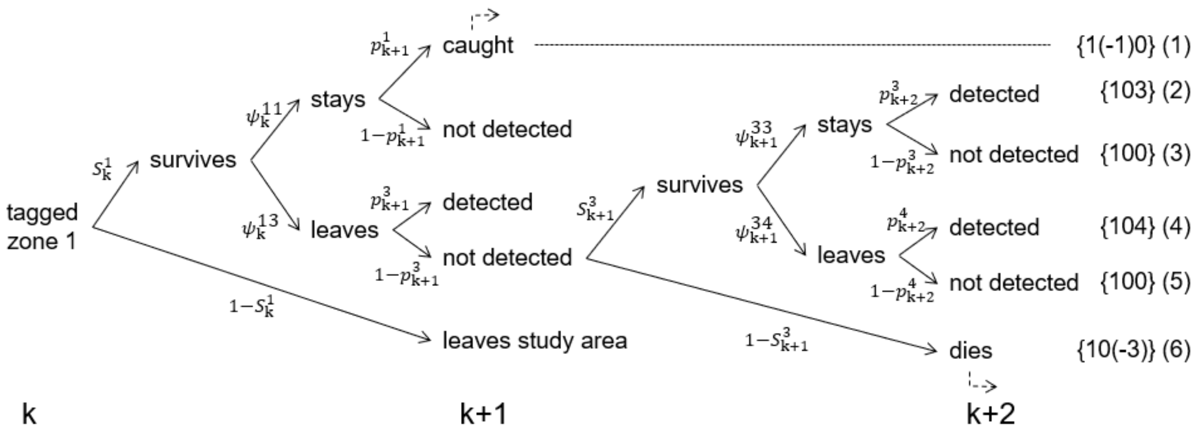

Figure 2.9: Fate diagram with corresponding Conditional Arnason-Schwarz (CAS) parameterization for a three occasion study system (see text for a detailed description). Angled and dashed right-pointing arrows indicate right-censoring (i.e., data is used up to this occasion but censored out of study beyond this point).

An overview of parameters from the 12 first occasions for the study system is given in Figure 2.10, apart from the ψ-parameter for which only a couple examples are given to ease readability. Candidate model structures with individual covariates were fitted and subjected to model selection by means of Akaike's Information Criterion (AIC).

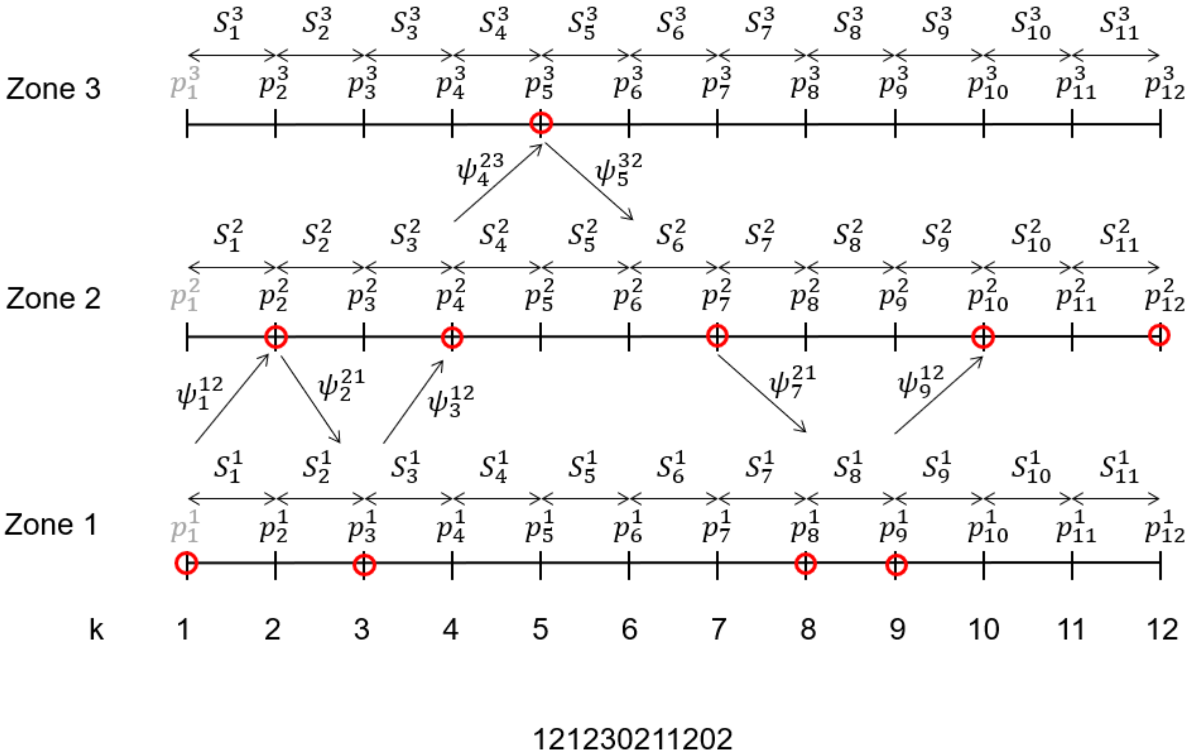

Figure 2.10: Overview of potential CAS parameters fitted for this study system (for 12 out of 14 occasions). k = occasion number, S_k^i represents survival over the k to k+1 period in zone i, p_k^i represents (re)capture probability at occasion k in habitat i (p_1 are indicated in grey as these are not estimable), ψ_k^i represents the dispersal probability from zone i to j over the k to k+1 period. The red circles denotes an example encounter trajectory (121230211202) described further in the main text.

3. Results

3.1 General aspects of the data

Data was retrieved from 118 (94,4% detection rate) brown trout in total, more specifically 55 (91,7%) from Eio, 31 (100%) from Granvin and 32 (94%) from Os. A total of 7 brown trout were never detected on any receivers, and therefore assumed to have tag rejections or died.

3.2 Migration to river mouth

Eio

The brown trout was detected in the Eio river mouth in the period from April 14th to June 29th, with the highest amount of migrating brown trout on May 11th, May 22nd and June 7th (Figure 3.1), and seem to be coherent with water discharge. 15 of the 55 detected individuals were never detected in the river mouth (27%) (Appendix Figure A – 1). The model selection procedure for candidate models estimating migration to the Eio river mouth favored a model with water discharge and day of year (DoY) as additive predictors (Table 3.1 and 3.2), followed by a model with an interaction between water discharge and day of year (DoY) as additive predictors (Appendix Table A – 1). The probability of migration into the Eio river mouth is shown in Figure 3.2.

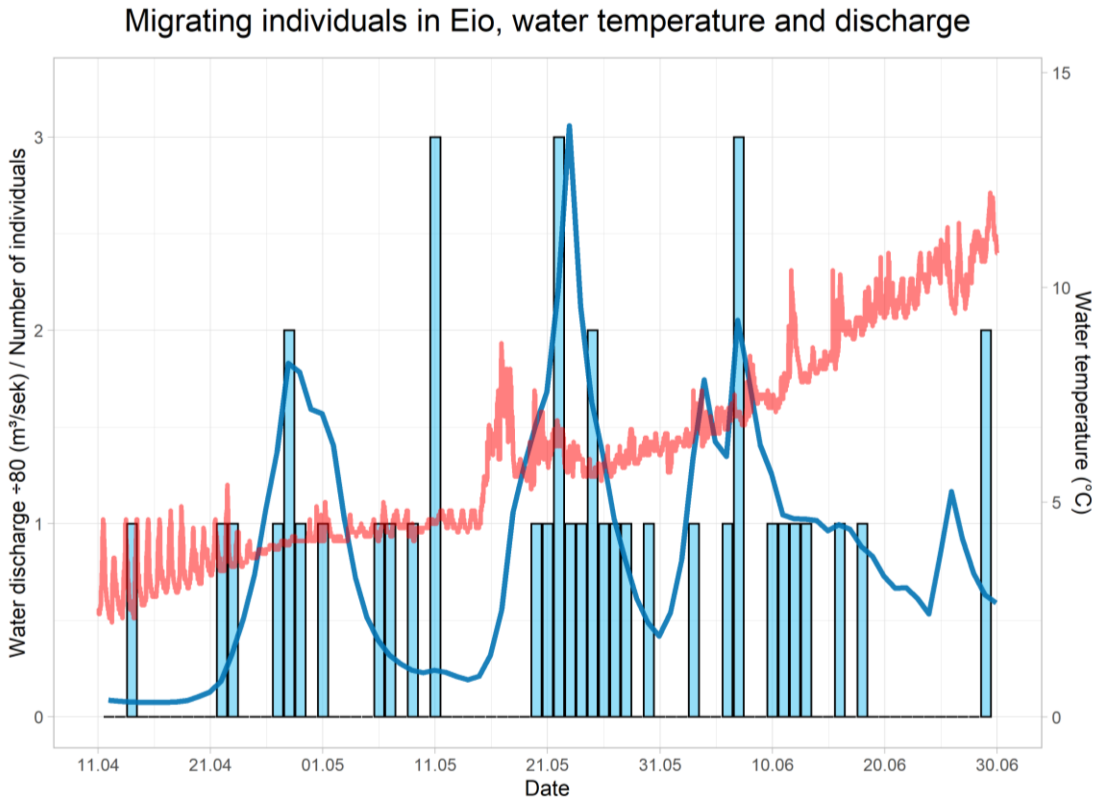

Figure 3.1: Migration to the river mouth over time in tagged brown trout from the River Eio, including water discharge (blue line) and water temperature (red line).

Table 3.1: Fixed effects parameter estimates (logit) for the most supported GLM-model water discharge+day of year (DoY) (Appendix Table A - 1).

Coefficients	Estimate	Std. Error	Z value	Pr (>|z|)
Intercept	-10.208	1.164	-8.769	< $2e^{-16}$
Water discharge	0.007	0.003	2.709	0.007
Day of year (DoY)	0.043	0.008	5.237	$1.63e^{-07}$
Null deviance	119.961 on 91 degrees of freedom			
Residual deviance	69.376 on 89 degrees of freedom			
AIC	140.84			

Table 3.2: ANOVA (logit) for the most supported GLM-model water discharge+day of year (DoY) (Appendix Table A - 1).

	Df	Deviance Resid.	Df	Resid. Dev	Pr (>Chi)
Water discharge	1	23.841	90	96.120	$1.046e^{-06}$
Day of year (DoY)	1	26.744	89	69.376	$2.323e^{-07}$

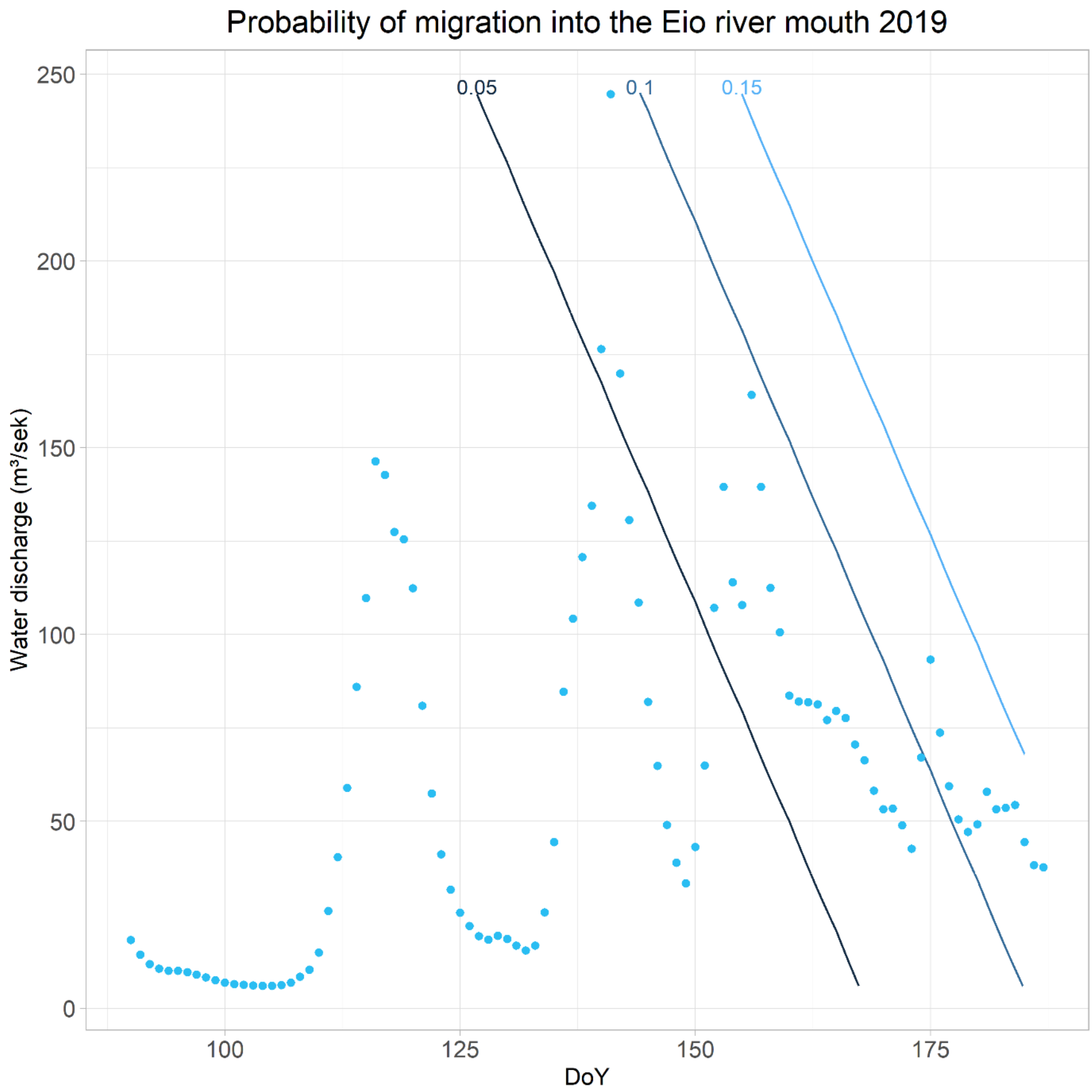

Figure 3.2: Probability of migration into the Eio river mouth based on water discharge and day of year (DoY). April 11th = 100 DoY, May 1st = 120 DoY, May 31st = 150 DoY, June 25th = 175 DoY. X-axis displays the day of year and the y-axis displays water discharge in m^3/sek. The contour lines represent the probability of migrating into the river mouth. The migration probabilities were estimated from the most supported model reported in Appendix Table A – 1.

Granvin

Detections of brown trout in the Granvin river mouth occurred in the period from April 17th to June 22nd, with the most fish detected on May 19th and May 23rd (Figure 3.3). This seems to be coherent with a combined effect of water level and water temperature. In total, 14 of the 31 detected individuals were never observed in the river mouth (45%) (Appendix Figure A – 2). The model selection procedure for candidate models estimating migration to the Granvin river mouth favored a model with water level and day of year (DoY) as additive predictors (Table 3.3 and 3.4), followed by a model with day of year (DoY) as additive predictors (Appendix Table A – 2). The probability of migration into the Granvin river mouth is shown in Figure 3.4.

