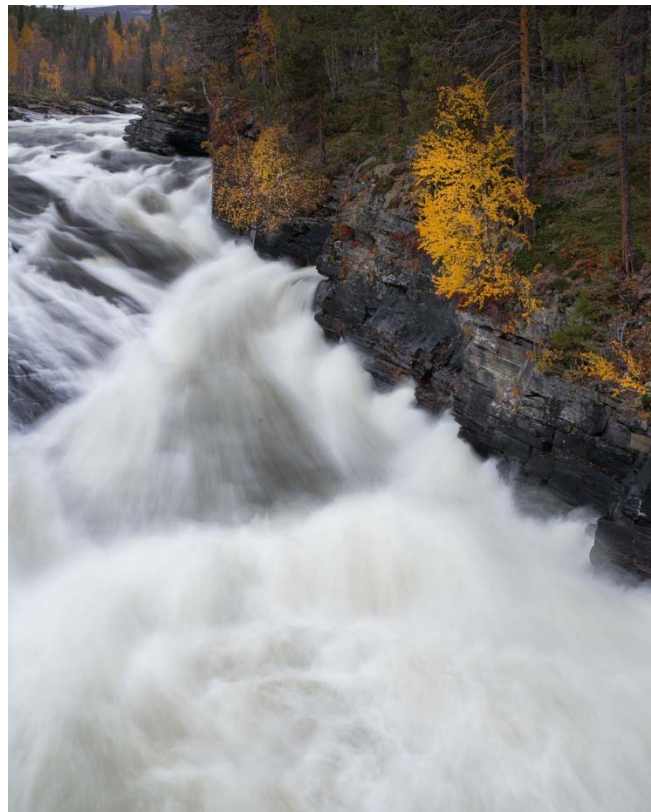


Sexual Dimorphism in the migratory dynamics of a land-locked population of Brown Trout (*Salmo trutta*) in central Sweden – A study at three temporal scales

Carl Vigren



Master's thesis • 60 credits

Jägmästarprogrammet

Examensarbete/Master's thesis, 2018:17

Umeå 2018

Sexual Dimorphism in the migratory dynamics of a land-locked population of Brown Trout (*Salmo trutta*) in central Sweden – A study at three temporal scales

Carl Vigren

Supervisor: Gustav Hellström, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies
Assistant supervisor: Kjell Leonardsson, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies
Examiner: Anders Alanärä, Swedish University of Agricultural Sciences, Department of Wildlife, Fish, and Environmental Studies

Credits: 60 credits
Level: Second cycle, A2E
Course title: Master degree thesis in Forest Sciences at the department of Wildlife, Fish, and Environmental Studies
Course code: EX0823
Programme/education: Jägmästarprogrammet
Course coordinating department: Department of Wildlife, Fish, and Environmental Studies

Place of publication: Umeå
Year of publication: 2018
Cover picture: Carl Vigren
Title of series: Examensarbete/Master's thesis
Part number: 2018:17
Online publication: <https://stud.epsilon.slu.se>

Keywords: trout, salmonid, salmo, trutta, migration, upstream, Storsjön, Storsjön, Damman, Dammån, regulated, fish ladder, behaviour, protandry

Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Department of Wildlife, Fish, and Environmental Studies

“As the poet [Vergilius] says of the sacred deity,
Wheresoever the god has turned his goodly head,
truly, whatever the person and eyes of the master are frequent visitors,
there the fruit abounds in richer measure”

Lucius Junius Moderatus Columella
De Re Rustica, 3.21.4
c. 60 A.D.

Acknowledgements

To my Family.
I owe it all to you.

Thank you to all those who have made this thesis possible. I wish to thank the Dammån FVOF for the monumental effort you have put in, collecting data through thick and thin.

Tack!

I am particularly grateful for the guidance and support offered and good fun I've had with my supervisor, Gustav Hellström!

A special thanks to
Alexandra Heinonen
Perry C. Nilsson
Simon Vallin
John P. Ball

I would also like to extend my appreciation to Virad Kisan, for teaching a man weak of faith how to go salmon fishing in the Yemen, and for inspiring my zest for science!

*Morfar,
for your love of nature,
which has inspired and guided me all the way.*

Abstract

In this study I use a 56 years long dataset to study the migratory behaviours of a land-locked population of Brown trout (*Salmo trutta*) in the river Dammån, positioned in central Sweden. I found that there was a mean female-to-male sex ratio in the spawning-run of approximately 2.31 with an average 50% run date on the 29th of July.

I principally investigated if there were any trends in 3 different temporal scales: diel, seasonal and interannual. The model investigating diel effect was not significant, likely due to the light summer nights at this latitude. I found that there was a seasonal trend, where the probability of an observation being female increased by 54.33% during the season, indicative of a protandric trait where males gain from an early arrival to the spawning-grounds. The interannual model displayed a decline of 13.85% in the proportion of females migrating over the 56 years investigated.

Keywords: trout, salmonid, salmo, trutta, migration, upstream, Storsjon, Storsjön, Damman, Dammån, regulated, fish ladder, behaviour, protandry

Table of contents

List of tables	8
Figurförteckning/List of figures	9
1 Introduction	13
1.1 Migratory Behaviour of the Brown Trout	13
1.2 Questions	17
2 Site	18
3 Method	20
3.1 General Migrational Statistics	22
3.2 Assessing diurnal patterns	22
3.3 Seasonal variation between the sexes	24
3.4 Assessing yearly trends in the sex quotient	24
3.5 Estimating a long-term weight loss trend.	25
4 Result	26
4.1 Seasonal Effect on female tendency to migrate.	29
4.2 GLM of male to female ratio	30
4.3 Variation in the timing of Peak Migration	31
4.4 Mean Fulton's K by sex and year	33
4.5 Total amount of trout passing through Dammån fish-ladder.	34
5 Discussion	36
5.1 Tendencies in migrational timing	36
5.1.1 Diel	36
5.1.2 Seasonal	36
5.1.3 Interannual	37
5.1.4 Timing of Spawning Migration	39
5.2 General Migration	40
5.2.1 Population Trends	40
5.3 Female to male ratio	40
5.4 Weight and Lengths	41
6 Future Directions	42
Appendix I	45
References	48

List of tables

Tabell 1. An aggregation describing the completeness of the dataset 1950-2006; as given from the most relevant cleaning process for each variable.	20
Tabell 2. Mean weights and length of migrants of respective sex.	26
Tabell 3. A broad range of reasons which could underlie a decrease in the proportion of migrating females.	37

Figurförteckning/List of figures

- Figur 1. Maps of differing scale showing the location of the fish ladder (indicated by black dot), and its surroundings.* 18
- Figur 2. A density plot illustrating how the catches of fish are related in time. The latest start and earliest closure of the fish-ladder are marked by the red intercepts. N.B. there is no data for 1955 or 1960. 18.36% of the data is outside of the boundaries in red. The bold lines emphasise the first and last day of the season for each year.* 21
- Figur 3. The mean weight of (A) female, and (B) male observations of *S. trutta* between 1950 and 2006.* 27
- Figur 4. Violin plots of the length (A) and weights (B) among the migrant sexes. Shaded area corresponds to the distribution of observations. Boxplot superimposed.* 28
- Figur 5. Graph illustrating the variation in the peak migration date. Earliest (25th of June) and latest (9th of September) values are dotted lines. N.B. by definition, years can have multiple peaks.* 31
- Figur 6. The coefficient of variance of the date of migration, by year.* 32
- Figur 7. Graph illustrating the mean Fulton's K for the migrant brown trout for each year; each sex illustrated individually. Black line depicts the average of the means.* 33
- Figur 8. Graph displaying the total amount of migrants passing through the fish-ladder between the day of year 175 and 241 over the years, including fish which were not successfully sexed.* 34
- Figur 9. Graph displaying the count totals of migrants which were successfully sexed.* 35

Abbreviations

GLM	General Linear Model
GLMMPQL	General Linear Model with Penalized Quasi- Likelihood.
FVOF	Fiskevårdsområdesförening – Fishing Conservation Area Ass.
Naturvårdsverket	Swedish Environmental Protection Agency
EPA	Environmental Protection Agency
M	Male
F	Female
NA	Not Applicable
DVM	See Diel vertical migration.

Latin in Academic Writing

N.B.	Nota Bene – Observe
Ceteris paribus	All other things equal
C.f.	Con ferra – Refer to ...
Sec.	Secundum – Along the thoughts of...
Op. Cit.	Opere Citatio – in the same work.
Et al.	Et alii – and others
In Sensu	In the sense of...