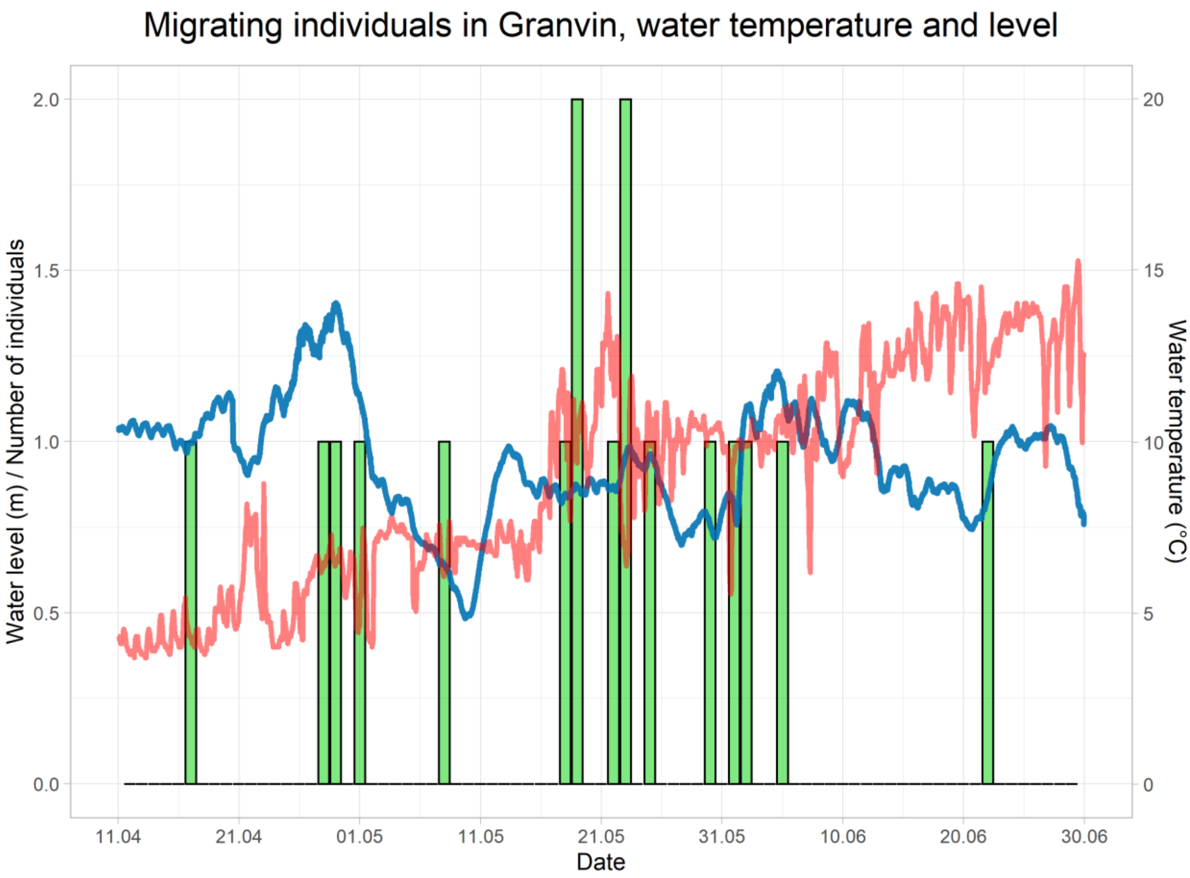

Figure 3.3: Migration to the river mouth over time in tagged brown trout from the River Granvinselva, including water level (blue line) and water temperature (red line).

Table 3.3: Fixed effects parameter estimates (logit) for the most supported GLM-model water level+day of year (DoY) (Appendix Table A - 2).

Coefficients	Estimate	Std. Error	Z value	Pr (>|z|)
Intercept	-14.660	2.752	-5.327	$9.99e^{-08}$
Water level	2.429	1.536	1.581	0.114
Day of year (DoY)	0.066	0.014	4.862	$1.16e^{-06}$
Null deviance	68.799 on 84 degrees of freedom			
Residual deviance	43.534 on 82 degrees of freedom			
AIC	78.066			

Table 3.4: ANOVA (logit) for the most supported GLM-model water level+day of year (DoY) (Appendix Table A - 2).

	Df	Deviance Resid.	Df	Resid. Dev	Pr (>Chi)
Water level	1	0.009	83	68.790	0.923
Day of year (DoY)	1	25.255	82	43.534	$5.022e^{-07}$

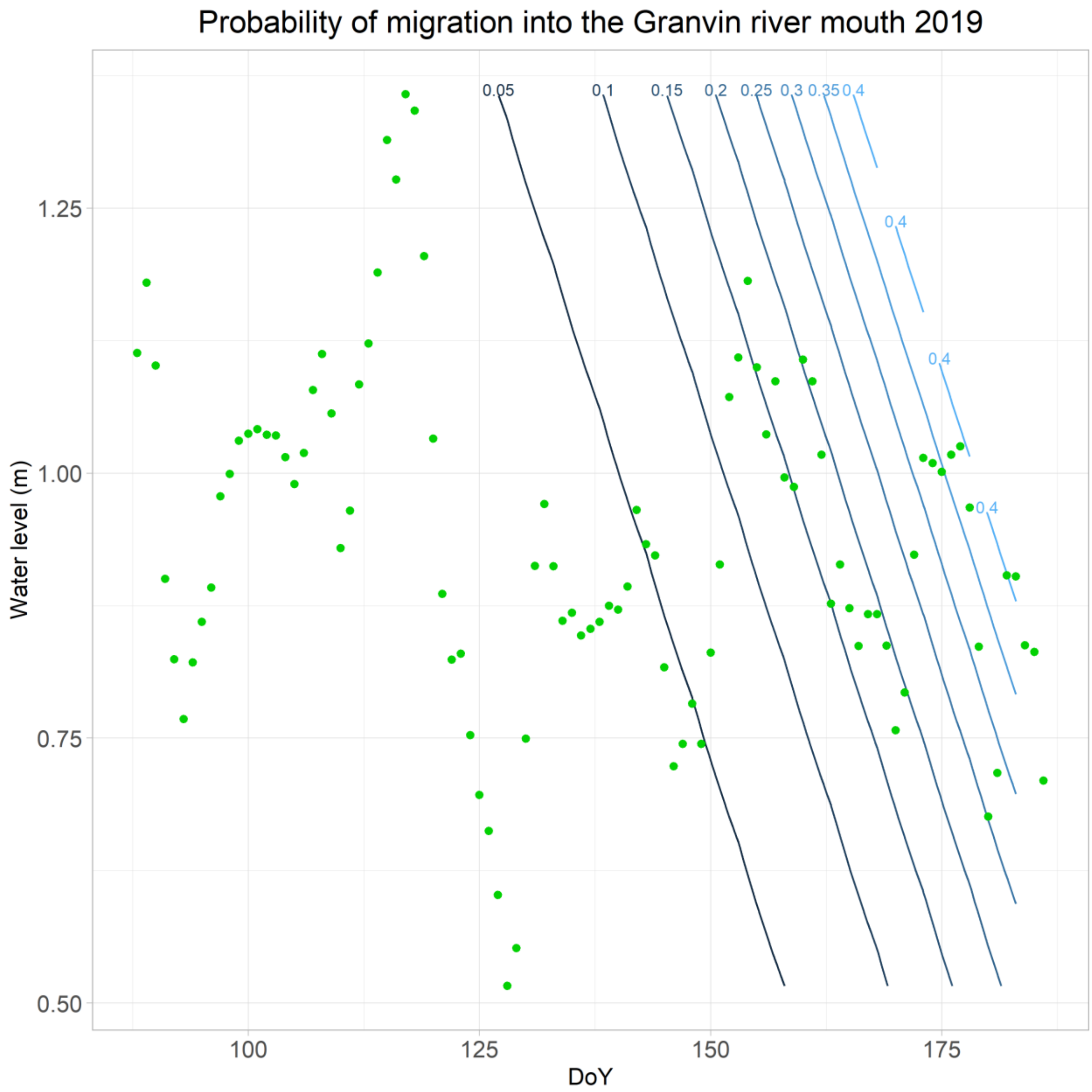

Figure 3.4: Probability of migration into the Granvin river mouth based on water level and day of year (DoY). April 11th = 100 DoY, May 1st = 120 DoY, May 31st = 150 DoY, June 25th = 175 DoY. X-axis displays the day of year and the y-axis displays water level in m. The contour lines represent the probability of migrating into the river mouth. The migration probabilities were estimated from the most supported model reported in Appendix Table A – 2.

Os

Detections of brown trout in the Os river mouth occurred in the period from April 12th to May 26th, peaking on April 13th (Figure 3.5). Most of the fish entered the river mouth in the middle to the end of April. All 32 detected individuals migrated to the river mouth (Appendix Figure A – 3). The model selection procedure for candidate models estimating migration to the Os river mouth favored a model with temperature and Δwater level as additive predictors (Table 3.5 and 3.6), followed by three models with temperature, temperature*water level and water level*day of year (DoY) respectively as additive predictors (Appendix Table A – 3). Figure 3.6 shows an increased probability for migration into the Os river mouth with increasing temperature and Δwater level.

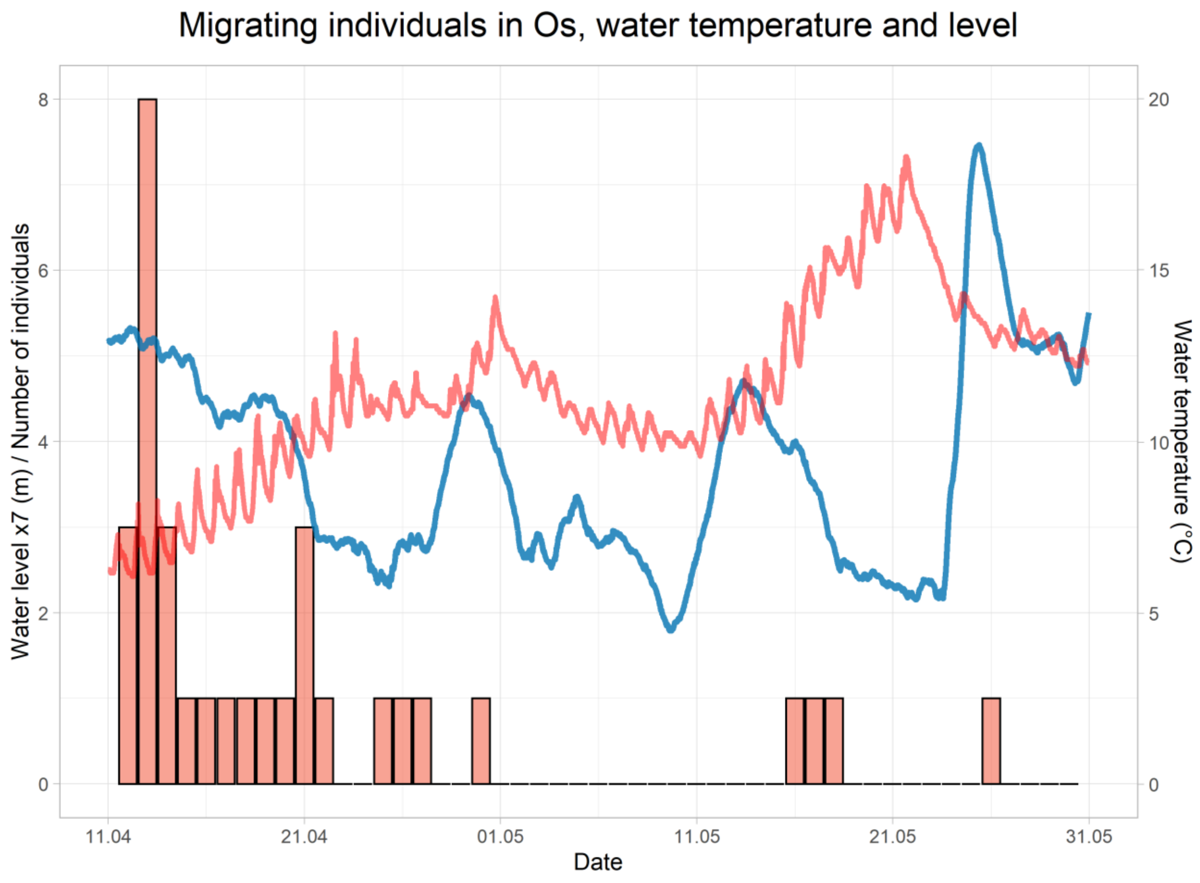

Figure 3.5: Migration to the river mouth over time in tagged brown trout from the River Oselva, including water level (blue line) and water temperature (red line).

Table 3.5: Fixed effects parameter estimates (logit) for the most supported GLM-model temperature∆water level (Appendix Table A - 3).*

Coefficients	Estimate	Std. Error	Z value	Pr (>|z|)
Intercept	-3.996	0.701	-5.698	$1.21e^{-08}$
Temperature	0.115	0.078	1.470	0.142
∆Water level	728.712	459.596	1.586	0.113
Temperature:∆water level	-92.331	46.598	-1.981	0.048
Null deviance	77.3551 on 55 degrees of freedom			
Residual deviance	59.669 on 52 degrees of freedom			
AIC	107.37			

Table 3.6: ANOVA (logit) for the most supported GLM-model temperature∆water level (Appendix Table A - 3).*

	Df	Deviance Resid.	Df	Resid. Dev	Pr (>Chi)
Temperature	1	11.749	54	65.606	0.001
∆Water level	1	0.164	53	65.442	0.686
Temperature: ∆water level	1	5.773	52	59.669	0.016

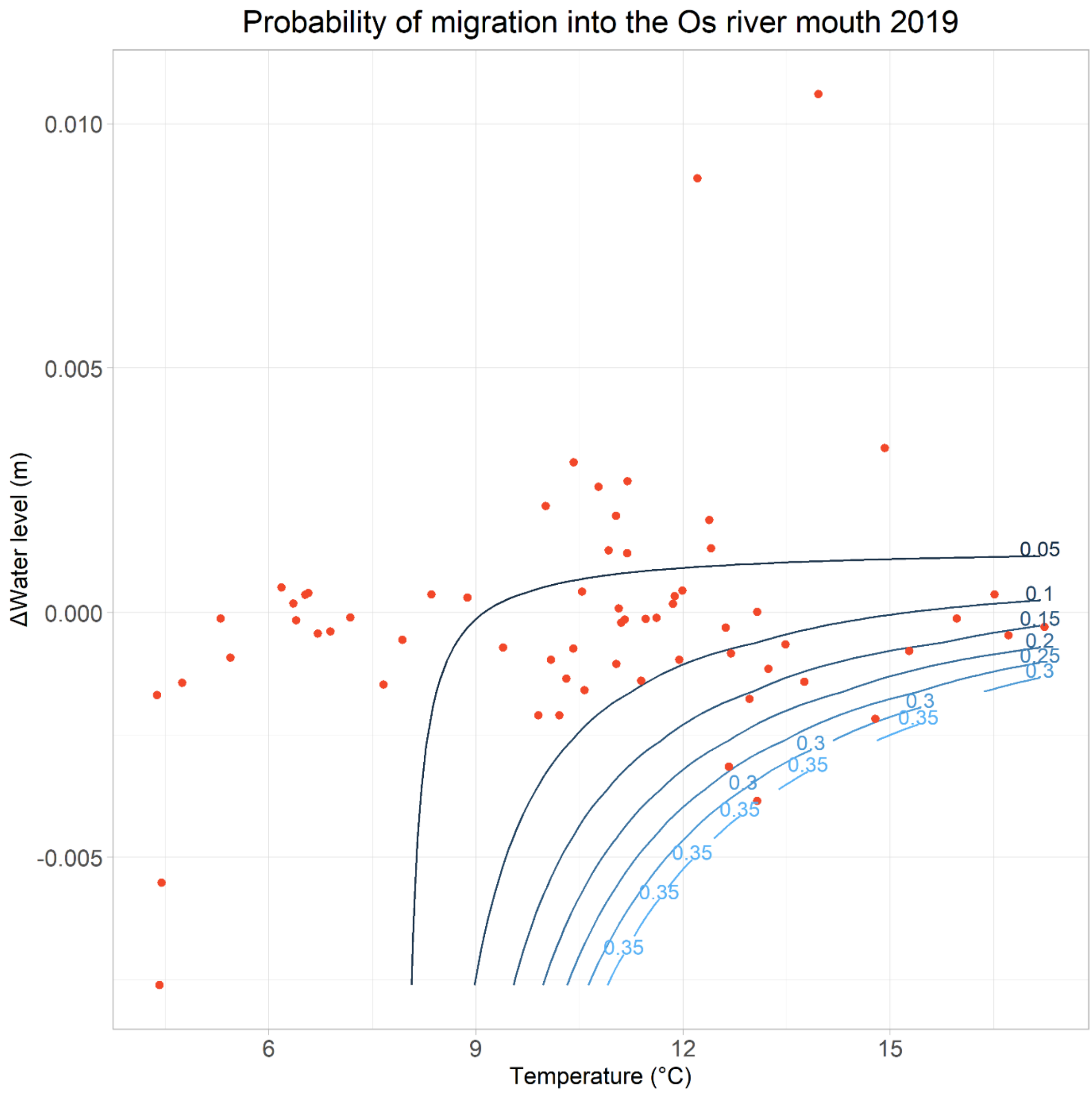

Figure 3.6: Probability of migration into the Os river mouth based on Δwater level and temperature. X-axis displays the temperature, and the y-axis displays Δwater level in m. The contour lines represent the probability of migrating into the river mouth. The migration probabilities were estimated from the most supported model reported in Appendix Table A – 3.

3.3 Fjord use

3.3.1 Arrival and residence time in different zones

Brown trout from Eio arrived in the inner to middle zones (a2 and b) at around June 25th, and only one individual was detected in the outer zones of the fjord (Figure 3.7). The brown trout from Granvin arrived to the inner to middle zones at approximately June 3rd and continued to the middle to outer zones (c, d) at around June 10th. They were observed to arrive in the outer zone close to Os (e1) at around July 9th (Figure 3.8). Lastly, brown trout from Os were observed in the outer zones (e2, d) on June 2nd, the middle zone (c) on August 15th, and the inner zone (a2) on September 23rd (Figure 3.9).

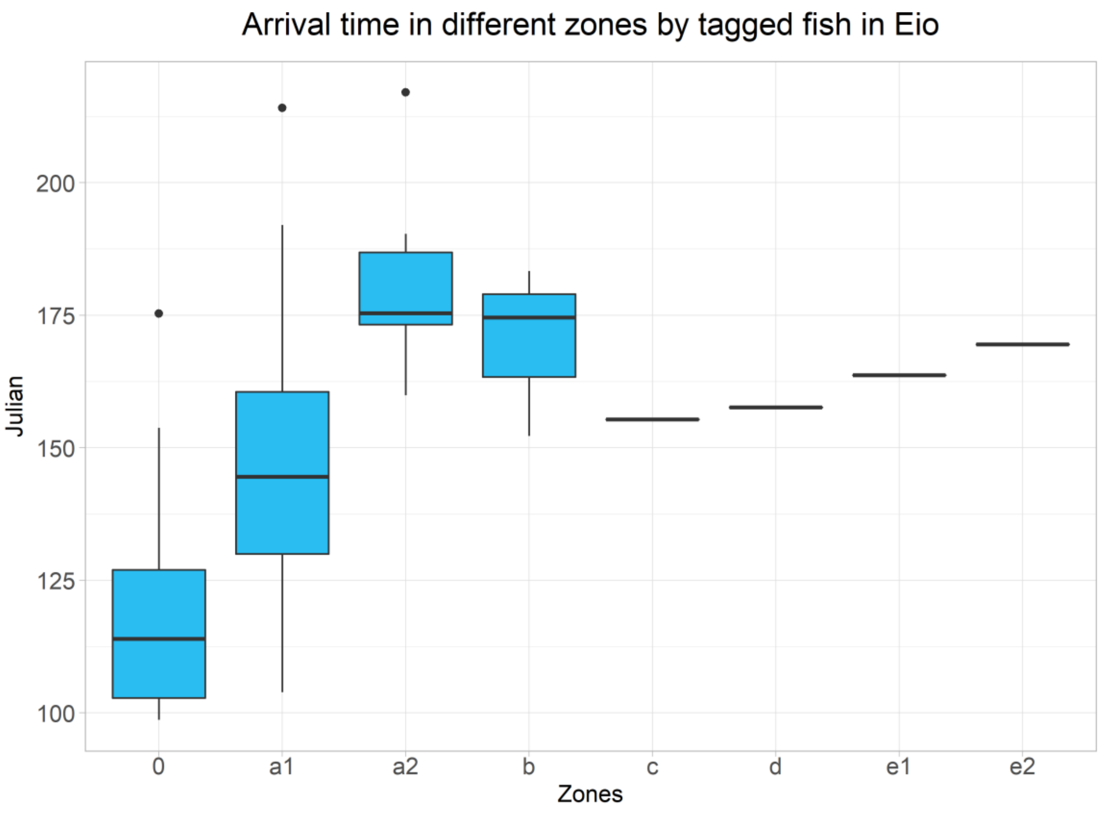

Figure 3.7: Arrival time in the different zones by tagged brown trout in Eio. Only one individual migrated to the four outer zones. Julian = the number of days since January 1st, 2019. 100 julian = April 11th, 125 julian = May 6th, 150 julian = May 31st, 175 julian = June 25th, 200 julian = July 20th.

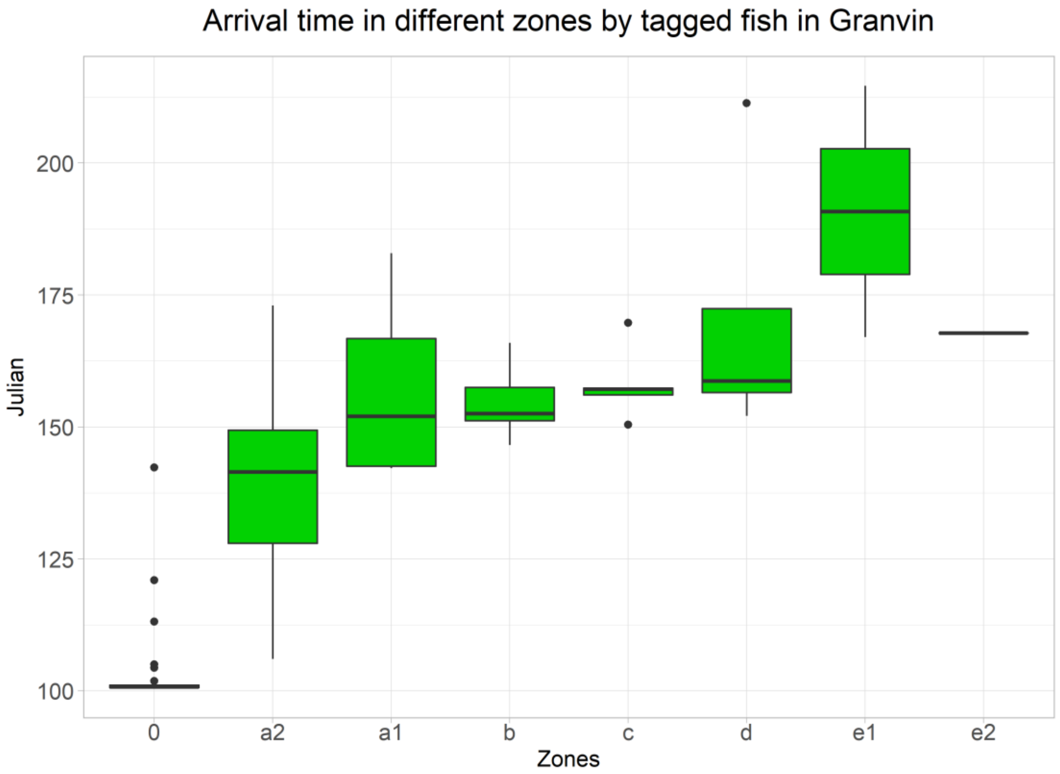

Figure 3.8: Arrival time in the different zones by tagged brown trout in Granvin. Julian = the number of days since January 1st, 2019. 100 julian = April 11th, 125 julian = May 6th, 150 julian = May 31st, 175 julian = June 25th, 200 julian = July 20th.

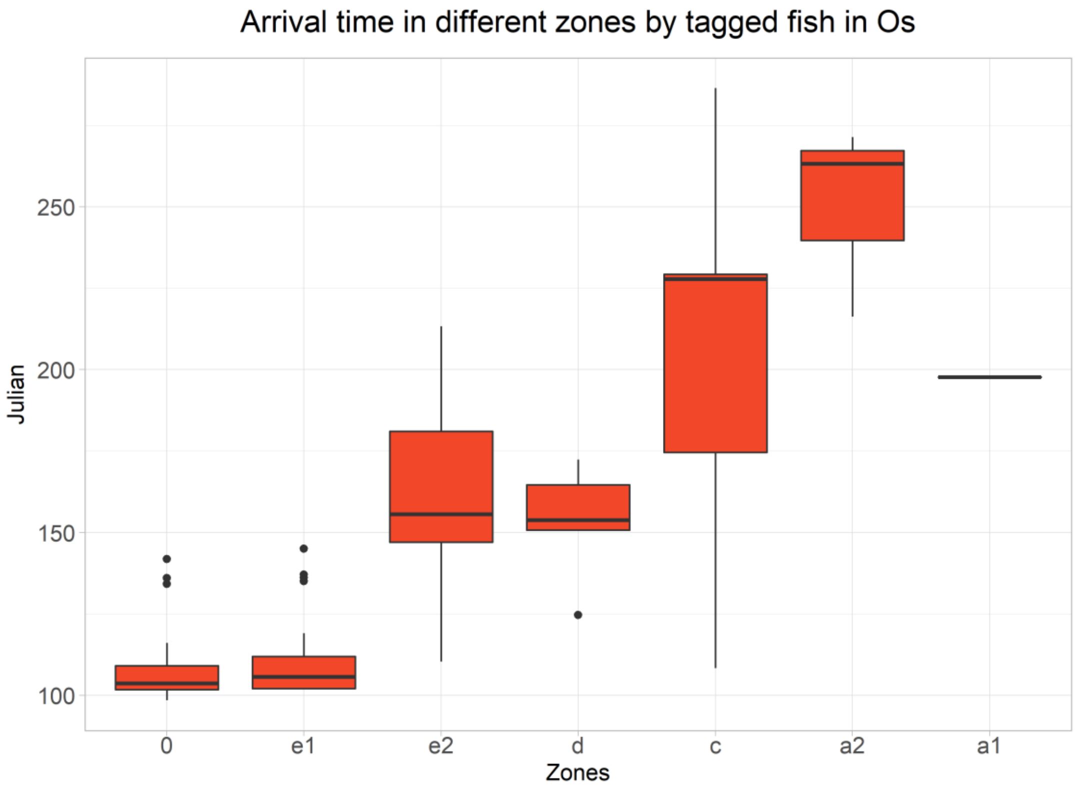

Figure 3.9: Arrival time in the different zones by tagged brown trout in Os. Julian = the number of days since January 1st, 2019. 100 julian = April 11th, 150 julian = May 31st, 175 julian = June 25th, 200 julian = July 20th, 250 julian = September 8th.

The residence time in different zones varied among individuals from all rivers (Figure 3.10). The Eio brown trout had the longest residence time in fresh water (approx. 55 days on average), while the Os brown trout had the shortest residence time in fresh water (approx. 44 days on average). The Granvin brown trout had a wider distribution of days spent in fresh water (approx. 135 days) compared to brown trout from Eio (approx. 85 days) and Os (approx. 92 days). The Eio brown trout spent approximately the same amount of time in the inner Hardangerfjord (a1) as in fresh water, while the Granvin brown trout spent less time in the inner Hardangerfjord (a2). The brown trout from Os had a little shorter residence time in the inner Bjørnafjord (e1, approx. 35 days on average) compared to its residence time in fresh water. Figure 3.10 also shows that brown trout from Granvin spent on average approximately 30 days in the inner part of Bjørnafjord (e1). The brown trout from Os seemed to utilize the outer and middle parts of the Hardangerfjord the most. No individuals were detected in the studied estuaries different from the estuaries in their home river. In general, the residence time in the middle parts of the Hardangerfjord (b, c, d) was short (< 12 days on average) for all three populations of brown trout.

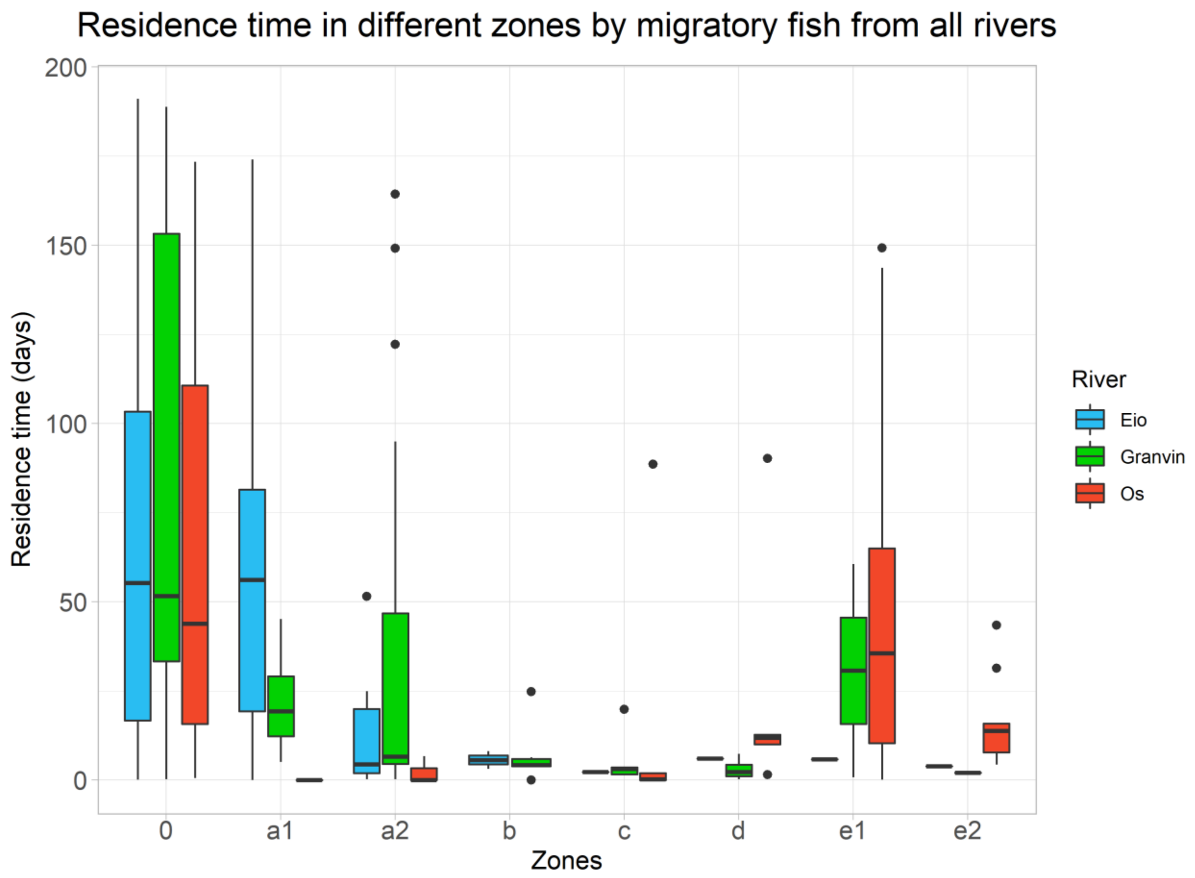

Figure 3.10: Boxplot of days spent in different zones by migratory brown trout from all rivers. The whiskers cover 90% of the group observations, the colored rectangles 50% and the bold vertical lines inside the rectangles represent the group medians.

3.3.2 Maximum distance travelled

The Granvin brown trout showed the longest distance travelled from the river mouth, while the brown trout from Eio and Os had approximately the same maximum distance travelled (Figure 3.11).

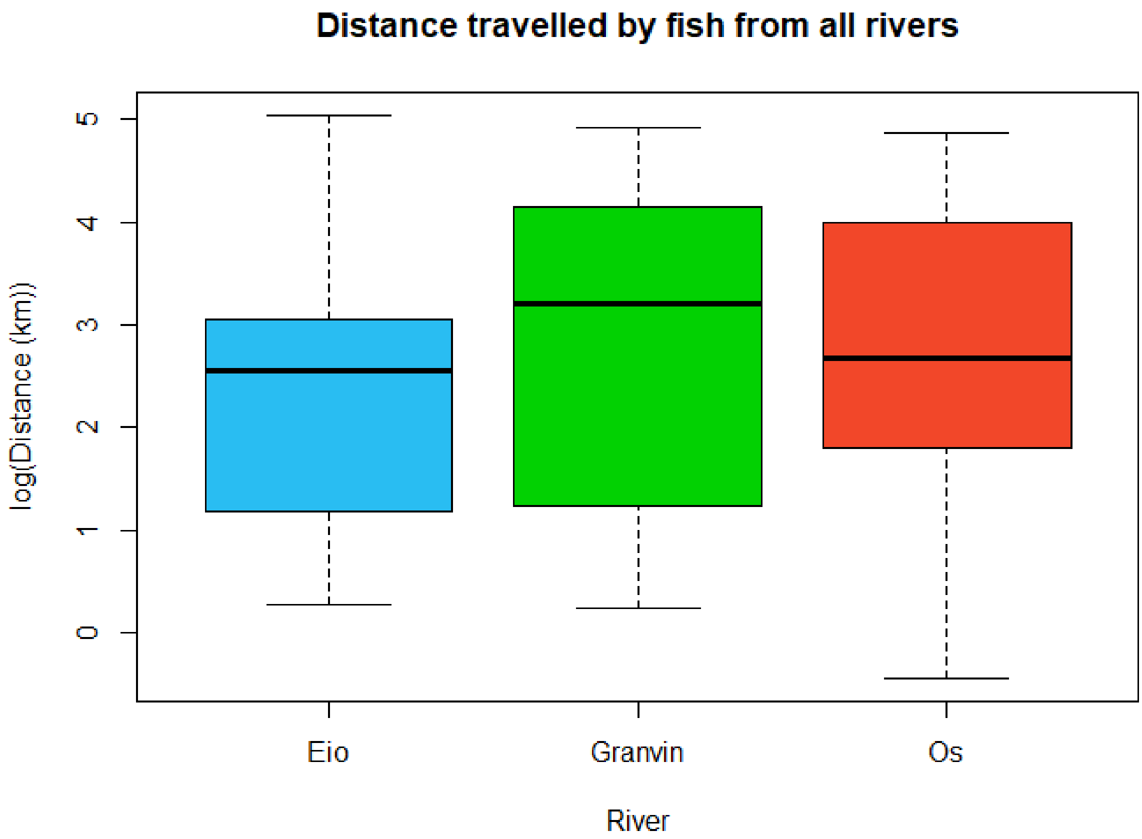

Figure 3.11: Boxplot of the logarithmic distance travelled (y) from respective river mouths (x) by migrating brown trout from all three populations.