Technical Terms

Adfluvial	Fish species which migrates between a spawning river and a lake.
Potamodromous	Fish species which migrate between a river and a lake.
Diel Vertical Migration	Depth-related migration with a 24-hour cycle.
Diadromous	Fish species which migrate between freshwater and the sea.
Anadromous	Diadromous fish species which migrate into freshwater to spawn.
Catadromous	Diadromous fish species which migrate into seawater to spawn.

1 Introduction

1.1 Migratory Behaviour of the Brown Trout

Great migrations are undertaken in all major animal taxa in pursuit of more bountiful lands, lower predation pressure, in order to avoid undue environmental adversity or to facilitate breeding.

Some of these form spectacular events, marvels of nature if you will, appreciated by laymen and scientists alike. Migrational phenomena of these scales are visible from the subspecies level, such as the Monarch Butterfly (*Danaus plexippus plexippus*, L. 1758); species level, e.g. Arctic tern (*Sterna paradisaea*, Pontoppidan 1763); to an interspecies level, e.g. Great Serengeti Migration – by Wildebeest, Gazelle, Zebra *et cetera*. Of these wonders, particularly associated with the salmonid family is the embodiment of self-sacrifice by semelparous (semel ‘once’, pario ‘to beget’) Sockeye salmon (*Oncorhynchus nerka*, Walbaum, 1792), which die in large numbers after they have spawned. Less known is the iteroparous (itero ‘repeat’) nature of many of its relatives, or the variation in migratory behavior displayed amongst them. Of these relatives, I have studied the migration of the brown trout (*Salmo trutta*) more closely.

The development of anadromy (Greek, *ana-* up; *dromos-* running) has been contested, wherein first Gross *et al.* (1988) suggested it developed as a response to the high productivity of marine waters compared to freshwaters at high northern latitudes. However, this has since been contested by one of the authors (McDowall, 2008), who instead suggests that it may have developed to facilitate colonization of newly deglaciated areas. Elliott (1994) suggests that diadromous behaviour may

have arisen in order to increase resource allocation of a stream to juveniles through the means of an intraspecific resource partitioning.

Nevertheless, brown trout demonstrate considerable variation in their capacity to adapt their life history. In general, these choices are assumed to reflect upon the individual's effort to maximize their evolutionary fitness (Chapman *et al.*, 2012b). Notably, *S. trutta* displays significant intraspecies variability in their migratory patterns. Elliott (1994) describes four types of life cycles which are differentiated between dependent on the individual's migratory habits:

- “1) the trout remain resident in their natal stream for their whole life-cycle;
- 2) after the first year, the juveniles migrate to the parent river and adults do not return until just before spawning;
- 3) similar to the previous type except that the migrations are to and from a neighbouring lake;
- 4) similar to the previous type except that the migrations are to and from an estuary (estuarine or slob trout) or the sea (sea-trout)”.

Partial migration and resultant phenotypic differences between individuals is common in salmonids cf. Elliot (*op. cit.*). Individual brown trout populations, such as that of Vangsvatnet lake, Norway, may express several or all of the by Elliot aforementioned life cycle divergences (Jonsson, 1985). Underlying an individual's migrational “decision”, may be environmental; inherited; and physiological conditions (Lucas & Baras, 2001). Differing returns for the Atlantic salmon's (*S. salar* L.) spawning migration between populations has been shown to be attributable to hereditary factors, rather than environmental influence (Hansen & Jonsson, 1991). Similarly, there is a larger genetic divergence between geographically distinct brown trout populations than there is between individuals of different life-cycles (Hindar *et al.*, 1991).

This polyphenic nature of brown trout migration is well covered in (Jonsson & Jonsson, 2011). There is a disparity in the number of each sex which choose to migrate – often amounting to a highly skewed ratio of females to males. An average ratio of 1.5 was found in 17 streams ≤ 1 m³/s in Norway (Jonsson *et al.*, 2001). Similarly, Campbell (1977) approximated a female to male ratio of 1.4 for sea-trout; female surplus is demonstrated also in Jonsson (1985), for graphic overview. This is thought to reflect on the differing return of investment from migratory behaviours as measured in evolutionary fitness between the sexes. As pointed out in Harris and Milner (2006), female surplus among migrants is largely mirrored by male overrepresentation among the resident demographic.

A longer upstream migratory distance is associated with higher energetic costs prior to spawning, limiting gonadal investment (Jonsson & Jonsson, 2006) cf. trade-off concept by Wright (1932). Fleming *et al.* (1996) found that body size alone could explain ~80% of the variance in female fecundity for wild Salmon (*S. salar*), measured as amount of viable eggs found in the redd. A larger body size in females is connected to an increased size and number of eggs oviposited (Fleming, 1996). A larger body size may also be an adaptation to facilitate the higher energy demands of longer or steeper upstream migrations (Bohlin *et al.*, 2001; Labeelund, 1991). However, females may be size limited by increased risk of injury in streams with low flow (Fleming, 1996).

This is closely related to the asset-protection principle (Clark, 1994), wherein I consider the environment to be considered analogous to predation risk. A brief overview of forces stabilizing spawning time is given by Fleming (1996), herein recounted briefly: The earliest time of spawning is limited by the initially higher exposure to predation of the earliest hatching juveniles, and the risk of redd destruction by subsequent female spawners or egg predation. The latest spawning time is limited by the lower quality of remaining redds the female can compete for; availability of resources which the juvenile can compete for.

In contrast, the breeding success by male spawners seems to be less governed by gonadal investment, but rather as a direct function of body size – as they otherwise have little chance in competing with larger males for breeding opportunities and must invest more time in searching for an unattended mate (Jonsson & Jonsson, 2011).

This masters' thesis considers the migrational variation at three temporal resolutions (diel, seasonal, interannual) between the sexes among migrating brown trout. Many different variables combine to affect the temporal variation displayed in the migration of different species.

In general, trout are noted to undertake migrations during nocturnal conditions, likely to avoid predation (Haraldstad *et al.*, 2017; Jonsson, 1991). Jonsson (Op. Cit.) however notes in the review that this condition is not absolute, and daylight migration seems to be facilitated by particularly high flow conditions, midnight sun, or when there is safety in numbers.

Diel vertical migrations with nocturnal ascent and diurnal descent occur widely among fishes – likely to maximize foraging efficiency or take advantage of an anti-predation window (Gutowsky *et al.*, 2013). Salmonids do not migrate efficiently on land due to the imminent risk of asphyxiation stemming from the collapse of the gill structure and lack of organs well developed to facilitate movement out of water. Smaller structures such as dams by beavers should however not be considered major obstacles to migrating salmonids (Ecke *et al.*, 2017).

Seasonal variation in salmonid migrants' time of arrival is known to correlate well with several variables and events, including: body size & maturity (Jonsson & Gravem, 1985), freshets cf. comprehensive review by (Jonsson & Jonsson, 2011); and to a lesser degree water temperature (Jonsson & Jonsson, 2002; Quinn & Adams, 1996).

Generally, an inherited sensitivity to photoperiod seems to synchronise the upstream migrations among Atlantic salmon (*Salmo salar*) and brown trout; the hypothesis being that a decrease in the amount of melatonin spurs maturation – and perhaps also the timing of spawning (Migaud *et al.*, 2010). This is most likely an inherited trait, as different populations may have to depart from shared feeding grounds several months before of spawning season, well-illustrated by the Klarälven trouts' 400 kilometre migration begun from mid-May in order to spawn in October, at the same time as the Gullspång trout, whose migration takes roughly 2 weeks (Ros, 1981).

Although there is still much to investigate on this matter, as an end result, brown trout males generally arrive at the spawning grounds earlier than the females (protandry) (Jonsson & Jonsson, 2011), s.271; in order to have the opportunity mate with as many females as possible (Morbey, 2002).

Size and composition of salmonids' spawning-run can change drastically throughout the years, cf. *Oncorhynchus* spp. decline in the Puget Sound region. Ohlberger *et al.* (2018), show that Chinook salmon (*O. tshawytscha*) populations on the east coast (both spawning and marine samples) – particularly the northern range - have had declining mean weights among the senior fish; mean age in general has decreased. Ohlberger *et al.* (2018) recount that common hypotheses include size-selective harvest, environmental pressure, introduction of hatchery-raised brethren, competition – but also suggest that the rebounding populations of larger marine predators (incl. killer whales (*Orcinus orca*) may be playing a role in shifting the composition towards smaller fish.

As the capacity for population growth and resilience is often limited by the amount of “Big Old Fat Fecund Female Fish” (Hixon *et al.*, 2013), certainly in heavily exploited populations, it is also of interest to explore the development of the sexes bodyweight in relation to any unearthed divergences.

Salmonid research has flourished as a result of society’s need to further comprehend the full scale of our impact on our natural resources; not only by our historic actions, but also our present. It is therefore of large interest to ensure that our mitigating interventions, such as implementation of fish-ladders and similar structures are functioning efficiently, and in an intended manner.