Several linear models combining length, weight and condition factor were fitted to the maximum distance travelled data, but the candidate model with most support was an average (Appendix Table A – 4). According to the chosen model, the brown trout in this study travelled 11.3 km on average, regardless of the different populations (Confidence interval 11.33 (8.45, 15.2)).

3.3.3 Use of estuaries in migratory brown trout

Migratory brown trout from Os spent the highest fraction of time in the estuary (approximately 34.7%), compared to the migratory brown trout from Eio that spent the least percentage of time in their respective estuary (approx. 31.2%) (Figure 3.12). However, a more effective way of modelling time spent in estuaries was used; a model selection procedure for candidate models estimating the usage of estuaries by the three populations favored a model with an interaction between river and length as the additive predictor (Table 3.7 and 3.8) (Appendix Table A – 5). The chosen model predicted that the largest individuals by length (> 24 cm) from Os and Eio spend more time in their respective estuary compared to smaller individuals (< 19 cm) (Figure 3.13). However, the smallest individuals from Granvin spent more time in their respective estuary compared to larger individuals, and compared to time spent in the estuary by smaller fish from Eio and Os.

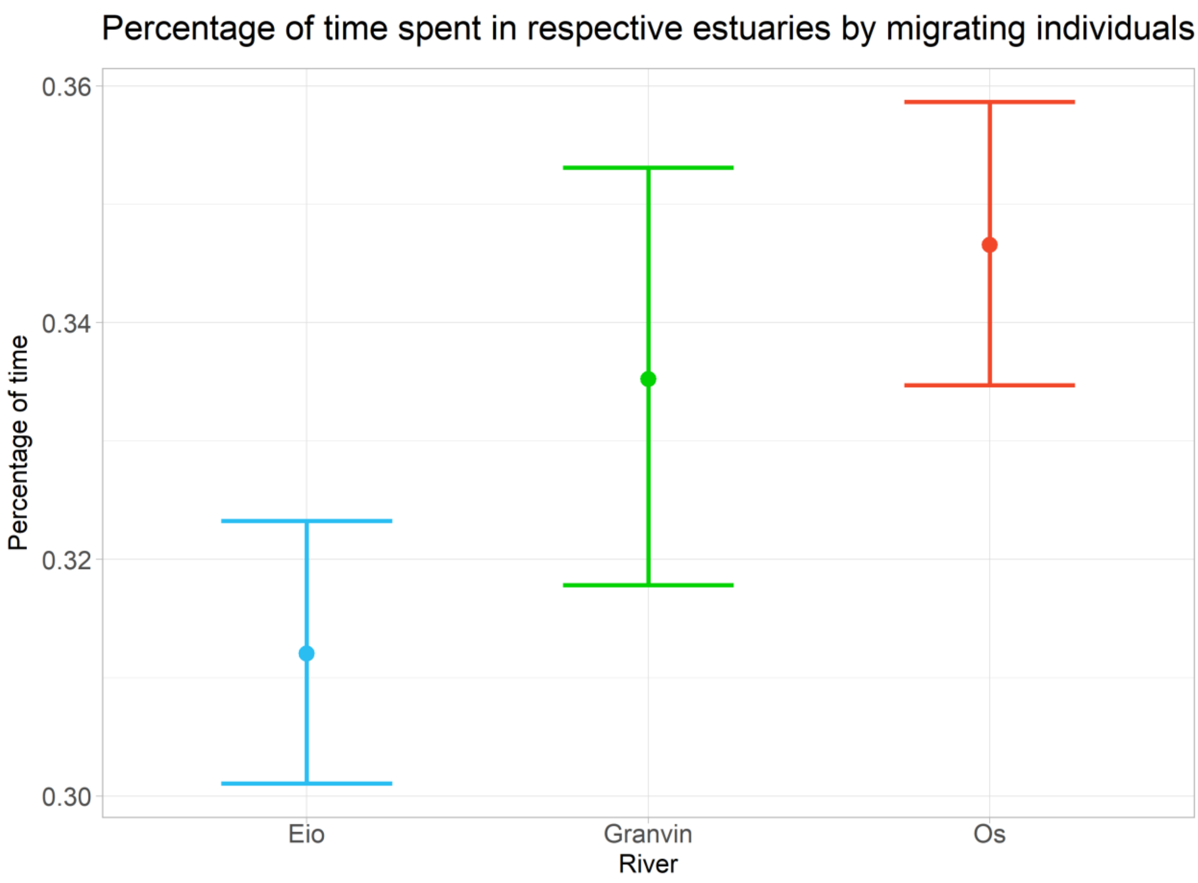

Figure 3.12: The percentage of time used in respective estuaries by migratory individuals from all rivers, Bars represent means and 95% confidence intervals (whiskers) predicted from the generalized linear model with river as the additive predictor. Stationary brown trout was excluded from the model.

*Table 3.7: Fixed effects parameter estimates (logit) for the most supported GLM-model river*length (Appendix Table A - 5).*

Coefficients	**Estimate**	**Std. Error**	**Z value**	**Pr (>|z|)**
Intercept	-1.301	0.133	-9.781	<2e-16
Granvin river	2.091	0.276	7.573	$3.65e^{-14}$
Os river	0.29	0.192	1.514	0.13
Length	0.025	0.006	3.929	$8.55e^{-05}$
Granvin river:length	-0.099	0.014	-7.263	$3.80e^{-13}$
Os river:length	-0.013	0.008	-1.609	0.108
Null deviance	1557.5 on 91 degrees of freedom			
Residual deviance	1478 on 86 degrees of freedom			
AIC	1928.9			

*Table 3.8: ANOVA (logit) for the most supported GLM-model river*length (Appendix Table A - 5).*

	Df	**Deviance Resid.**	**Df**	**Resid. Dev**	**Pr (>Chi)**
River	2	17.701	89	1539.8	0.00014
Length	1	6.090	88	1533.8	0.014
River:length	2	55.763	86	1478.0	$7.785e^{-13}$

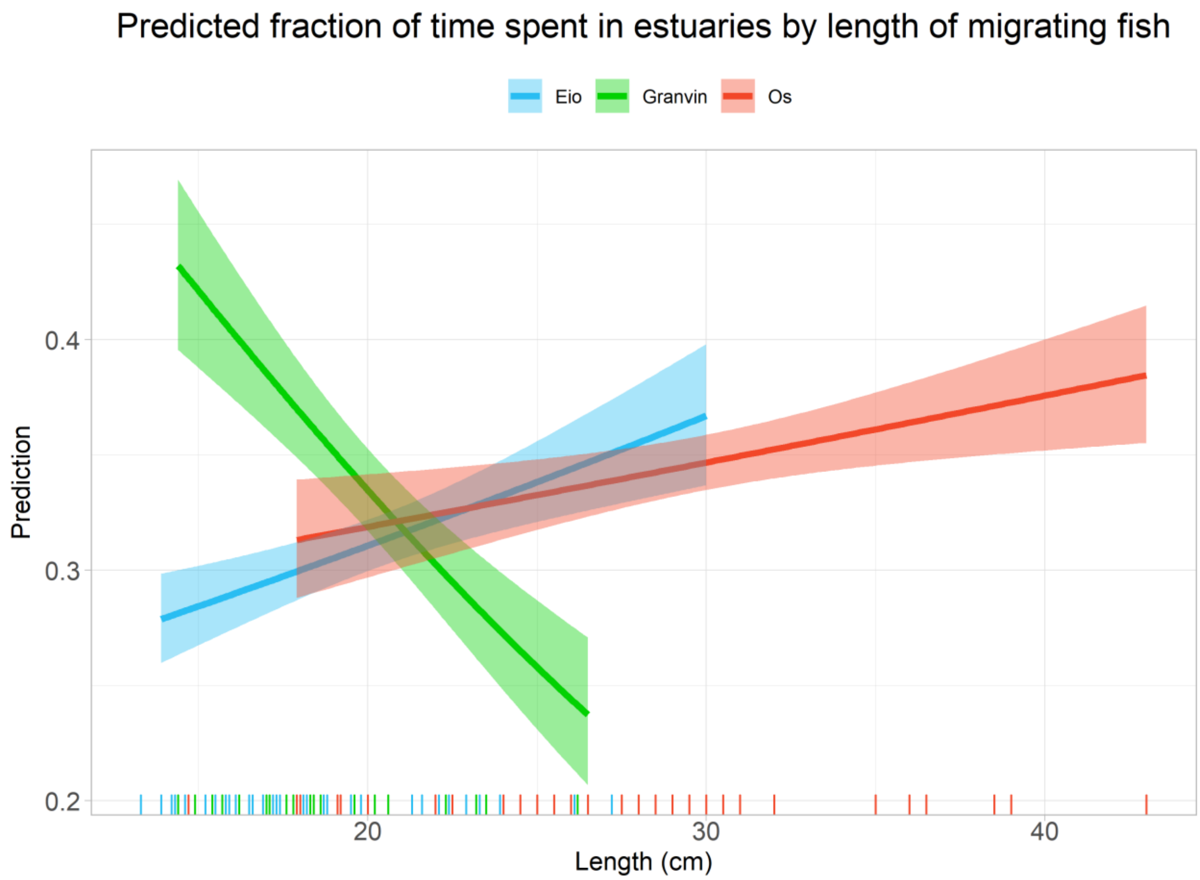

Figure 3.13: Predicted fraction of time spent in respective estuaries as a function of length for migratory brown trout from all three populations including the respective 95% confidence intervals. X-axis represent the length (cm) including each sample length for all individuals, while y-axis is the predicted residence time in the respective estuaries.

3.3.4 Mark-recapture analysis

A successfully fitted fully factorial CAS-model [S(period*zone*river)p(zone*river) ψ (period*zone*river)] (Parameter estimates table: Appendix Table A – 6) revealed that bi-weekly survival in fresh water was generally high for tagged brown trout from all three populations, but it decreased in the late period (August 12th to October 13th) (Figure 3.14). Survival in the near fjord-zone was at its highest during the middle period (June 17th to August 11th), while it decreased for some populations in the distant fjord-zone, specifically for the Os and Eio brown trout in the middle and late periods respectively.

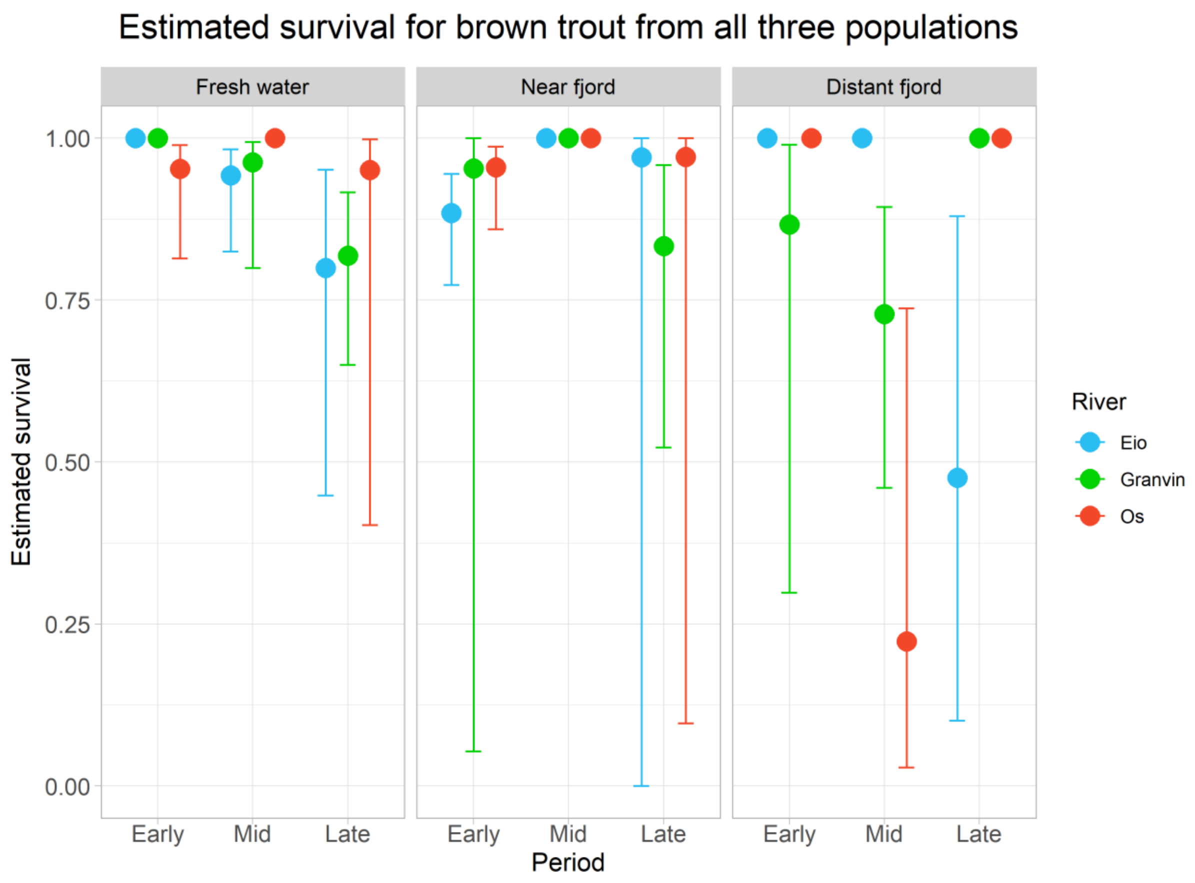

Figure 3.14: Estimated survival in each zone (S) in three different time periods for all three populations. Early period = from April 8th to June 16th, mid period = from June 17th to August 11th, late period = from August 12th to October 13th. The survival estimates were estimated from the most supported model reported in the main text.

The CAS-model indicated that the bi-weekly probability of being detected (p) was high for the Eio and Granvin brown trout in fresh water, brown trout from Os had a detection probability of approximately 47% in fresh water (Figure 3.15). The detection probability in the near fjord-zone was high for all three populations, while it was close to 1% for the Eio brown trout in the distant fjord-zone. The Os brown trout had the highest detection probability in the distant fjord-zone (25%).