1.2 Questions

1. Is there a difference between males and female brown trout in the propensity to migrate during night or day?
2. Is there a difference between male and female brown trout in seasonal migration intensity?
3. Is there a trend in the sex ratio of brown trout over years?

3 Method

A migration can be defined in several ways, depending on its' scope and purpose. For the purposes of this study, I have defined migration as the homeostatic annual venture between a lake and the tributary spawning grounds. Disrupted migration is common, although I assume that repeated migration past the Dammån power station and fish-ladder is negligible. I also assume that the trout belong to the same population.

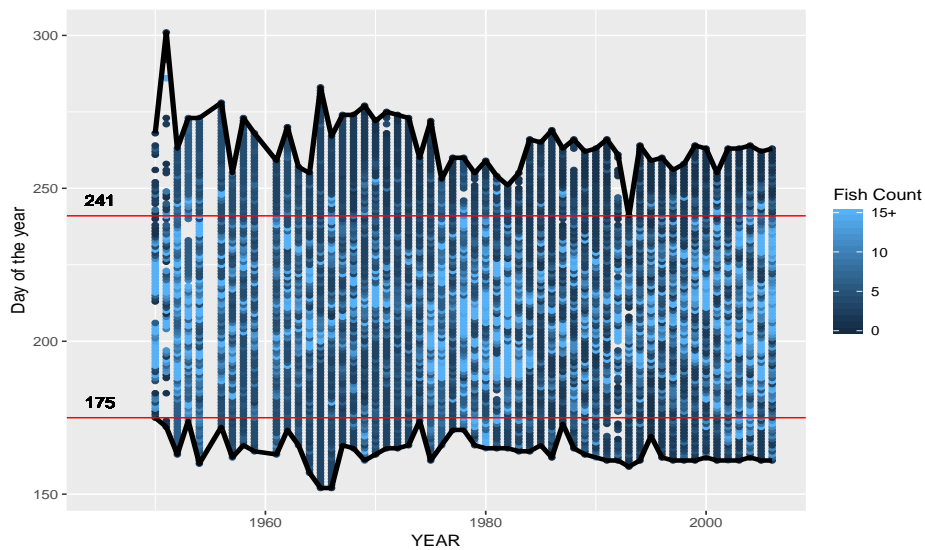
As the hypotheses required different levels of resolution, I've used R Studio to reshape, clean and analyse the data. A complete disclosure of the used packages and their version is included in Appendix. Below, I will outline by which rules I sorted the data, beginning with the most comprehensive cleaning. An overview of the structure of the data is given in table 1 below.

Tabell 1. *An aggregation describing the completeness of the dataset 1950-2006; as given from the most relevant cleaning process for each variable.*

Variable	Valid	NotAvailable
Time	34'610	3'164
Sex	29'862	7'912
Weight	30'197	7'577
Length	30'144	7'630
Date	5'446 unique	37'774 total

The Dammån Brown trout dataset is detailed, given that the FVOF has maintained operation for an excess of 55 years. In total between 1950 to the end of the 2006 season, the fish-ladder was operational on a total of 5446 days; despite that there is no data 1955 and 1960. This has amounted to a total of 37'774 trout observations, the vast majority for which sex, weight and length have been successfully recorded.

As the season the fish ladder is active has not been uniform throughout the years, and it is uncertain that such should represent the full migrational season, I have employed a cut-off on the basis of the latest season start and earliest season closure as measured in day of year. This as to ensure that each years' "total" count is based on a similar expedited effort. As shown in figure 2, this has led to discarding 18.36% of the total available data.



Figur 2. A density plot illustrating how the catches of fish are related in time. The latest start and earliest closure of the fish-ladder are marked by the red intercepts. N.B. there is no data for 1955 or 1960. 18.36% of the data is outside of the boundaries in red. The bold lines emphasise the first and last day of the season for each year.

Fulton's Condition Factor, K , was calculated with a slight modification to the formula as given in Tesch (1978):

$$K = 100 \times W \text{ (g)} \times L \text{ (cm)}^{-3}$$

Fulton's K was used to eliminate erroneous data, where: $K \notin [0.35, \dots, 1.5]$. In total this removed 22.0% of the records when calculating mean weight and length.

3.1 General Migrational Statistics

The 50% run date was calculated as the median run date each year.

N.B. in the R language, Julian date refers to the day of year!

To explore whether the means of the two sexes weights and lengths were significantly different, I conducted Welch's Two Sample t-test as the variances were unequal.

The variation in peak migration date was graphed visually and the earliest and latest migrational date was observed. All dates are given as a day of year out of 366.

3.2 Assessing diurnal patterns

The fish ladder is emptied twice daily, at 08:00 and 16:00. During primarily earlier years, the fish ladder was emptied less regularly. In order to make these more directly comparable, I have standardized all times to 08:00 or 16:00 with the following statement:

For $t > 16 \mid t \leq 8 \rightarrow t = 8$.

For $9 \leq t \leq 16 \rightarrow t = 16$

- Obvious errors such as "1600" were corrected manually. I also filtered out NA time-stamps.
- There were no records for the years 1955 and 1960. The years 1950, 1951, 1992, 1995 do not detail the hour during which the fish-ladder was emptied. They were discarded in this analysis.
- To avoid presenting unduly high numbers of fish when the fish ladder has not been emptied for an interim longer than 1 day, the first day following an interim is discarded.
 - If the fish ladder has been emptied only once per day, it is discarded.

Filtering for times removed $\approx 10.10\%$ of the observations included in the dataset, in total 3814 records.

After removing the unsuccessfully sexed fish and fish which were caught but not given a valid time-stamp; as well as filtering for the abovementioned: there remained 26'459 observations, c. 70.0% of the total amount of observed fish.

The data was then aggregated to reflect the total amount of male and female migrants per day and collection.

As is visible in figures 3 & 4, the *number* of migrants of respective sex is highly variable. An analysis of solely the abundance of migrants would therefore skew the data towards those years with a high or low number of migrants. Similarly, if one were to compare the *proportion* of migrants, one would be remiss to disregard the bias of, particularly in hypotheses referring to a higher temporal resolution, chance causing heavy skewing when there are very few migrants. I have therefore chosen to weight the sex ratio of the migrants by the number in which they have arrived.

To investigating any diel patterns, I used a general linear mixed-effect model (GLMM) with a binomial distribution and logit function. I modeled Diel cycle as a two-level nominal variable (Day / Night) with season as an integer variable constituting the day of year to account for changes in photoperiod during the season which the fish-ladder is operational each year. The different years were included in the model as a random effect in order to account for dependence in-between years. I assumed that μ_i is stationary. The full model took on the form:

$$\text{logit}(p_{ij}) = \alpha + \text{Season} * \text{Diurnal}_{ij} + a_j$$

Where p is the probability of observation i in year j being female. $\text{Season} * \text{Diurnal}_{ij}$ is shorthand for the interaction term $\beta_1 \text{Season} + \beta_2 \text{Diurnal} + \beta_1 \beta_2 \text{Season} * \text{Diurnal}$.

α is an intercept and a_j is a random effect to account for between-year dependence.

Thus, the predicted values represent the probability of the next migrant being female, given a certain time of day, season and year. The model was overdispersed, and this was corrected for by adding an observational level random effect based on Zuur *et al.* (2012).

3.3 Seasonal variation between the sexes

In order to assess the importance of potential seasonal effects on the respective sexes tendency to migrate past the fish-ladder, as indicated by Jonsson and Jonsson (2011) and Morbey (2002); my data preparation consisted of removing fish which were unsuccessfully sexed, and subsequently aggregating the data by date of observation and sex. In total 29'560 fish were successfully sexed, amounting to $\approx 78.5\%$ of the amount of observations being able to be used for this model.

This model is similar to model in 4.1; it is also a GLMM with a binomial distribution which accounts for the effect of season, and interdependence between years and additionally, the time of season. This interdependence is modelled by the integer variable *observationday*. *Observationday* ensures an internal order of the days of observation by numbering the dates during the fish-ladder was active through all seasons.

$$\text{logit}(p_{ijk}) = \alpha + \text{Season}_{ijk} + 1|\text{observationday}_k + 1|\text{Year}_j$$

This model also accounted for overdispersion in the predicted values and used the same function by Zuur *et al.* (2012) as described in 3.1.

3.4 Assessing yearly trends in the sex quotient

Aggregation consisted of summarizing the dataset by given year and sex. This was modelled by a general linear model (GLM) which took the following form:

$$\text{logit}(p_{ij}) = \alpha + \beta_1 \text{Year}_j$$

Where p_{ij} represents the log-odds of the next observation, i , being female in the year j . Again, α represents the intercept.

4 Result

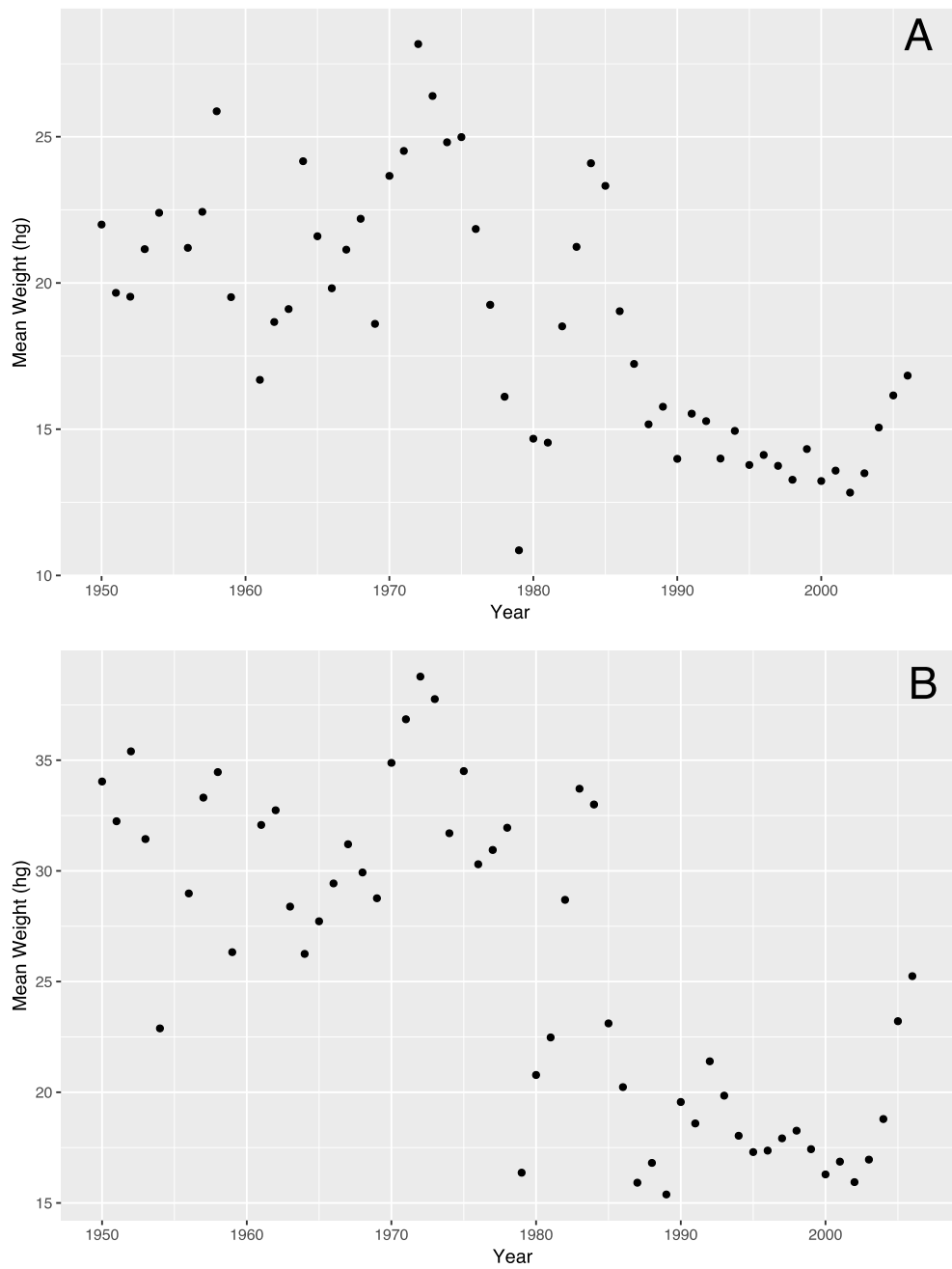
Mean 50% run date for the Dammån population was calculated as the average median run date across all years: 29th of July \pm 5.61 days (95% C.I.).

The mean female-to-male ratio of the migrants is 2.31 (95% CI=2.16-2.45). For means taken over years, the mean weight and lengths for respective sex can be viewed in table 2. Males are significantly larger than the females.

Tabell 2. *Mean weights and length of migrants of respective sex.*

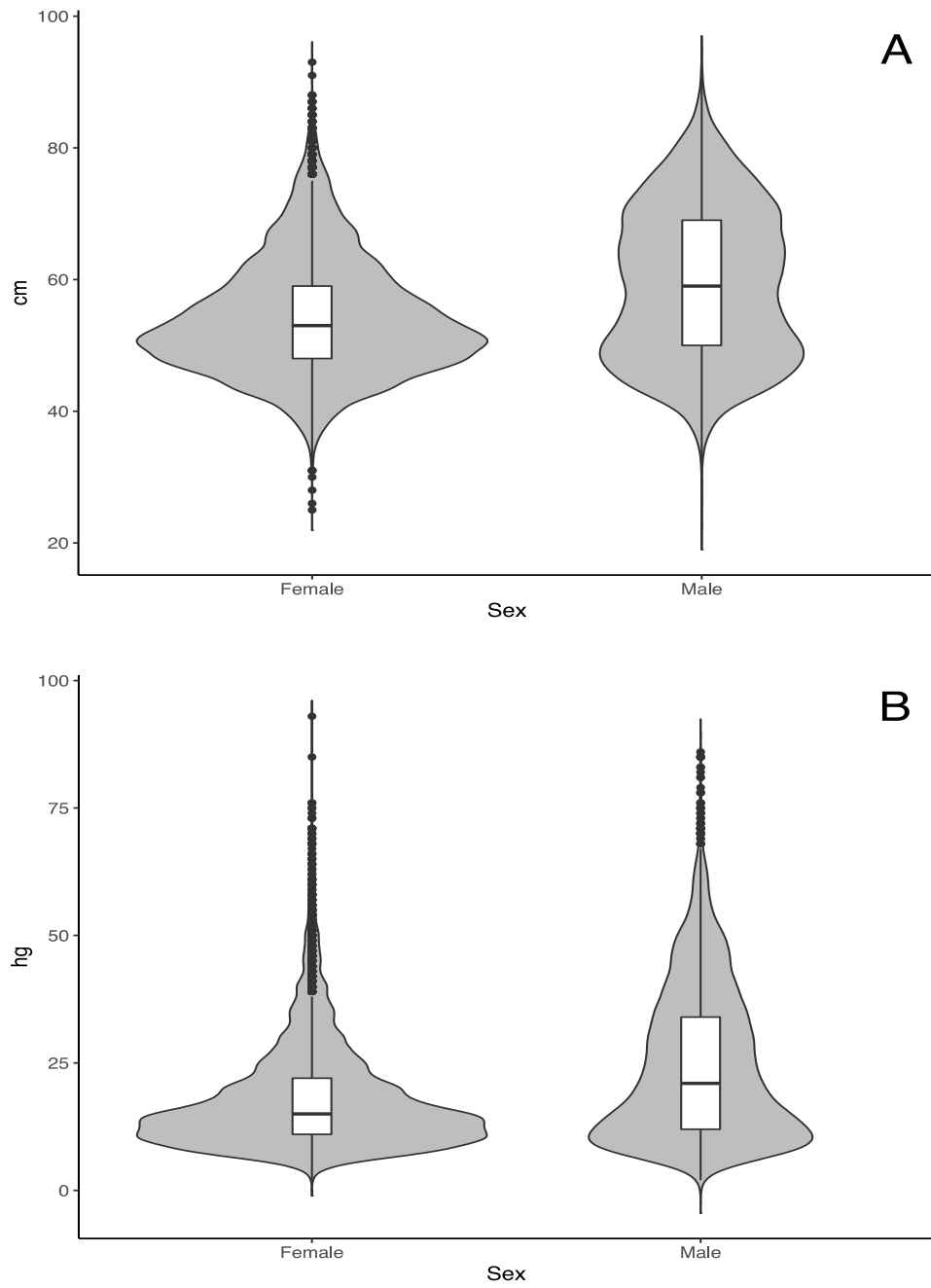
Sex	Mean Weight	Mean Length
Female	1799g	54.2 cm
Male	2454g	59.3 cm

The diel nominal variable for day or night did not significantly explain the variation in when the migrants passed the fish-ladder. The model was therefore discarded.



Figur 3. The mean weight of (A) female, and (B) male observations of *S. trutta* between 1950 and 2006.

There is a very sudden change in weights after 1978, which is particularly clear in the male demographic, although it is also visible among females. There is a tendency beginning 2002 for both female and male weights to recover.



Figur 4. Violin plots of the length (A) and weights (B) among the migrant sexes. Shaded area corresponds to the distribution of observations. Boxplot superimposed.