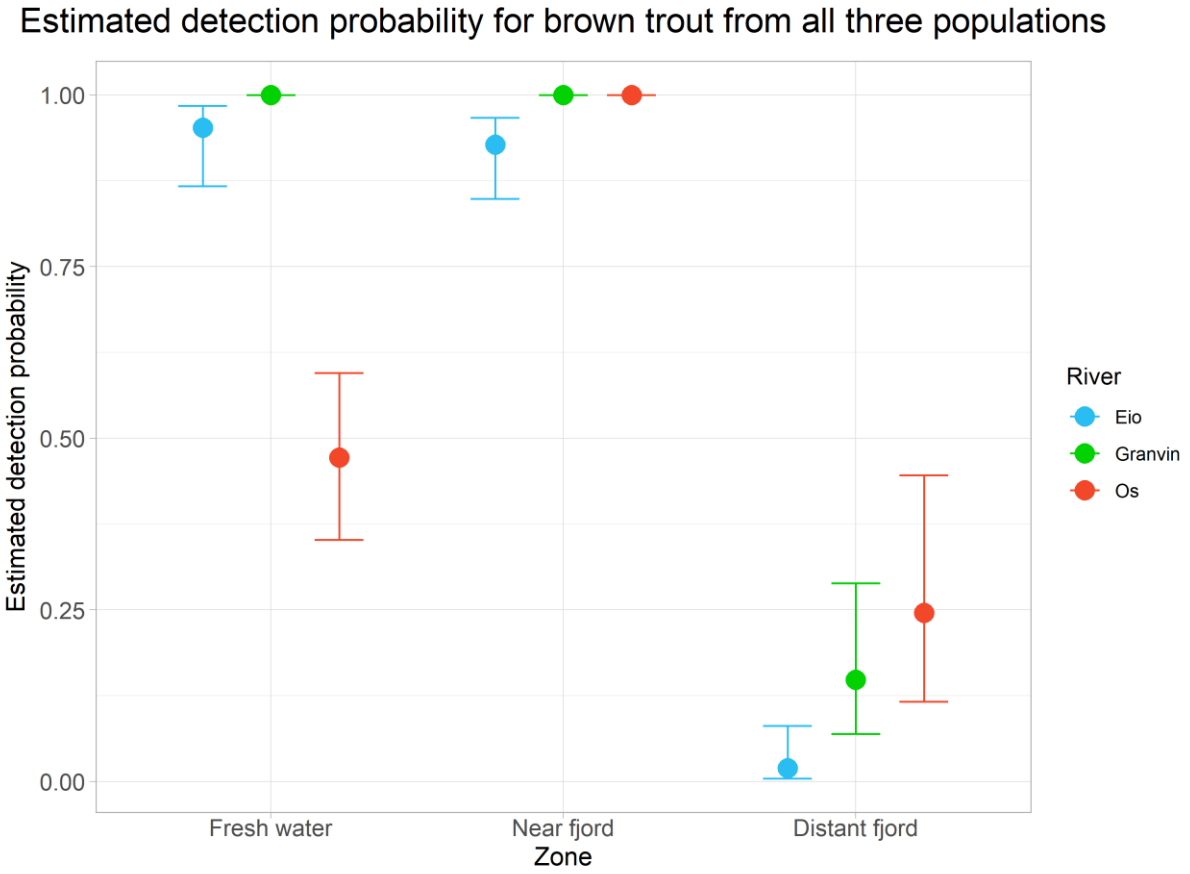

Figure 3.15: Estimated detection probability (p) in three different zones of the Hardangerfjord for all three populations. Early period = from April 8th to June 16th, mid period = from June 17th to August 11th, late period = from August 12th to October 13th. The detection probabilities were estimated from the most supported model reported in the main text.

It is indicated by the CAS-model that the bi-weekly likelihood of migrating from fresh water to the near fjord-zone (ψ) was higher for the Os brown trout compared to the Eio and Granvin brown trout (Figure 3.16). Fewer of the Granvin brown trout individuals were migratory (55%), but those who were, migrated early and far. Migration from the near fjord-zone to fresh water increased during the mid and late periods.

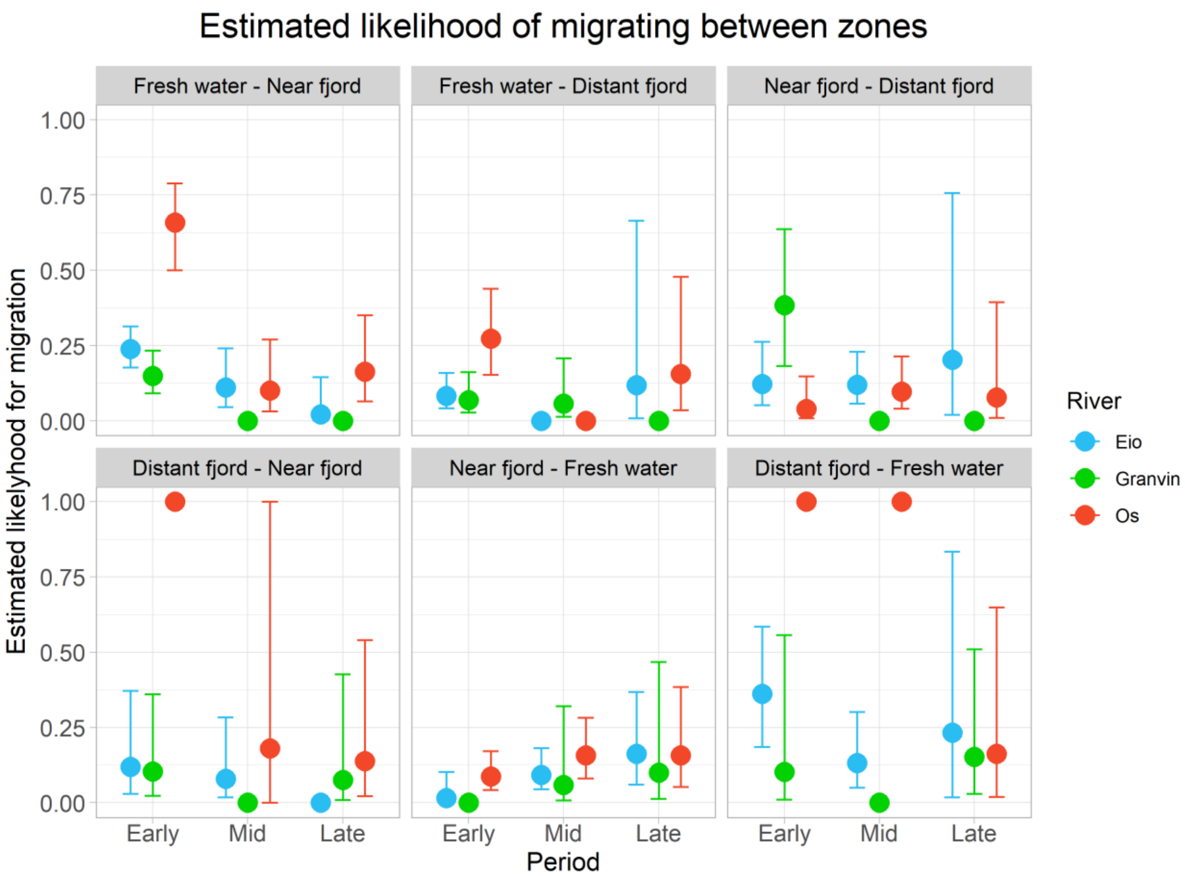

Figure 3.16: Estimated likelihood of migrating among zones (ψ) in three different time periods for all three populations. Early period = from April 8th to June 16th, mid period = from June 17th to August 11th, late period = from August 12th to October 13th. The estimated likelihoods of migrating among zones were estimated from the most supported model reported in the main text.

4. Discussion

4.1 Time of migration to the river mouth and influencing factors

The observed time of migration to the respective river mouths in this study occurred between April and June in all three populations. The Eio individuals portrayed the broadest time period of migration (April 14th to June 29th), while Os had the narrowest migration time span in the study (April 12th to May 26th). The seaward migration among the Os brown trout seemed to be more coordinated among the individuals compared to the Eio and Granvin brown trout. This coincided with the Os brown trout having the highest estimated biweekly likelihood of migrating from fresh water to near fjord areas in the early period. The migration of brown trout smolts in a Danish stream was observed to occur from early March until June (Rasmussen, 1986, cited in Jonsson & Finstad, 1995). Flaten et al. (2016) observed that the downstream migration occurred within a period of 5-6 weeks between May and the middle of June in Hemnfjord and Snillfjord, mid-Norway. In Norumsån, south-Sweden 90% of the downstream migration was observed over the course of 29 days, from the middle of April until the middle of May (Bohlin et al, 1993, cited in Klemetsen et al., 2003). Hembre et al. (2001) studied the smolt run in the River Stjørdalselva, mid-Norway, and observed that the main smolt run took place over 7-10 days in the middle of and towards the end of May. Altogether, the time of seaward migration has been reported to vary among watercourses and development stages of the fish (Klemetsen et al., 2003), which coincides with the results of this study.

I hypothesized that the brown trout migrated to the river mouth with increasing water discharge and water temperature. This was partially supported by the study results for all three populations. Water flow and day of year were favored additive predictors for the estimated migration to the river mouth in Eio and Granvin, while temperature and daily change in water level was favored in Os. This is in accordance with several other studies (Aldvén et al., 2015; Jensen et al., 2012; Jonsson & Jonsson, 2011; Jonsson & Finstad, 1995). Jensen et al. (2012) found that water flow explained day-to-day variations in smolt runs made by both Atlantic salmon and brown trout in the River Halselva in northern Norway, with water flow being the most important factor for the brown trout. In contrast, Solomon (1978) reported that smolt runs in the River Piddle, England, was correlated with increasing water temperatures. Jonsson and Jonsson (2002) reported that the downstream migration of anadromous brown trout in the River Imsa was influenced by water temperature, where approximately 50% of the tagged fish smaller than 30 cm, migrated downstream in temperatures ranging from 7.5 °C to 12.5 °C. Individuals larger than 30 cm was observed to migrate downstream in temperatures under 7.5 °C. A combination of water discharge and water temperature has also been reported to influence downstream migration of brown trout in the River Himleån, Sweden and the River Stjørdalselva, mid-Norway (Aldvén et al., 2015; Hembre et al., 2001). In 2011 Aldvén et al. (2015) observed that brown trout in the River Himleån remained in the river even when the temperature reached 10 °C, as a consequence of low precipitation and thus low water discharge. Observations made the following year showed that smolts had a tendency of migrating in periods of high discharge in highly turbid water, indicating that the increased water turbidity during intensified water flow could provide a greater protection from visual predators such as gulls and cormorants (Gregory & Levings, 1998). Altogether, the results in this study corroborate that the influence of water discharge and water temperature on downstream migration likely vary among populations, watercourses and years, and could consist of combinations of influencing factors (Aldvén et al., 2015; Hembre et al., 2001; Jonsson & Finstad, 1995; Klemetsen et al., 2003).

4.2 Fjord use

The arrival time to the different zones of the Hardangerfjord varied among the three populations. Brown trout from Granvin arrived in the inner to middle zones 22 days prior to the Eio brown trout, and were observed to arrive in the outer fjord areas in early July. The tagged brown trout from Eio seemed to utilize the inner middle zones of the Hardangerfjord the most and only one individual was detected in the outer Hardangerfjord. The tagged Granvin brown trout spent less time in the inner Hardangerfjord compared to brown trout from Eio, however they were also observed to spend on average approximately 30 days in the inner part of Bjørnafjord. This coincided with the Granvin brown trout having the highest estimated biweekly likelihood of migrating from the near fjord to distant fjord areas in the early period. The Os brown trout mostly utilized the inner Bjørnafjord area but were detected in the middle to inner zones from August through September. Similarly, observations made by Middlemas et al. (2009) in North-Scotland showed that the brown trout tended to slowly migrate from their natal river. The results of this study could imply that the inner Hardangerfjord is an important area for anadromous brown trout from both Eio and Granvin.

The inner Bjørnafjord also seems to be an important area for the anadromous brown trout from Os in addition to the long-distance migrating individuals from Granvin. The Eio brown trout residence times are in accordance with studies of brown trout in the inner Sognefjord, west-Norway (Haugen et al., 2019), where the residence time in the inner zones of the Sognefjord was considerably longer than residence time in the outer zones. 77% of the tagged brown trout smolts (n=15) in the Romsdalsfjord, west-Norway, were observed to remain in and utilize the inner fjord system (Finstad et al., 2005). It has been argued by Flaten et al. (2016) that the use of habitat can be influenced by a combination of feeding opportunities and the risk of predation. Near shore habitats have more hiding places and vegetation than the open areas in the outer fjord areas, as well as suitable prey (Flaten et al., 2016; Knutsen et al., 2001), which could explain why the Eio brown trout in this study remained in the inner fjord areas. One could also speculate that the food availability is sufficient in the innermost area of the Hardangerfjord, resulting in no need for long-distance migration to find energy-rich prey. In the present study, one individual from Eio and five individuals from Granvin were detected in the outer zones of the Hardangerfjord. Similar observations of brown trout have been reported in the Stryn river system, where only a small amount of the tagged individuals migrated to the outer fjord areas (Urke et al., 2018). However, studies have observed variations in marine residence time among and within populations with several factors affecting the individual marine residence time (Jonsson, 1985; Middlemas et al., 2009). Altogether, the results in this study could imply that the majority of brown trout from watercourses located in the inner parts of the Hardangerfjord, tended to utilize the inner parts and near shore habitats of for grazing, while a smaller amount of individuals migrated to the outer parts of the Hardangerfjord system to possibly find pelagic prey of higher energy-richness.

I hypothesized that the maximum distance travelled from their respective rivers increased with fish size. However, the results did not support my hypothesis. The maximum distance travelled by the anadromous brown trout in this study was not size dependent and did not vary among the three populations. Long-distance veteran migrants of brown trout in Hemnfjord and Snillfjord in 2012-2013 were observed to have poorer body condition in spring prior to migration (Eldøy et al., 2015). There was a high variance in individual distance migrated (40% migrated less than 4 km from the river mouth, 18% migrated between 4-13 km, and 42% migrated more than 13 km), and individuals of all size categories performed long-distance migrations. Eldøy et al. (2015) argued that fast growing individuals shift to a more piscivorous diet at a smaller size and younger age than slower-growing individuals, and that differences in genetics and behavior could explain the observed variation in migratory strategies. Flaten et al. (2016) observed the same fjord system in 2014 and found that the distribution of post smolts in the fjord was size dependent, with larger individuals utilizing the outer fjord area and portraying earlier returns to fresh water. Flaten et al. (2016) argued that their findings could indicate that brown trout with a high metabolism and growth rate had a higher likelihood of being long-distance migrants, in order to find suitable food items. Similarly, Jensen et al. (2014) observed that smaller individuals were less likely to be long-distance migrants than large individuals in the Alta fjord, suggesting that this was due to a higher abundance of suitable fish prey for large individuals in the outer areas of the fjord. Knutsen et al. (2001) reported that small post-smolt brown trout on the Norwegian Skagerrak coast fed inshore, while larger individuals fed further offshore on pelagic fish. Small fish in poor condition in the Etnefjord, a side-fjord of the outer Hardangerfjord, were observed to spend less time in the outer parts of the Etnefjord compared to large individuals in good condition (Halttunen et al., 2018). Altogether, the results in this study could be explained by individuals with a high metabolism and growth rate shifting to a more piscivorous diet at a smaller size, and portraying long-distance migrations to find suitable prey, compared to small and slower-growing individuals. On the contrary, the distribution of small individuals that migrated long-distance could be random, or a result of competition with conspecifics in inshore areas, as argued by Eldøy et al. (2015).

I hypothesized that individuals that migrated to the outer fjord areas with high salmon lice densities spent a higher fraction of time in their respective estuaries than those that only used inner and mid parts of the fjord. The tendency observed in this study supported this hypothesis. Although the difference in percentages was low (approx. 3.5%), the brown trout from Os had a higher fraction of time spent in their respective estuary (approx. 34.7%) compared to the Eio brown trout (approx. 31.2%). Of the three studied estuaries and subsequently the three brown trout populations, none of the brown trout appeared to ever enter the counterpart estuaries. In 2019, the infestation pressure of salmon lice was considered moderate to high in certain areas of the Hardanger- and Bjørnafjord (Vollset et al., 2019). The density of infectious salmon lice was observed to be high in the inner area of the Bjørnafjord on May 21st, 2019, and moderate in the outer part of the Bjørnafjord and middle areas of the Hardangerfjord (Vollset et al., 2019). The induced mortality caused from salmon lice in 2019 was considered moderate (Vollset et al., 2019). Thus, the infestation pressure in the

Bjørnafjord and middle parts of the Hardangerfjord, could explain the observed tendency in this study; the Os brown trout spending a higher fraction of time in their respective estuary compared to the Eio brown trout. The Eio brown trout had a lower likelihood of migrating from fresh water to the fjord compared to the Os brown trout, and overall a low likelihood of migrating towards the outer areas of the Hardangerfjord affected by salmon lice. The Eio brown trout spent most of its time in the inner parts of the Hardangerfjord (zone a1, Figure 2.8), an area that has no fish farms and is less affected by the salmon lice. The Granvin brown trout spent the intermediate fraction of time in their estuary, which could be explained by them utilizing the inner middle areas of the fjord (zone a2, Figure 2.8) the most, which are in proximity to the innermost located fish farms in the Hardangerfjord (located between zone a2 and b, Figure 2.8). The fish farms located in the inner to middle Hardangerfjord therefore could facilitate a higher abundance of salmon lice in these areas, causing more salmon lice exposure for the Granvin brown trout. The observed tendencies in this study coincide with a three-year study of anadromous brown trout in the Etnefjord by Halttunen et al. (2018). Halttunen et al. (2018) observed that the brown trout spent more time in delousing areas in years with high infestation pressure compared to years with low infestation pressure. In years with low infestation pressure the brown trout travelled further out and had longer periods of marine migration compared to years with high infestation pressure. However, Halttunen et al. (2018) found no difference in survival between years of low and high infestation pressure and suggested that the brown trout adapted their behavior in compensation for the direct mortality risks caused by salmon lice. Altogether, these adaptions could lead to reduced growth, thus reduced fecundity and extended exposure to size dependent predation risk, as the opportunities for foraging and growth are lost due to the increased time spent in delousing areas. This could make the cost of migration higher than the benefit, reducing or even eliminating the likelihood of seaward migration in the affected population.