Violin plots in figure 4 display the distribution of weight and lengths among the migrant sexes. Using Welch's two sample t-test of respective variables, we cannot cast aside the alternative hypothesis that the means for the sexes are unequal ($p < 0.001$ for both length and weight). Females display a single peak around 50 cm of length and slightly above 12 hg of weight. The male demographic displays the same peaks, but the distributions have much longer tails, showing a higher variance among the male migrants. Male lengths display a bimodal distribution, with a first peak at c. 50 cm, followed by a second peak at c. 70 cm.

4.1 Seasonal Effect on female tendency to migrate.

The seasonal variable *observationdate* was very well correlated with seasonal changes. In conclusion, the model of how the probability of female observations changes throughout the season was very significant ($\chi^2 = 29.486$, $DF=1$, $\Pr(> \chi^2 < 0.0001, n=4113)$). For every day during the season, the log-odds of an observation being female increases by 0.00364. For a season between the earliest and latest observations, i.e. a total of 119 days; using equations (1.) and (2.) below, and inserting the intercept and term coefficient for the day of the season we see that the chance of a female observation on day 119 is 54.32% higher than that of a female observation on the first day of the season.

Calculating the Log-Odds:

$$\begin{aligned} \ln\left(\frac{p}{1-p}\right) &= \beta_0 + \beta_1(\text{Sex})(\text{day of season}) \Rightarrow \\ \ln\left(\frac{p}{1-p}\right) &= 0.04368647 + 0.00364632(\text{Sex})(\text{length of season}) \Rightarrow \\ \ln\left(\frac{p}{1-p}\right) &= 0.04368647 + 0.00364632(1)(119) \Rightarrow \\ \ln\left(\frac{p}{1-p}\right) &= 0.47759855 \end{aligned} \tag{1.}$$

Calculating the Log-Odds Ratio:

$$\frac{\text{Odds at end of season}}{\text{Odds at start of season}} = \frac{e^{0.47759855}}{e^{0.04368647}} = 1.543283 \tag{2.}$$

4.2 GLM of male to female ratio

The GLM of the male to female ratio throughout the years indicates a 13.85% decline in the probability of a female observation throughout the 56 years the study has been ongoing. The model was highly significant ($\chi^2 = 13.45$, DF=1, $\Pr(>\chi^2)=0.0002$).

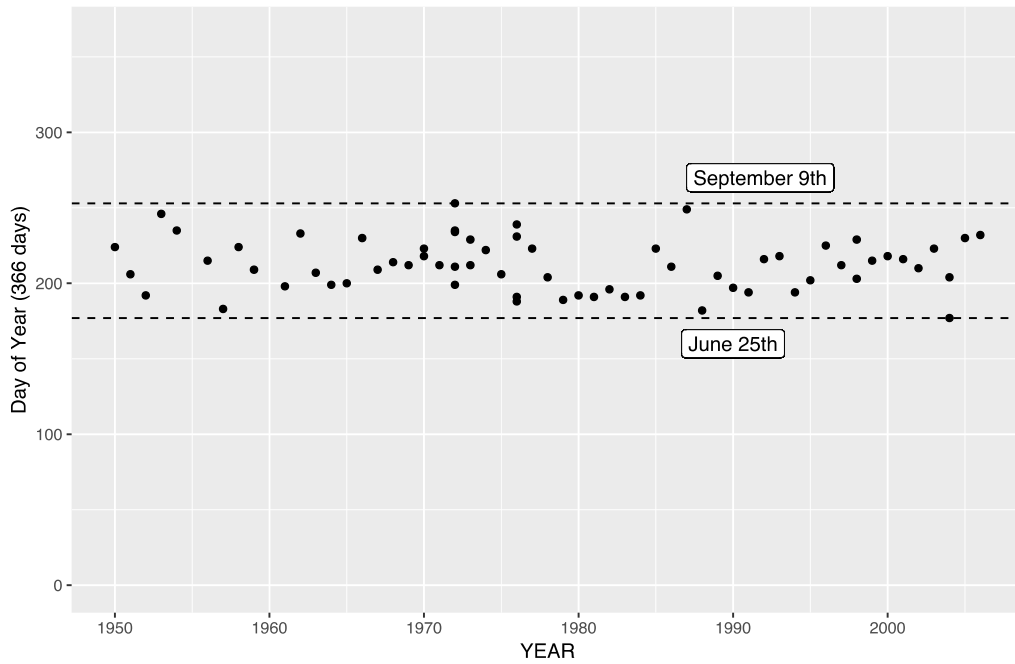
$$\begin{aligned}\ln\left(\frac{p}{1-p}\right) &= \beta_0 + \beta_1(\text{Sex})(\text{Year}) \Rightarrow \\ \ln\left(\frac{p}{1-p}\right) &= 6.0573110 - 0.0026625(\text{Sex})(\text{Year}) \Rightarrow \\ \ln\left(\frac{p}{1-p}\right) &= 6.0573110 - 0.0026625(1)(56) \Rightarrow\end{aligned}\tag{3.}$$

$$\ln\left(\frac{p}{1-p}\right) = 5.908211$$

$$\frac{\text{Odds during the last year}}{\text{Odds during the first year}} = \frac{e^{5.908211}}{e^{6.0573110}} = 0.861483\tag{4.}$$

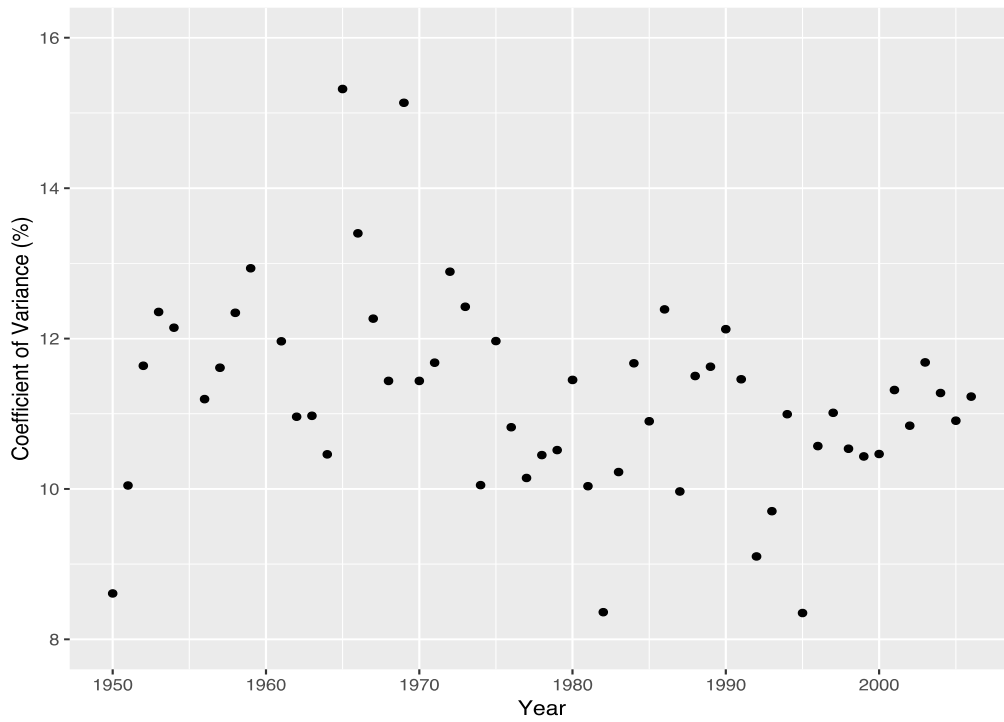
$$1 - 0.861483 = 0.138517$$

4.3 Variation in the timing of Peak Migration



Figur 5. Graph illustrating the variation in the peak migration date. Earliest (25th of June) and latest (9th of September) values are dotted lines. N.B. by definition, years can have multiple peaks.

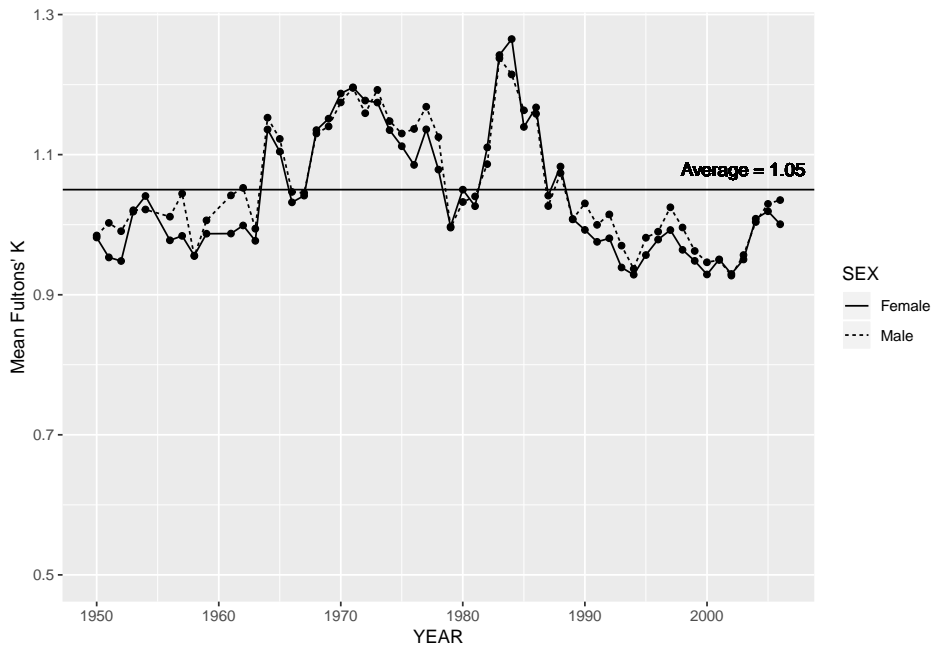
Looking at when the peak migration (day of highest number of migrants) occurred in figure 5, we can see that it has kept steady around the mean peak migration date, 30th of July, with the most extreme year having its peak migration date 41 days away (September 9th).



Figur 6. The coefficient of variance of the date of migration, by year.

The variation in the populations migrational timing has stabilized at $\sigma \approx 23$ days. As visible in fig. 6, there was marginally higher volatility during the earlier years.

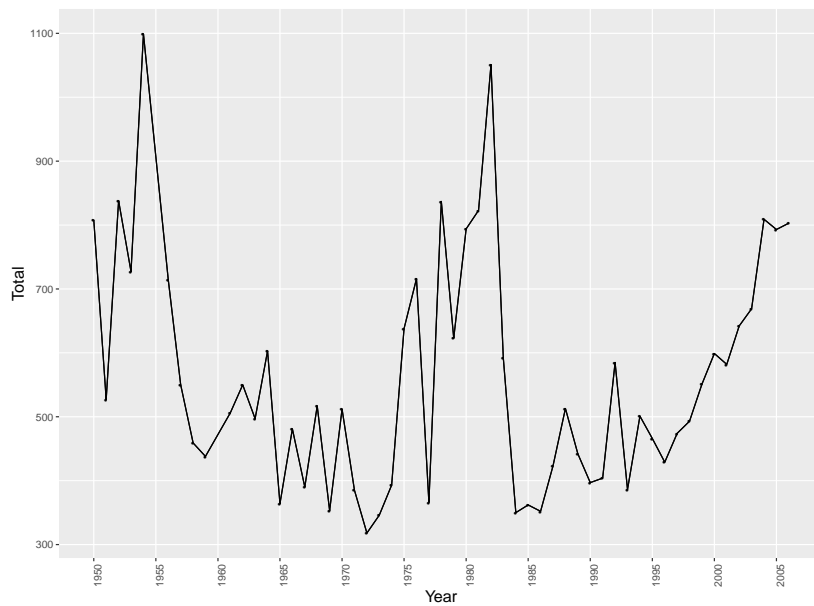
4.4 Mean Fulton's K by sex and year



Figur 7. Graph illustrating the mean Fulton's K for the migrant brown trout for each year; each sex illustrated individually. Black line depicts the average of the means.

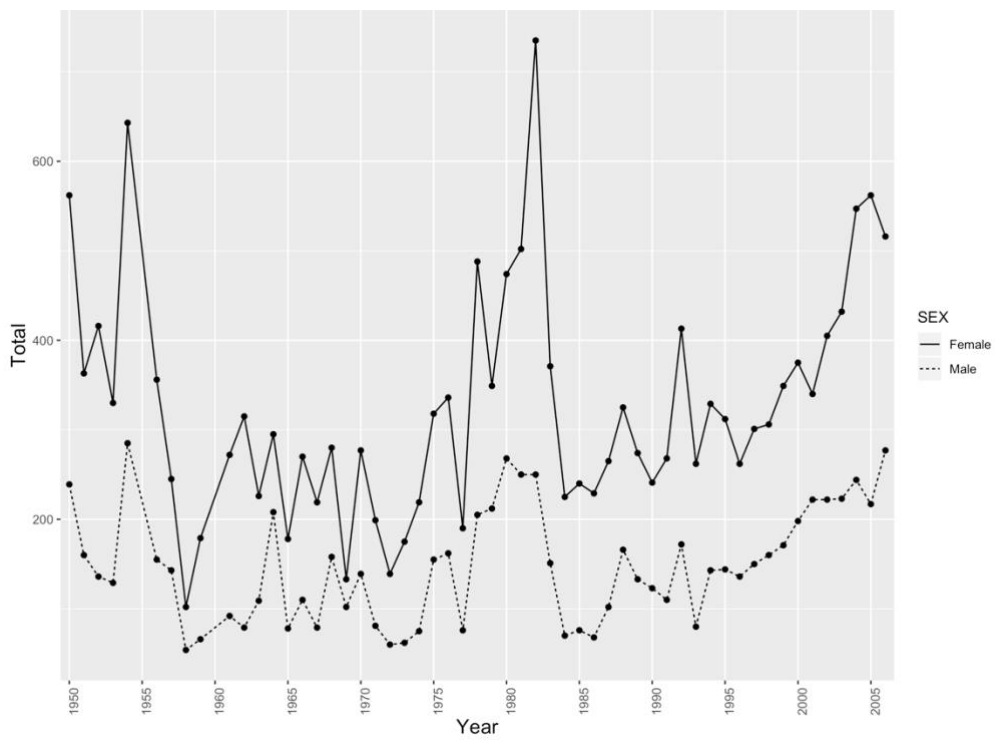
Figure 7 displays the development of Fulton's K throughout the years. There is no clear trend; values remain close to 1, with the exception of the 1970's and a peak in 1984.

4.5 Total amount of trout passing through Dammån fish-ladder.



Figur 8. Graph displaying the total amount of migrants passing through the fish-ladder between the day of year 175 and 241 over the years, including fish which were not successfully sexed.

The total amount of trout which has passed the fish-ladder (fig. 8) has been highly variable through the years, with some explosive increases prior to the clear peaks in 1954, 1982. 2004-2006 is also a period of high numbers of migrants, although the precursory increase has not occurred as rapidly. My visual observation is that there is a bi-decadal cyclic fluctuation. An all-time low was observed in 1972, when 318 migrants were observed. The maximum number of migrants, 1099 fish, was observed in 1954.



Figur 9. Graph displaying the count totals of migrants which were successfully sexed.

When the migrants are divided into their respective sexes, it is clear that the sexes closely follow one another.

5 Discussion

5.1 Tendencies in migrational timing

5.1.1 Diel

The diel model with a two-category nominal variable of day and night was not significant. It is likely that the very long summer days at the sites' latitude may significantly overlap the times when the fish-ladder is emptied.

5.1.2 Seasonal

I observed in the seasonal model a tendency for female migrants to arrive later in the season than males. The chance of an observation being female increases by 54.33% during a season of 119 days (formulae 1 & 2). This can be compared to the protandry predicted by Morbey (2002) to be predominant among Pacific salmon, and also commonly observed in adfluvial trout populations (Jonsson & Jonsson, 2011).

This tendency could also be coupled with the asset-protection principle, wherein the larger the current reproductive investment, the larger the interest to protect it (Clark, 1994). As brought up in the introduction, I see the consequent anti-predatory responses as both analogous and complementary to environmental risk responses – which would favour that females would be more risk averse as a result of their body

size being intimately connected to their absolute reproductive capacity. For migratory males, however, the asset-protection principle should relate more to ensure an early return to the spawning grounds in order to breed with as many females as possible – certainly as their absolute capacity to impregnate eggs is limited by competition, not the production rate of spermatozoa. As such, it is of higher importance that they arrive to the spawning grounds before as many females as possible.

5.1.3 Interannual

Differences in returning migrants as shown in the GLM of the probability of a return of female sex (formulae 3 & 4), can be argued to arise as a result of divergent pressures acting on the sexes as a result of spatial segregation as presented by Haraldstad and Jonsson (1983). In total, the model suggests that there is a total of 13.85% lower chance of an observation being female during the 2006 season compared to the 1955 season. This trend among upstream migrants could be attributed to several factors, see table 3 for overview.

Tabell 3. *A broad range of reasons which could underlie a decrease in the proportion of migrating females.*

Cause	Enabling Assumption
Harvest Pressure	Spatial segregation in lake
Predation Pressure	Change in trophic composition.
Environmental Pressure	Predisposition determined in embryonic development; resident or migrational mortality.
Male Residential Premium	Diminished habitat complexity decreases possibility for male parr maturation.
Female Migrational Premium	Relaxed intrasexual competition for redd habitat.