H4: Large individuals have a higher rate of return to their respective estuaries than smaller individuals.

I hypothesized that large individuals had a higher rate of return to delousing areas than smaller individuals. The results of this study supported this for the Eio and Os brown trout, but not for the Granvin brown trout. It was predicted that the largest individuals by length (> 24 cm) from Os and Eio spent more time in their respective estuary compared to smaller individuals (< 19 cm). In contrast, the smaller individuals from Granvin spent more time in their respective estuary compared to larger individuals. Halttunen et al. (2018) observed that larger brown trout spent more time in the outer fjord areas on average compared to smaller individuals, which would make them more exposed to salmon lice and thus more likely to spend increased time in delousing areas. Similarly, results from a study of salmon lice abundance by Heuch et al. (2009) in the Hardangerfjord indicated that larger fish had a higher abundance of salmon lice. This could imply that the large individuals from Os in this study experienced a higher infestation pressure from salmon lice compared to the smaller individuals, and therefore spent more time in the estuary. However, the high fraction of time spent in the respective estuary by large individuals in Eio is most likely not explained by a higher abundance of salmon lice, as only one individual was detected in the middle and outer areas of the Hardangerfjord. The remaining individuals utilized the innermost parts of the Hardangerfjord with low abundances of salmon lice. The Granvin brown trout differed from Eio and Os, with small individuals spending the highest fraction of time in the respective estuary. As observed in this study, the migratory individuals from Granvin migrated early and far, and were observed to spend on average approximately 30 days in the inner parts of the Bjørnafjord, an area with moderate to high infestation pressure in 2019. Speculations can be made that medium and large sized individuals from Granvin migrated towards the outer areas fjord areas as observed in Halttunen et al. (2018), but sought refuge in estuaries that were not included in this study, giving the impression that the smaller individuals spent a higher fraction of time in the Granvin estuary. Altogether, this study seems to indicate a tendency for larger fish from Os and possibly Granvin to be affected by salmon lice densities in the outer fjord areas, while salmon lice is most likely not the main reason for the same tendency observed in Eio.

I hypothesized that the survival probabilities were lowest in the outer Hardangerfjord (salmon lice-induced). This was not supported by the results in this study. The brown trout from Os had high survival probabilities in the outer areas of the Hardangerfjord in general, but it decreased in the middle to inner areas. The Granvin brown trout had generally high survival probabilities (>70%), while the Eio brown trout had lower survival probabilities in the outer fjord areas (<50%) in the late period. Only one individual from the River Eio was detected the outer areas of the fjord and was not observed to have migrated back to the inner parts of the Hardangerfjord. Halttunen et al. (2018) found no differences in survival between years of high and low infestation pressure from the salmon lice in the Etnefjord. As previously discussed in relation to time spent in estuaries, this could imply that the brown trout in this study adapted its behavior to compensate for the risk of mortality. Altogether, the high survival probabilities in this study could be an indication of behavioral adaptations to avoid immediate mortality risks caused by the salmon lice. In the long run, this adaptation could lead to reduced amounts or elimination of anadromy in the populations affected, as the cost of migration outweighs the benefits.

I also hypothesized that the survival probabilities were at their lowest right after migration from fresh water to the fjord (predation-induced). The results in this study partially supported my hypothesis. The survival probabilities were high in general, but the Eio and Os brown trout had the lowest probabilities during the early period (April 8th to June 16th) after migration to the near fjord area. In contrast, the Granvin brown trout had lower probabilities during the late periods (August 8th to October 13th). Previous studies have revealed an increased mortality rate shortly after brown trout smolts migrated to the river mouth and into the sea (Dieperink et al., 2001; Middlemas et al., 2009), which could be in accordance with the results for the Eio and Os brown trout in this study. Dieperink et al. (2001) observed a high daily predation rate in the Horsens Fjord, Denmark, 2 days after the seaward migration. This supported his hypothesis that the risk of predation increased shortly after the smolts were exposed to full-strength sea water, but also indicated that osmoregulatory problems could be another factor influencing mortality (Dieperink et al., 2001). Middlemas et al. (2009) had similar findings in Loch Torridon, Scotland; the post-smolts had an increased mortality due to predation in the river mouth during the first 14 days after seaward migration. However, the lower survival probabilities following the seaward migration in this study were observed over a longer period of time (April 8th to June 16th) compared the studies of Middlemas et al. (2009) and Dieperink et al. (2001). In addition, Jonsson and Jonsson (2009) observed that the brown trout smolts in the River Imsa migrated downstream together with the Atlantic salmon smolts, implying that the brown trout smolt avoided predation in the river mouth by seeking shelter in schools consisting of Atlantic salmon. Altogether, the generally high survival probabilities (>88%) presented in this study following seaward migration, could imply low predation pressures, or possibly that brown trout could have migrated together with Atlantic salmon smolts to decrease the risk of predation in the river mouths.

4.3 Shortcomings and suggestions of improvement

Collection and tagging of fish happened from April 8^{th} to 11^{th} 2019. The tagged brown trout in Os seemed to migrate to the river mouth shortly after release (April 13^{th}). Earlier tagging of the fish could possibly have given more information on the exact migration time, seeing as the downstream migration could have already been initiated in Os at the time of collection and tagging. The handling and tagging procedure of the fish could have altered its natural behavior, such as reducing its swimming performance. However, tags of similar size as the ones used in this study did not cause a significant decrement to the swimming performance of hatchery-reared Atlantic salmon (McCleave & Stred, 1975). Similarly, Moore et al. (1990) found that swimming behavior, feeding and growth did not seem to be impacted by implantations of tags in hatchery-reared Atlantic salmon smolts. However, the tagging procedures and environmental conditions can differ from the laboratory, and cause wild fish to react differently to tagging procedures than hatchery-reared fish (Peake et al., 1997). Peake et al. (1997) urges to exercise caution in interpreting data gathered from wild Atlantic salmon smolts during the first day after tagging. The survival in this study was generally high and does not seem have been significantly impacted by the handling and tagging procedure. No control group was used in this study, and thus we cannot be sure that the observed behavior of our tagged individuals was unaffected by the handling and tagging procedure.

The study samples varied among the three locations, 60 brown trout in Eio, 31 in Granvin and 34 in Os. There was an almost doubled amount of tagged fish in Eio thanks to NORCE collecting and providing us with brown trout, in addition to the fish we collected ourselves. Anglers in Os also helped with catching larger brown trout individuals for tagging, which explains the difference in fish size for Os compared to Eio and Granvin. We also received brown trout caught by net fishing in the Granvin lake from Rådgivende Biologer. This could explain the observed higher percentage of resident brown trout in Granvin in this study.

The Hardangerfjord is a large and complex fjord system, making it challenging to cover the entire system with receivers and ensure as accurate detections as possible throughout the fjord system. Areas like the Sørfjord towards Odda was not covered, and the area between Granvin and Norheimsund did not have as frequent placements of receivers as the remaining parts of the Hardangerfjord. The Bjørnafjord is also a more open system, making it more challenging to cover with receivers compared to the Hardangerfjord. There is a chance that the migratory brown trout spent time in locations where the cover of receivers was scarce, thereby leading to misinterpreted residence times in these parts of the fjord. In addition, the Os brown trout had a detection probability of approximately 47% in fresh water, which is explained by there being only one receiver in the outlet of the River Oselva. Several receivers were placed in the Eidfjord and Granvin lakes, resulting in a higher detection probability for the Eio and Granvin brown trout compared to the Os brown trout.

The infestation pressure from salmon lice in the Hardangerfjord system in 2019 was based on pervious findings by Vollset et al. (2019), Nilsen, R. et al. (2019) and (Heuch et al., 2009). Maps simulating this was intended to be made but was dependent on data from the Norwegian Veterinary Institute, which was not received in time to be presented in this study. In addition, the Hardangerfjord is a complex system with several river outlets and estuaries that the brown trout could utilize. Receivers were only placed in the estuary belonging to each study area, meaning that the tagged brown trout could have undetectably utilized other estuaries in the fjord system.

4.4 Management implementations and further studies

Several knowledge gaps have been reported to exist about the life history, population status, migratory route and behavior of the brown trout (Nilsen, F. et al., 2019), and this knowledge is needed in order to make sure that the measures implemented and planned have the desired effect. However, the tendencies observed in this study are based on observations during a narrow time span from April to October 2019. This is a very short amount of time for such a complex system, and studies over longer periods of time in addition to new tagged individuals over several years is needed before any substantial conclusions could be drawn. The conditions during the summer of 2019 could also have been less representative for the fjord system in general. Further investigations of depth use and how the salinity and temperatures throughout the Hardangerfjord affects the behavior of brown trout would be of interest. The knowledge obtained from the Salmon Tracking 2020 project could potentially contribute to a national model for monitoring and preserving the wild salmonid stocks, by managing the negative impacts of salmon lice.

5. Conclusion

This study has obtained information on the migrations and utilization of the Hardangerfjord by brown trout from the Rivers Eio, Granvinselva and Oselva in 2019.

The time of seaward migration varied among the three studied watercourses. The Os brown trout portrayed the narrowest migration time span in the study and had the highest estimated biweekly likelihood of migrating from fresh water to near fjord areas in the early period. The factors influencing downstream migration varied among the three rivers. Water flow and day of year seemed to influence the migration in the Rivers Eio and Granvinselva, while a combination of temperature and daily change in water level affected the migration in the River Oselva.

The Granvin brown trout tended to utilize the inner middle fjord areas, but had individuals that migrated early and far, to the inner areas of the Bjørnafjord. The Eio brown trout seemed to mostly utilize the inner fjord areas, with only one individual that was detected further out in the fjord system. The Os brown trout mostly utilized the inner Bjørnafjord areas.
Brown trout of both small and large size, and from all three rivers seemed to travel the same number of kilometers from their respective rivers.

There was a tendency of individuals in fjord areas with high salmon lice densities spending a higher fraction of time in delousing areas, compared to individuals in areas with less salmon lice densities. There were also indications that larger individuals from Os and possibly Granvin were affected by the high salmon lice density in the outer fjord areas, while the tendency of large individuals in Eio having the highest fraction of time spent in delousing areas most likely is not caused by high salmon lice densities.

The survival probabilities presented in this study was generally high for all three populations. The probability of survival did not seem to be induced by the salmon lice. However, an adaptation in behavior could explain these results, as changes in behavior could lead to the brown trout avoiding any immediate mortality risks caused by salmon lice. The probability of survival seemed to somewhat induced by predation, as they were at their lowest in the period of seawards migration for the Eio and Os brown trout.

References

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19: 716-723.

Aldvén, D., Degerman, E. & Höjesjö, J. (2015). Environmental cues and downstream migration of anadromous brown trout (Salmo trutta) and Atlantic salmon (Salmo salar) smolts. *Boreal Env. Res.*, 20: 35–44.

Bjørn, P. A., Finstad, B., Nilsen, R., Uglem, I., Asplin, L., Skaala, Ø., Boxaspen, K. K. & Øverland, T. (2009). *Nasjonal lakselusovervåkning 2008 på ville bestander av laks, sjøørret og sjørøye langs Norskekysten samt i forbindelse med evaluering av nasjonale laksevassdrag og laksefjorder*. NINA Rapport 447.

Bohlin, T., Hamrin, S., Heggberget, T., Rasmussen, G. & Saltveit, S. (1989). Electrofishing—Theory and Practice with Special Emphasis on Salmonids. *Hydrobiologia*, 173: 9-43. doi: 10.1007/BF00008596.

Dieperink, C., Pedersen, S. & Pedersen, M. I. (2001). Estuarine predation on radiotagged wild and domesticated sea trout (Salmo trutta L.) smolts. *Ecology of Freshwater Fish*, 10 (3): 177-183. doi: 10.1034/j.1600-0633.2001.100307.x.

Direktoratet for naturforvaltning. (2009). *Bestandsutvikling hos sjøørret og forslag til forvaltningstiltak.* Notat 2009-1.

Einum, S. & Fleming, I. A. (1999). Maternal effects of egg size in brown trout (Salmo trutta): norms of reaction to environmental quality. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266 (1433): 2095-2100. doi: doi:10.1098/rspb.1999.0893.

Eldøy, S. H., Davidsen, J. G., Thorstad, E. B., Whoriskey, F., Aarestrup, K., Næsje, T. F., Rønning, L., Sjursen, A. D., Rikardsen, A. H. & Arnekleiv, J. V. (2015). Marine migration and habitat use of anadromous brown trout (Salmo trutta). *Canadian Journal of Fisheries and Aquatic Sciences*, 72 (9): 1366-1378. doi: 10.1139/cjfas-2014-0560.

Finstad, B., Økland, F., Thorstad, E. B., Bjørn, P. A. & McKinley, R. S. (2005). Migration of hatchery-reared Atlantic salmon and wild anadromous brown trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology*, 66 (1): 86-96. doi: 10.1111/j.0022-1112.2005.00581.x.

Flaten, A. C., Davidsen, J. G., Thorstad, E. B., Whoriskey, F., Rønning, L., Sjursen, A. D., Rikardsen, A. H. & Arnekleiv, J. V. (2016). The first months at sea: marine migration and habitat use of sea trout Salmo trutta post-smolts. *Journal of Fish Biology*, 89 (3): 1624-1640. doi: 10.1111/jfb.13065.

Forseth, T. & Forsgren, E. (2008). *El-fiskemetodikk – Gamle problemer og nye utfordringer*. NINA Rapport 488. Available at: https://brage.nina.no/nina-xmlui/handle/11250/2393936 (accessed: 29.04.2020).

Forskrift om bruk av dyr i forsøk. (2015). *Forskrift om bruk av dyr i forsøk*. Available at: https://lovdata.no/dokument/SF/forskrift/2015-06-18-761 (accessed: 19.05.2020).

Froese, R. (2006). Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology*, 22 (4): 241-253. doi: 10.1111/j.1439-0426.2006.00805.x.

Gregory, R. S. & Levings, C. D. (1998). *Turbidity Reduces Predation on Migrating Juvenile Pacific Salmon*, 127. p. 275.

Gross, M. R., Coleman, R. M., McDowall, R. M. & Gross, M. R. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science (New York, N.Y.)*, 239 (4845): 1291-1293. doi: 10.1126/science.239.4845.1291.

Halttunen, E., Gjelland, K. Ø., Hamel, S., Serra-Llinares, R. M., Nilsen, R., Arechavala-Lopez, P., Skarðhamar, J., Johnsen, I. A., Asplin, L., Karlsen, Ø., et al. (2018). Sea trout adapt their migratory behaviour in response to high salmon lice concentrations. *Journal of Fish Diseases*, 41 (6): 953-967. doi: 10.1111/jfd.12749.

Haugen, T. O., Urke, H. A., Kristensen, T., Ulvund, J. B., Lunde, R., Hawley, K. & Thaulow, J. (2019). *Områdebruk og vandringer i fjord og ferskvann hos sjøaure i indre Sognefjorden 2012-2015: konsekvenser for erfart lakseluseksponering (KUSTUS-rapporten)*. MINA fagrapport 53.

Havforskningsinstituttet. (2018a). *Effekter av lakselus på vill laksefisk*. Available at: https://www.hi.no/hi/temasider/arter/lakselus/effekter-av-lakselus-pa-vill-laksefisk (accessed: 14.11.2019).

Havforskningsinstituttet. (2018b). *Hvordan spres lakselusa*. Available at: https://www.hi.no/hi/temasider/arter/lakselus/hvordan-spres-lakselusa (accessed: 14.11.2019).