The constituents comprising high quality habitat among aquatic organisms are not uniform –we have a need to simplify the mechanisms and structures which substantiate an improvement to any degraded site or area. The Danish EPA, cf. Madsen and Denmark. Miljøstyrelsen. (1995), has developed a triad approach towards general watercourse quality: ensuring continuity in water quality, quantity; and habitat structure.

Sala *et al.* (2000) show that freshwater lakes & streams may experience significant change in the species community and/or biodiversity dependent upon the pressure from anthropogenic disturbances, most notably land-use change, climate change, or

biotic exchange; *in sensu* the threat posed to the native community by invasive species.

Scandinavian freshwater systems are no strangers to abovementioned factors, and have, at least in northern Scandinavia, been extensively employed for timber floating. In 1959 there were some 33'000 kilometres of public channels in Sweden (Sundberg, 1978). Interventions to facilitate the floating, e.g.: straightening the channel, installing stone piers, and clearing the riverbed of boulders and coarse woody debris with the aid of dynamite and bulldozers were commonplace (*pers. obs.*). It's thought that these interventions, as an extension of niche theory, have had an adverse impact upon the limnic biodiversity: largely due to the homogenization of habitat, recurring stressors or removal of disturbances.

As such, restoration efforts in Sweden have been focused on recreating larger structural heterogeneity, however this approach has been critiqued for its lack of empirical backing. Lepori *et al.* (2005) could show that restored sites did not majorly differ in macroinvertebrate or fish diversity; however, due to the increase of habitat area, restored sites could host a larger population. The inconclusive results of geomorphic restructuring for gains in biodiversity is seconded in the subject review by Palmer *et al.* (2010), who suggest that geomorphic heterogeneity is of lesser importance than anthropogenic interventions, catchment variables, riparian vegetation, disturbance regimes and water flow. Several papers suggest that this may be due to the scale of interventions failing to address critical structures (Chapman *et al.*, 2012a; Tews *et al.*, 2004). If the restoration attempts in Dammån (1973 & 1982) were of a short-term nature only, and in conjunction with the continuous timber-floating up until 1967 increased the male residential premium by providing much debris from logs and log-jams; this could have contributed to a higher female representation among the migrant demographic during the earlier and middle years of the study.

It is also possible that the decrease in the chance of an observation being female is due to a successive increase in abundance of inherited epigenetic methylations (not relating to the base DNA) which predispose male offspring to display migratory behaviour. Transgenerational epigenetic changes have been displayed in salmonids (Baerwald *et al.*, 2016) & several other taxa (Eva Jablonka & Gal Raz, 2009).

Additionally, Lake Storsjön has had several invasive species introduced which have had the potential to bring about the trophic changes discussed by Sala *et al.* (2000). Lansstyrelsen Jamtlands län (2015) give a report on different introduced species,

including: Brook trout (*S. fontinalis*, Mitchell 1814), Lake trout (*S. namaycush*, Walbaum 1792) & Rainbow trout (*O. mykiss*, Walbaum 1792). If any resultant trophic changes have affected the sexes differently, see Haraldstad and Jonsson (1983), they are also capable of bringing about a decrease in the number of female migrants.

5.1.4 Timing of Spawning Migration

Averaged over all years, the median run date I observed in Dammån was the 29th of July.

Carlsson *et al.* (2004) studied two tributaries to the river Ammerån, which has its confluence into Indalsälven roughly 150 kilometers downstream of Dammån fish ladder; the tributaries, whereof one was passable for migratory trout, experienced their upstream migratory peak mid-July. This peak is largely comparable to the peak migration dates in Dammån.

Dahl *et al.* (2004) studied the migration time of brown trout from 1960-2002 in Dalälven, located at 60°08'40"N 16°15'48"E, roughly 350 kilometers south of Dammån fish ladder: 50% run date of females was the 20th of August ± 14.9 days. For males, the 50% run date was 29th of August ± 17.2 days. The later upstream migration observations by Dahl *et al.* (2004) might be expected in a latitudinal cline, where the window of opportunity might occur earlier at higher latitudes, in order to avoid the freeze.

As can be deduced by the low amounts of observations migrating at the very start or end of the season (figure 2), the current season at the fish-ladder seems appropriate. As seen in figure 5, the day(s) of peak migration have remained stable throughout the course of this study. Similarly, as can be seen in figure 6, the volatility in migrational timing as measured by COV has not changed to a noteworthy degree.

5.2 General Migration

5.2.1 Population Trends

I believe that there is some indication of a bi-decadal population cycle, peaking in 1954, 1982, 2004 (see figure 8). These fluctuations are not exclusive to one sex (figure 9). Population cycles of various lengths are known in several other species, notably among Lynx (*Lynx canadensis*) & Snowshoe hares (*Lepus americanus*) in Canada (Elton & Nicholson, 1942); in British populations of Red Grouse (*Lagopus lagopus scotica*) (Hudson *et al.*, 1998) and in Skagerrak Cod (*Gadus morhua* L.) outside the Norwegian coast (Bjornstad *et al.*, 1999). It is generally understood that these cycles may be the result of density-dependent structures, climatic fluctuations, predation, inter- or intraspecies interactions, parasitism and the interaction of any combinations or all of the above mentioned (Bjornstad & Grenfell, 2001). As there are no obvious visual indications that the conditional index changes negatively as an immediate result of the total amount of spawning trout, it is possible that there is a density-dependent lag affecting other life-stages or life cycle choices.

Blanchfield and Ridgway (2005) demonstrate for lacustrine *S. fontinalis* a situation where the egg loss owing to a sub-par redd habitat is far higher than the respective loss owing to female competition. If the same were to apply to our study, it is possible that the combination of a stochastic negative environmental effect and an increasing amount of superimposed redds leverage a supra-additive mortality among the eggs.

5.3 Female to male ratio

Contrary to the summarization by Jonsson and Jonsson (2011) who found that the female-to-male ratio of partially migrant, anadromous brown trout populations in coastal streams roughly amounted to 1.5, I instead find in the migrant demographic of land-locked adfluvial brown trout a female-to-male ratio of 2.31.

I interpret the high ratio, compared to Jonsson and Jonsson (2011), as illustrative of a disproportionally high intrasexual competition among females for limited nest sites in Dammån.

5.4 Weight and Lengths

I observed a very rapid drop in the mean weights among the migrants, first in 1978, which quickly recovered in the following years before dropping again to the lower level which has since persisted (figure 3). As the population recovered quite quickly after the first drop, I am hesitant to suggest that any obstacle has hindered larger fish from migrating. Quite interestingly, the violin plots of the migrant lengths' show that the females very much concentrate around a single peak, which would suggest that there is a stabilising selection occurring. Among female weights, I observe the same trend, albeit not as clearly. The two sexes do not display similar distributions, and Welch's two-sample t-test indicates that we cannot rule out that the means are unequal; males do not seem to be affected by this stabilizing selection to the same degree, instead assuming a bimodal distribution. If the anthropogenic harvesting pressure is significant, is there a preference among fishermen to release mature males? Do the females require more time to regain lost condition post-spawning, and as a result do not fill the largest classes before they die if they spawn iteratively? As the selection seems to mostly impact the largest sizes, I find it difficult to assume a non-human predation as any notable cause.

6 Future Directions

As reviewed by Subbey *et al.* (2014), there remains tremendous challenges in modelling recruitment, despite the inclusion of environmental variables – certainly since organisms with high fecundity may display quite some chaotic dynamics, and there is outstanding difficulty in determining an appropriate scale of detail in complex processes. I generally agree with Subbey *et al.* (2014) that there exist two major reasons to develop recruitment models; either to i) guide policy, or ii) understand underlying processes.

Szuwalski and Hollowed (2016) discuss how some forecasts can become biased - perhaps most importantly, if there is driven change in an underlying variable, this can to differing degrees introduce bias through its non-stationarity. This type of bias may be apparent in longer time-series. Good examples might include changes in harvest strategy, crossing climatic tipping points, or the introduction of an invasive species. While recognizing some information from the long-term data, e.g. carrying capacity; it may be prudent to consider a shorter time-span during which it is reasonable to assume that there have been no major structural changes. Similarly, individual interventions may have an unduly strong effect on the model depending on what degree of smoothing which is applied, or what type of model is chosen.

As the history of the tributary is well known, and we have a high-resolution data set, it would be interesting to conduct an intervention analysis to see if it is possible to correlate individual events to the migrational dynamics. In such an analysis, it would become increasingly pressing to also include a temporal autocorrelation in the model in order to be able to clearer root out trends. In particular, I would recommend to further implore how the sudden weight loss in 1978 came about.

Imputational method becomes increasingly important with a growing amount of incomplete data; by adjusting the length of the time-series it may be possible to

avoid more significant gaps. This is also concluded by Bjornstad and Grenfell (2001), whom note that restructuring capacities provides great value as it is not always feasible to measure all variables.

I would encourage an effort to include later years of the time series in order to see if the periodicity of the perceived population cycle has been maintained, and if further time series analyses can confirm a pattern. It is possible to connect further environmental variables which have fallen outside of the scope of my current work. Perhaps fishing records from the County Administrative Board are available and can be used to model an approximation of the harvest pressure.

Pertaining to the adaptive management of fisheries, it is my firm belief that developing predictive models is a sound research objective – beyond the basic monitoring which facilitates the development, statistical models may allow us to continually evaluate potential structural changes while simultaneously providing managers with valuable short and midterm guidance.

Appendix I

R Session Info

R version 3.4.0 (2017-04-21)

Platform: x86_64-apple-darwin15.6.0 (64-bit)

Running under: macOS 10.13.1

Matrix products: default

BLAS:

/System/Library/Frameworks/Accelerate.framework/Versions/A/Frameworks/vec
Lib.framework/Versions/A/libBLAS.dylib

LAPACK:

/Library/Frameworks/R.framework/Versions/3.4/Resources/lib/libRlapack.dylib

locale:

[1] en_US.UTF-8/en_US.UTF-8/en_US.UTF-8/C/en_US.UTF-8/en_US.UTF-8

attached base packages:

[1] stats graphics grDevices utils datasets methods base

other attached packages:

[1] rgeos_0.3-28 ggmap_2.6.1 forcats_0.3.0 stringr_1.3.1
[5] purrr_0.2.5 readr_1.1.1 tibble_1.4.2 tidyverse_1.2.1
[9] maptools_0.9-2 tmap_1.11-2 rgdal_1.3-3 sp_1.3-1
[13] sjPlot_2.6.0 xtable_1.8-2 car_3.0-0 carData_3.0-1
[17] mgcv_1.8-24 zoo_1.8-2 doBy_4.6-1 tidyr_0.8.1
[21] sqldf_0.4-11 RSQLite_2.1.1 gsubfn_0.7 proto_1.0.0
[25] magrittr_1.5 ggplot2_3.0.0 lme4_1.1-17 Matrix_1.2-14
[29] nlme_3.1-137 MASS_7.3-50 dplyr_0.7.6 plyr_1.8.4
[33] lubridate_1.7.4

loaded via a namespace (and not attached):

[1] R.utils_2.6.0 tidyselect_0.2.4 htmlwidgets_1.2 grid_3.4.0
[5] munsell_0.5.0 codetools_0.2-15 units_0.6-0 chron_2.3-52
[9] withr_2.1.2 colorspace_1.3-2 knitr_1.20 rstudioapi_0.7

[13] stats4_3.4.0 bayesplot_1.6.0 emmeans_1.2.3 RgoogleMaps_1.4.2
 [17] mnormt_1.5-5 bit64_0.9-7 glmmTMB_0.2.2.0 coda_0.19-1
 [21] LearnBayes_2.15.1 TH.data_1.0-9 R6_2.2.2 bitops_1.0-6
 [25] assertthat_0.2.0 promises_1.0.1 scales_0.5.0 multcomp_1.4-8
 [29] nnet_7.3-12 gtable_0.2.0 sandwich_2.4-0 rlang_0.2.1
 [33] splines_3.4.0 TMB_1.7.14 lazyeval_0.2.1 dichromat_2.0-0
 [37] mapview_2.4.0 broom_0.4.5 yaml_2.1.19 reshape2_1.4.3
 [41] prediction_0.3.6 abind_1.4-5 modelr_0.1.2 crosstalk_1.0.0
 [45] httpuv_1.4.4.2 gdalUtils_2.0.1.14 rmapshaper_0.4.0 tools_3.4.0
 [49] tcltk_3.4.0 psych_1.8.4 spData_0.2.9.0 raster_2.6-7
 [53] RColorBrewer_1.1-2 ggridges_0.5.0 jsonvalidate_1.0.0 Rcpp_0.12.17
 [57] base64enc_0.1-3 classInt_0.2-3 RCurl_1.95-4.10 deldir_0.1-15
 [61] tmaptools_1.2-4 haven_1.1.2 survey_3.33-2 data.table_1.11.4
 [65] openxlsx_4.1.0 gmodels_2.18.1 effects_4.0-2 mvtnorm_1.0-8
 [69] sjmisc_2.7.4 hms_0.4.2 mime_0.5 XML_3.98-1.11
 [73] leaflet_2.0.1 rio_0.5.10 sjstats_0.17.0 jpeg_0.1-8
 [77] readxl_1.1.0 ggeffects_0.5.0 compiler_3.4.0 maps_3.3.0
 [81] KernSmooth_2.23-15 V8_1.5 crayon_1.3.4 minqa_1.2.4
 [85] R.oo_1.22.0 htmltools_0.3.6 later_0.7.3 spdep_0.7-7
 [89] expm_0.999-2 DBI_1.0.0 sjlabelled_1.0.13 sf_0.6-3
 [93] boot_1.3-20 cli_1.0.0 R.methodsS3_1.7.1 gdata_2.18.0
 [97] parallel_3.4.0 bindr_0.1.1 pkgconfig_2.0.1 geosphere_1.5-7
 [101] coin_1.2-2 foreign_0.8-70 xml2_1.2.0 foreach_1.4.4
 [105] geojsonlint_0.2.0 stringdist_0.9.5.1 webshot_0.5.0 estimability_1.3
 [109] rvest_0.3.2 snakecase_0.9.2 digest_0.6.15 cellranger_1.1.0
 [113] curl_3.2 shiny_1.1.0 gtools_3.8.1 satellite_1.0.1
 [117] modeltools_0.2-21 rjson_0.2.20 pwr_1.2-2 nloptr_1.0.4
 [121] jsonlite_1.5 bindrcpp_0.2.2 mapproj_1.2.6 viridisLite_0.3.0
 [125] pillar_1.2.3 lattice_0.20-35 httr_1.3.1 survival_2.42-4
 [129] glue_1.2.0 zip_1.0.0 png_0.1-7 iterators_1.0.9
 [133] bit_1.1-14 class_7.3-14 stringi_1.2.3 blob_1.1.1
 [137] memoise_1.1.0 osmar_1.1-7 e1071_1.6-8

References

- Anon. *Hot mot Dammån*. Available at:
<http://www.fishersguide.com/inlaga/om%20damman/hot%20mot%20Damman.htm> [08-20].
- Baerwald, M.R., Meek, M.H., Stephens, M.R., Nagarajan, R.P., Goodbla, A.M., Tomalty, K.M.H., Thorgaard, G.H., May, B. & Nichols, K.M. (2016). Migration-related phenotypic divergence is associated with epigenetic modifications in rainbow trout. *Molecular Ecology*, 25(8), pp. 1785-1800.
- Bjornstad, O.N., Fromentin, J.M., Stenseth, N.C. & Gjosaeter, J. (1999). Cycles and trends in cod populations. *Proceedings of the National Academy of Sciences of the United States of America*, 96(9), pp. 5066-5071.
- Bjornstad, O.N. & Grenfell, B.T. (2001). Noisy clockwork: Time series analysis of population fluctuations in animals. *Science*, 293(5530), pp. 638-643.
- Blanchfield, P.J. & Ridgway, M.S. (2005). The relative influence of breeding competition and habitat quality on female reproductive success in lacustrine brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62(12), pp. 2694-2705.
- Bohlin, T., Pettersson, J. & Degerman, E. (2001). Population density of migratory and resident brown trout (*Salmo trutta*) in relation to altitude: evidence for a migration cost. *Journal of Animal Ecology*, 70(1), pp. 112-121.
- Campbell, J.S. (1977). Spawning Characteristics of Brown Trout and Sea Trout *Salmo-Trutta-L* in Kirk Burn, River Tweed, Scotland. *Journal of Fish Biology*, 11(3), pp. 217-&.
- Carlsson, J., Aarestrup, K., Nordwall, F., Naslund, I., Eriksson, T. & Carlsson, J.E.L. (2004). Migration of landlocked brown trout in two Scandinavian streams as revealed from trap data. *Ecology of Freshwater Fish*, 13(3), pp. 161-167.
- Chapman, B.B., Hulthen, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.A. & Bronmark, C. (2012a). Partial migration in fishes: causes and consequences. *Journal of Fish Biology*, 81(2), pp. 456-478.
- Chapman, B.B., Skov, C., Hulthen, K., Brodersen, J., Nilsson, P.A., Hansson, L.A. & Bronmark