Havforskningsinstituttet. (2019). *Rapport om sjøørret og lakseluspåvirkning*. Available at: https://www.hi.no/hi/nyheter/2019/mai/rapport-om-sjoorret-og-lakseluspavirkning (accessed: 15.05.20).

Hembre, B., Arnekleiv, J. V. & L'Abée-Lund, J. H. (2001). Effects of water discharge and temperature on the seaward migration of anadromous browntrout, Salmo trutta, smolts. *Ecology of Freshwater Fish*, 10 (1): 61-64. doi: 10.1111/j.1600-0633.2001.tb00195.x.

Heuch, P. A., Olsen, R. S., Malkenes, R., Revie, C. W., Gettinby, G., Baillie, M., Lees, F. & Finstad, B. (2009). Temporal and spatial variations in lice numbers on salmon farms in the Hardanger fjord 2004–06. *Journal of Fish Diseases*, 32 (1): 89-100. doi: 10.1111/j.1365-2761.2008.01002.x.

Jensen, A. J., Finstad, B., Fiske, P., Hvidsten, N. A., Rikardsen, A. H. & Saksgard, L. (2012). Timing of smolt migration in sympatric populations of Atlantic salmon (Salmo salar), brown trout (Salmo trutta), and Arctic char (Salvelinus alpinus). *Canadian Journal of Fisheries and Aquatic Sciences*, 69 (4): 711-723. doi: 10.1139/f2012-005.

Jensen, A. J., Diserud, O. H., Finstad, B., Fiske, P. & Rikardsen, A. H. (2015). Between-watershed movements of two anadromous salmonids in the Arctic. *Canadian Journal of Fisheries and Aquatic Sciences*, 72 (6): 855-863. doi: 10.1139/cjfas-2015-0015.

Jensen, J. L. A., Rikardsen, A. H., Thorstad, E. B., Suhr, A. H., Davidsen, J. G. & Primicerio, R. (2014). Water temperatures influence the marine area use of Salvelinus alpinus and Salmo trutta. *Journal of Fish Biology*, 84 (6): 1640-1653. doi: 10.1111/jfb.12366.

Jonsson, B. (1985). Life History Patterns of Freshwater Resident and Sea-Run Migrant Brown Trout in Norway. *Transactions of the American Fisheries Society*, 114 (2): 182-194. doi: 10.1577/1548-8659(1985)114<182:Lhpofr>2.0.Co;2.

Jonsson, B. & Jonsson, N. (2009). Migratory timing, marine survival and growth of anadromous brown trout Salmo trutta in the River Imsa, Norway. *Journal of Fish Biology*, 74 (3): 621-638. doi: 10.1111/j.1095-8649.2008.02152.x.

Jonsson, B. & Jonsson, N. (2011). *Ecology of Atlantic salmon and Brown Trout: Habitat as A Template For Life Histories*: Springer.

Jonsson, N. & Finstad, B. (1995). *Sjøørret: økologi, fysiologi og atferd*. NINA Fagrapport 06: 1-32. Available at: https://www.nina.no/archive/nina/PppBasePdf/fagrapport/006.pdf (accessed: 02.03.2020).

Jonsson, N. & Jonsson, B. (2002). Migration of anadromous brown trout Salmo trutta in a Norwegian river. *Freshwater Biology*, 47 (8): 1391-1401. doi: 10.1046/j.1365-2427.2002.00873.x.

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O' Connell, M. F. & Mortensen, E. (2003). *Atlantic salmon Salmo salar L., brown trout Salmo trutta L. and Arctic charr Salvelinus alpinus (L.): a review of aspects of their life histories*, 12. Oxford, UK. pp. 1-59.

Knutsen, J. A., Knutsen, H., Gjøsæter, J. & Jonsson, B. (2001). Food of anadromous brown trout at sea. *Journal of Fish Biology*, 59 (3): 533-543. doi: 10.1111/j.1095-8649.2001.tb02359.x.

Lyse, A. A., Stefansson, S. O. & Fernö, A. (1998). Behaviour and diet of sea trout post-smolts in a Norwegian fjord system. *Journal of Fish Biology*, 52 (5): 923-936. doi: 10.1111/j.1095-8649.1998.tb00593.x.

McCleave, J. D. & Stred, K. A. (1975). Effect of Dummy Telemetry Transmitters on Stamina of Atlantic Salmon (Salmo salar) Smolts. *Journal of the Fisheries Research Board of Canada*, 32 (4): 559–563. doi: 10.1139/f75-071.

McCormick, S. D., Hansen, L. P., Quinn, T. P. & Saunders, R. L. (1998). Movement, migration, and smolting of Atlantic salmon (Salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 77–92. doi: 10.1139/d98-011.

McCullagh, P. & Nelder, J. A. (1989). *Generalized linear models. 2nd edition*. 2nd ed. ed. Monographs on statistics and applied probability, vol. 37. London: Chapman and Hall.

Middlemas, S. J., Stewart, D. C., Mackay, S. & Armstrong, J. D. (2009). Habitat use and dispersal of post-smolt sea trout Salmo trutta in a Scottish sea loch system. *Journal of Fish Biology*, 74 (3): 639-651. doi: 10.1111/j.1095-8649.2008.02154.x.

Miljødirektoratet. (2013). *Lakseregisteret*. Available at: www.lakseregisteret.no (accessed: 15.03.2019).

Moore, A., Russell, I. C. & Potter, E. C. E. (1990). The effects of intraperitoneally implanted dummy acoustic transmitters on the behaviour and physiology of juvenile Atlantic salmon, Salmo salar L. *Journal of Fish Biology*, 37 (5): 713-721. doi: 10.1111/j.1095-8649.1990.tb02535.x.

Neil Arnason, A. (1973). The estimation of population size, migration rates and survival in a stratified population. *Researches on Population Ecology*, 15 (2): 1-8. doi: 10.1007/BF02510705.

Nilsen, F., Ellingsen, I., Finstad, B., Helgesen, K. O., Karlsen, Ø., Qviller, L., Sandvik, A. D., Sægrov, H., Ugedal, O. & Vollset, K. W. (2019). *Vurdering av kunnskapsgrunnlaget for å implementere lakselus på sjøørret som en bærekraftsindikator i «produksjonsområdeforskriften»*. Rapport fra ekspertgruppe for vurdering av lusepåvirkning. Available at: https://slrc.w.uib.no/files/2019/05/Rapport-ekspertgruppe-om-Sj%C3%B8aure-2019.pdf (accessed: 15.05.20).

Nilsen, R., Llinares, R. M. S., Sandvik, A. D., Elvik, K. M. S., Kjær, R., Karlsen, Ø., Finstad, B., Berg, M. & Lehmann, G. B. (2019). *Lakselusinfestasjon på vill laksefisk langs Norskekysten i 2019*. Rapport frå Havforskningsinstituttet 09/2019. Available at: https://www.mattilsynet.no/fisk_og_akvakultur/fiskehelse/fiske_og_skjellsykdommer/lakselus/havforskningsinstituttet_rapport_2019_om_overvaaking_av_lakselus_paa_vill_laksefisk.35283/binary/Havforskningsinstituttet%20Rapport%202019%20om%20overv%C3%A5king%20av%20lakselus%20p%C3%A5%20vill%20laksefisk (accessed: 07.11.19).

Norges Sjømatråd. (2019). *Sjømateksport for 99 milliarder i 2018*. Available at: https://seafood.no/aktuelt/nyheter/sjomateksport-for-99-milliarder-i-2018-/ (accessed: 22.04.2019).

Nærings- og fiskeridepartementet. (2017). *Regjeringen skrur på trafikklyset*. Available at: https://www.regjeringen.no/no/aktuelt/regjeringen-skrur-pa-trafikklyset/id2577032/ (accessed: 15.04.2019).

Peake, S., McKinley, R. S., Scruton, D. A. & Moccia, R. (1997). Influence of Transmitter Attachment Procedures on Swimming Performance of Wild and Hatchery-Reared Atlantic Salmon Smolts. *Transactions of the American Fisheries Society*, 126 (4): 707-714. doi: 10.1577/1548-8659(1997)126<0707:Iotapo>2.3.Co;2.

QGIS Development Team. (2020). *QGIS Geographic Information System* Open Source Geospatial Foundation Project. Available at: http://qgis.osgeo.org (accessed: 05.05.2020).

R Development Core Team. (2019). *R: a language and environment for statistical computing. 3.63 edition. R Foundation for Statistical Computing*. Available at: https://www.r-project.org/.

Rikardsen, A. H., Amundsen, P. A., Knudsen, R. & Sandring, S. (2006). Seasonal marine feeding and body condition of sea trout (Salmo trutta) at its northern distribution. *Ices Journal of Marine Science* 63: 466-475. doi: 10.1016/j.icesjms.2005.07.013.

Schwarz, C. J., Schweigert, J. F. & Arnason, A. N. (1993). Estimating Migration Rates Using Tag-Recovery Data. *Biometrics*, 49 (1): 177-193. doi: 10.2307/2532612.

Skoglund, H., Vollset, K. W., Barlaup, B. & Lennox, R. (2019). *Gytefisktelling av laks og sjøaure på Vestlandet – status og utvikling i perioden 2004-2018*. LFI Norce rapport nr. 357 10/2019. Available at: https://norce.s3.amazonaws.com/NORCE-LFI-rapport-nr-357-Gytefisktelling-Vestlandselver.pdf (accessed: 19.11.19).

Solomon, D. J. (1978). Migration of smolts of Atlantic salmon (Salmo salar L.) and sea trout (Salmo trutta L.) in a chalkstream. *Environmental Biology of Fishes*, 3: 223–229. doi: 10.1007/BF00691946.

Thorstad, E. B., Todd, C. D., Bjørn, P. A., Gargan, P. G., Vollset, K. W., Halttunen, E., Kålås, S., Uglem, I., Berg, M. & Finstad, B. (2014). *Effects of salmon lice on sea trout*. NINA report 1044. Available at: https://www.nina.no/archive/nina/PppBasePdf/rapport/2014/1044.pdf (accessed: 10.05.2020).

Thorstad, E. B., Forseth, T. & Fiske, P. (2019). *Klassifisering av tilstanden til 430 norske sjøørretbestander*. Temarapport fra Vitenskapelig råd for lakseforvaltning; 7. Available at: https://brage.nina.no/nina-xmlui/handle/11250/2629316 (accessed: 21.11.19).

Urke, H. A., Haugen, T. O., Kjærstad, G., Alfredsen, J. A. & Kristensen, T. (2018). *Laks- og aurebestanden i Strynevassdraget; vandringsmønsteret hjå laksesmolt og aure, ungfiskproduksjon og botndyr*. MINA fagrapport 48.

Vollset, K. W., Nilsen, F., Ellingsen, I., Finstad, B., Helgesen, K. O., Karlsen, Ø., Sandvik, A. D., Sægrov, H., Ugedal, O., Qviller, L., et al. (2019). *Vurdering av lakselusindusert villfiskdødelighet per produksjonsområde i 2019*. Rapport fra ekspertgruppe for vurdering av lusepåvirkning
Available at: https://www.hi.no/resources/ekspertgruppe-rapport_2019.pdf (accessed: 29.05.2020).

Wedemeyer, G. A., Saunders, R. L. & Clarke, W. C. (1980). Environmental factors affecting smoltification and early marine survival of anadromous salmonids. *Mar Fish Rev*, 42: 1–14.

Zuur, A. F., Leno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R.* New York: Springer.

Appendix

Table A - 1: Model selection (GLM) for estimating the determinates of arrival in the Eio river mouth. The top ten models according to the corrected Akaike's Information Criterion (AICc). Temp = water temperature, depth = water discharge, DoY = day of year.

Model number	Model structure	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
6	depth+DoY	3	141,092	0,000	1,000	0,483	-67,418	0,483
5	depth*DoY	4	142,577	1,485	0,476	0,230	-67,073	0,713
7	temp+depth	3	145,102	4,010	0,135	0,065	-69,423	0,779
4	DoY	2	145,628	4,536	0,104	0,050	-70,751	0,829
1	temp*depth	4	146,762	5,670	0,059	0,028	-69,166	0,857
17	DoY+rel.delta.temp	3	147,280	6,188	0,045	0,022	-70,512	0,879
18	DoY+rel.delta.depth	3	147,496	6,405	0,041	0,020	-70,621	0,898
19	DoY+delta.temp	3	147,748	6,657	0,036	0,017	-70,747	0,916
20	DoY+delta.depth	3	147,755	6,663	0,036	0,017	-70,750	0,933
15	DoY*delta.temp	4	148,966	7,875	0,020	0,009	-70,268	0,943

Table A - 2: Model selection (GLM) for estimating the determinates of arrival in the Granvin river mouth. The top ten models according to the corrected Akaike's Information Criterion (AICc). Temp = water temperature, depth = water discharge, DoY = day of year.

Model number	Model structure	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
6	depth+DoY	3	78,319	0,000	1,000	0,199	-36,033	0,199
4	DoY	2	78,663	0,345	0,842	0,167	-37,269	0,366
5	depth*DoY	4	80,422	2,104	0,349	0,069	-35,998	0,436
17	DoY+rel.delta.temp	3	80,530	2,211	0,331	0,066	-37,139	0,502
19	DoY+delta.temp	3	80,688	2,369	0,306	0,061	-37,218	0,563
20	DoY+delta.depth	3	80,783	2,464	0,292	0,058	-37,265	0,621
18	DoY+rel.delta.depth	3	80,786	2,467	0,291	0,058	-37,267	0,679
7	temp+depth	3	81,726	3,407	0,182	0,036	-37,736	0,715
14	DoY*rel.delta.depth	4	81,798	3,479	0,176	0,035	-36,686	0,750
16	DoY*delta.depth	4	81,997	3,678	0,159	0,032	-36,786	0,781

Table A - 3: Model selection (GLM) for estimating the determinates of arrival in the Os river mouth. The top ten models according to the corrected Akaike's Information Criterion (AICc). Temp = water temperature, depth = water discharge, DoY = day of year.

Model number	Model structure	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
34	temp*delta.depth	4	108,043	0,000	1,000	0,254	-49,683	0,254
2	temp	2	109,499	1,456	0,483	0,123	-52,651	0,377
1	temp*depth	4	109,578	1,535	0,464	0,118	-50,450	0,495
5	depth*DoY	4	109,836	1,793	0,408	0,104	-50,579	0,598
33	temp*rel.delta.depth	4	110,325	2,282	0,320	0,081	-50,823	0,679
16	DoY*delta.depth	4	110,342	2,299	0,317	0,080	-50,832	0,760
7	temp+depth	3	111,544	3,501	0,174	0,044	-52,572	0,804
14	DoY*rel.delta.depth	4	112,146	4,103	0,129	0,033	-51,734	0,837
4	DoY	2	112,714	4,670	0,097	0,025	-54,258	0,861
19	DoY+delta.temp	3	113,004	4,961	0,084	0,021	-53,302	0,883

Table A - 4: Model selection (LM) for estimating the determinates of maximum distance travelled by all three populations. The top ten models according to the corrected Akaike's Information Criterion (AICc).

Model number	Model structure	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
11	1	2	317,126	0,000	1,000	0,238	-156,493	0,238
3	weight	3	317,859	0,733	0,693	0,165	-155,788	0,403
2	length	3	318,019	0,893	0,640	0,152	-155,868	0,555
1	river	4	318,021	0,895	0,639	0,152	-154,772	0,707
4	cfactor	3	319,194	2,069	0,355	0,085	-156,456	0,791
9	river+weight	5	319,681	2,555	0,279	0,066	-154,479	0,858
8	river+cfactor	5	319,685	2,559	0,278	0,066	-154,481	0,924
10	river+length	5	320,006	2,880	0,237	0,056	-154,642	0,980
5	river*cfactor	7	324,075	6,949	0,031	0,007	-154,346	0,988
6	river*weight	7	324,299	7,173	0,028	0,007	-154,458	0,994

Table A - 5: Model selection (GLM) for estimating the determinates of residence time in the respective estuaries among migratory brown trout from all three populations (stationary brown trout excluded). The top ten models according to the corrected Akaike's Information Criterion (AICc).

Model number	Model structure	K	AICc	Delta_AICc	ModelLik	AICcWt	LL	Cum.Wt
8	river*length	6	1929,925	0,000	1,000	0,989	-958,468	0,989
7	river*weight	6	1938,960	9,035	0,011	0,011	-962,986	1,000
6	river*cfactor	6	1969,067	39,142	$3{,}17e^{-09}$	$3{,}13e^{-09}$	-978,039	1,000
10	river+weight	4	1975,555	45,630	$1{,}23e^{-10}$	$1{,}22e^{-10}$	-983,548	1,000
9	river+cfactor	4	1976,137	46,212	$9{,}23e^{-11}$	$9{,}13e^{-11}$	-983,839	1,000
4	weight	2	1977,801	47,876	$4{,}02e^{-11}$	$3{,}97e^{-11}$	-986,833	1,000
11	river+length	4	1979,124	49,199	$2{,}07e^{-11}$	$2{,}05e^{-11}$	-985,332	1,000
3	length	2	1980,343	50,418	$1{,}13e^{-11}$	$1{,}11e^{-11}$	-988,104	1,000
2	river	3	1982,517	52,592	$3{,}80e^{-12}$	$3{,}76e^{-12}$	-988,122	1,000
5	cfactor	2	1987,842	57,917	$2{,}65e^{-13}$	$2{,}62e^{-13}$	-991,854	1,000

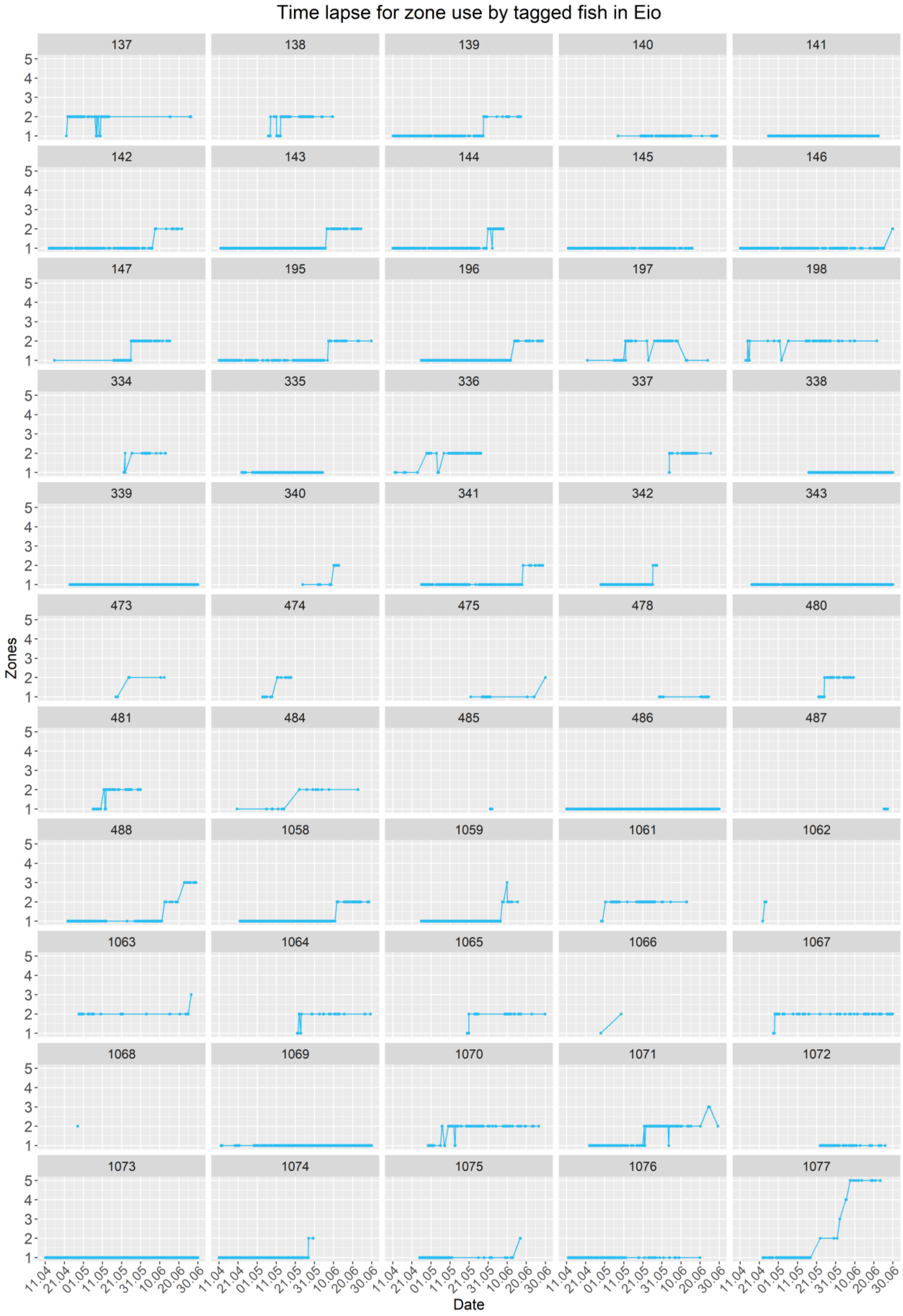

Figure A - 1: Time lapse for zone use by tagged brown trout from Eio from spring 2019. Zone 1= 0 (fresh water), zone 2= a1, zone 3= a2+b, zone 4= c, zone 5= d+e1+e2 (see Figure 2.8).

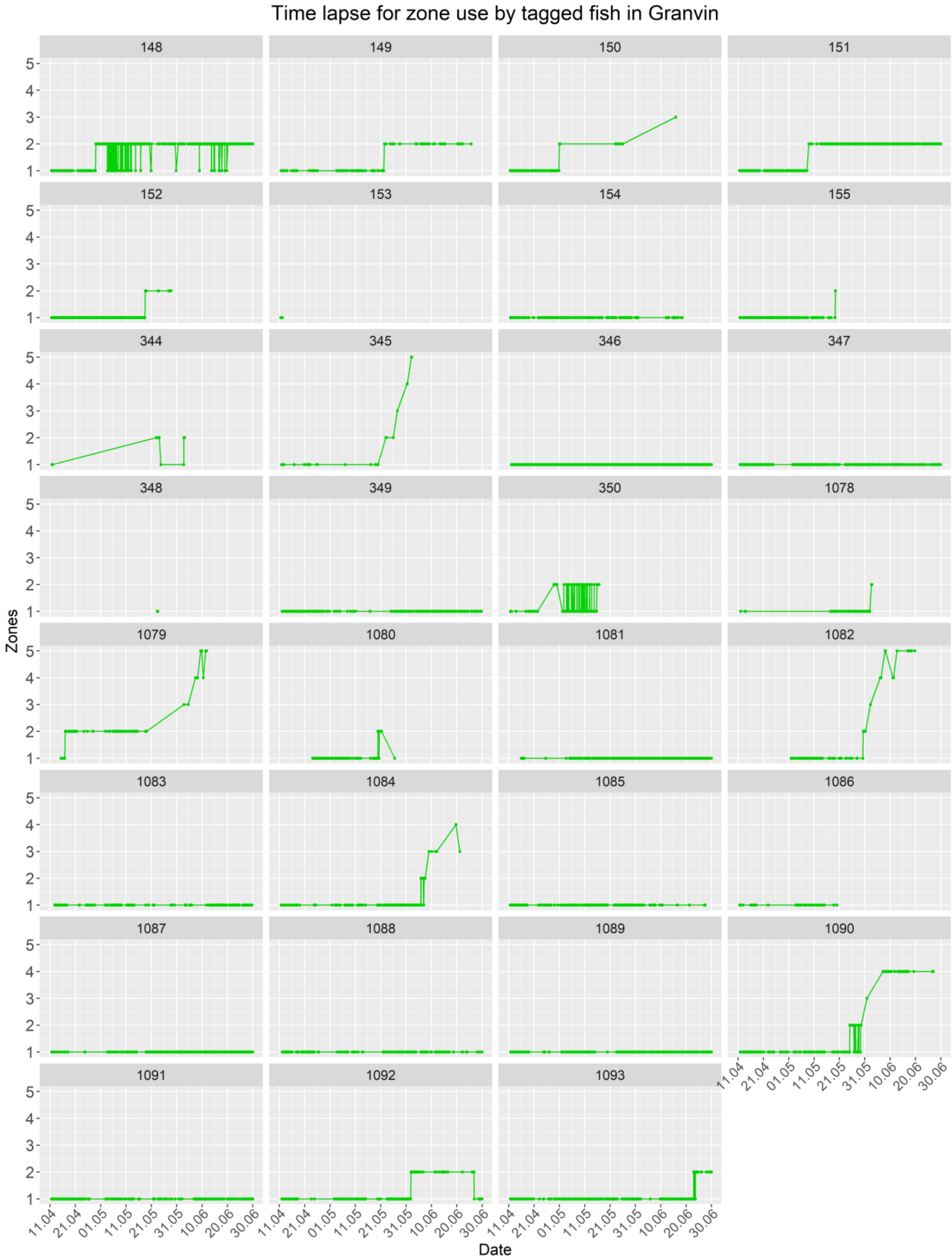

Figure A - 2: Time lapse for zone use by tagged brown trout from Granvin from spring 2019. Zone 1= 0 (fresh water), zone 2= a1+a2, zone 3= b, zone 4= c, zone 5= d+e1+e2 (see Figure 2.8).

Figure A - 3: Time lapse for zone use by tagged brown trout from Os from spring 2019. Zone 1= 0 (fresh water), zone 2= e1, zone 3= e2+d, zone 4= c, zone 5= b+a2+a1 (see Figure 2.8).

Table A - 6: CAS-analysis, real parameter estimates. FW = fresh water, NF = near fjord, DF = distant fjord. Early period = from April 8th to June 16th, mid period = from June 17th to August 11th, late period = from August 12th to October 13th.

Type	Zone	River	Period	Est	SE	LCL	UCL
S	FW	Eio	Early	1,00	0,00	1,00	1,00
S	FW	Eio	Mid	0,94	0,03	0,82	0,98
S	FW	Eio	Late	0,80	0,13	0,45	0,95
S	FW	Granvin	Early	1,00	0,00	1,00	1,00
S	FW	Granvin	Mid	0,96	0,03	0,80	0,99
S	FW	Granvin	Late	0,82	0,07	0,65	0,92
S	FW	Os	Early	0,95	0,04	0,81	0,99
S	FW	Os	Mid	1,00	0,00	1,00	1,00
S	FW	Os	Late	0,95	0,08	0,40	1,00
S	NF	Eio	Early	0,88	0,04	0,77	0,94
S	NF	Eio	Mid	1,00	0,00	1,00	1,00
S	NF	Eio	Late	0,97	0,24	0,00	1,00
S	NF	Granvin	Early	0,95	0,13	0,05	1,00
S	NF	Granvin	Mid	1,00	0,00	1,00	1,00
S	NF	Granvin	Late	0,83	0,11	0,52	0,96
S	NF	Os	Early	0,95	0,03	0,86	0,99
S	NF	Os	Mid	1,00	0,00	1,00	1,00
S	NF	Os	Late	0,97	0,08	0,10	1,00
S	DF	Eio	Early	1,00	0,00	1,00	1,00
S	DF	Eio	Mid	1,00	0,00	1,00	1,00
S	DF	Eio	Late	0,48	0,27	0,10	0,88
S	DF	Granvin	Early	0,87	0,16	0,30	0,99
S	DF	Granvin	Mid	0,73	0,12	0,46	0,89
S	DF	Granvin	Late	1,00	0,00	1,00	1,00
S	DF	Os	Early	1,00	0,00	1,00	1,00
S	DF	Os	Mid	0,22	0,20	0,03	0,74
S	DF	Os	Late	1,00	0,00	1,00	1,00
p	FW	Eio		0,95	0,03	0,87	0,98
p	FW	Granvin		1,00	0,02	0,00	1,00
p	FW	Os		0,47	0,06	0,35	0,60
p	NF	Eio		0,93	0,03	0,85	0,97
p	NF	Granvin		1,00	0,00	1,00	1,00
p	NF	Os		1,00	0,00	1,00	1,00
p	DF	Eio		0,02	0,01	0,00	0,08
p	DF	Granvin		0,15	0,05	0,07	0,29
p	DF	Os		0,25	0,09	0,12	0,45
Psi	FW-NF	Eio	Early	0,24	0,03	0,18	0,31
Psi	FW-NF	Eio	Mid	0,11	0,05	0,05	0,24
Psi	FW-NF	Eio	Late	0,02	0,02	0,00	0,15
Psi	FW-NF	Granvin	Early	0,15	0,04	0,09	0,23
Psi	FW-NF	Granvin	Mid	0,00	0,00	0,00	0,00
Psi	FW-NF	Granvin	Late	0,00	0,00	0,00	0,00
Psi	FW-NF	Os	Early	0,66	0,08	0,50	0,79
Psi	FW-NF	Os	Mid	0,10	0,06	0,03	0,27

Psi	FW-NF	Os	Late	0,16	0,07	0,07	0,35
Psi	FW-DF	Eio	Early	0,08	0,03	0,04	0,16
Psi	FW-DF	Eio	Mid	0,00	0,00	0,00	0,00
Psi	FW-DF	Eio	Late	0,12	0,14	0,01	0,67
Psi	FW-DF	Granvin	Early	0,07	0,03	0,03	0,16
Psi	FW-DF	Granvin	Mid	0,06	0,04	0,01	0,21
Psi	FW-DF	Granvin	Late	0,00	0,00	0,00	0,00
Psi	FW-DF	Os	Early	0,27	0,07	0,15	0,44
Psi	FW-DF	Os	Mid	0,00	0,00	0,00	0,00
Psi	FW-DF	Os	Late	0,16	0,11	0,04	0,48
Psi	NF-FW	Eio	Early	0,02	0,02	0,00	0,10
Psi	NF-FW	Eio	Mid	0,09	0,03	0,05	0,18
Psi	NF-FW	Eio	Late	0,16	0,08	0,06	0,37
Psi	NF-FW	Granvin	Early	0,00	0,00	0,00	0,00
Psi	NF-FW	Granvin	Mid	0,06	0,06	0,01	0,32
Psi	NF-FW	Granvin	Late	0,10	0,09	0,01	0,47
Psi	NF-FW	Os	Early	0,09	0,03	0,04	0,17
Psi	NF-FW	Os	Mid	0,16	0,05	0,08	0,28
Psi	NF-FW	Os	Late	0,16	0,08	0,05	0,38
Psi	NF-DF	Eio	Early	0,12	0,05	0,05	0,26
Psi	NF-DF	Eio	Mid	0,12	0,04	0,06	0,23
Psi	NF-DF	Eio	Late	0,20	0,21	0,02	0,76
Psi	NF-DF	Granvin	Early	0,38	0,12	0,18	0,64
Psi	NF-DF	Granvin	Mid	0,00	0,00	0,00	0,00
Psi	NF-DF	Granvin	Late	0,00	0,00	0,00	0,00
Psi	NF-DF	Os	Early	0,04	0,03	0,01	0,15
Psi	NF-DF	Os	Mid	0,10	0,04	0,04	0,21
Psi	NF-DF	Os	Late	0,08	0,07	0,01	0,39
Psi	DF-FW	Eio	Early	0,36	0,11	0,18	0,59
Psi	DF-FW	Eio	Mid	0,13	0,06	0,05	0,30
Psi	DF-FW	Eio	Late	0,23	0,26	0,02	0,83
Psi	DF-FW	Granvin	Early	0,10	0,11	0,01	0,56
Psi	DF-FW	Granvin	Mid	0,00	0,00	0,00	0,00
Psi	DF-FW	Granvin	Late	0,15	0,12	0,03	0,51
Psi	DF-FW	Os	Early	1,00	0,00	1,00	1,00
Psi	DF-FW	Os	Mid	1,00	0,00	1,00	1,00
Psi	DF-FW	Os	Late	0,16	0,16	0,02	0,65
Psi	DF-NF	Eio	Early	0,12	0,08	0,03	0,37
Psi	DF-NF	Eio	Mid	0,08	0,06	0,02	0,28
Psi	DF-NF	Eio	Late	0,00	0,00	0,00	0,00
Psi	DF-NF	Granvin	Early	0,10	0,08	0,02	0,36
Psi	DF-NF	Granvin	Mid	0,00	0,00	0,00	0,00
Psi	DF-NF	Granvin	Late	0,08	0,08	0,01	0,43
Psi	DF-NF	Os	Early	1,00	0,00	1,00	1,00
Psi	DF-NF	Os	Mid	0,18	1175,05	0,00	1,00
Psi	DF-NF	Os	Late	0,14	0,12	0,02	0,54

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway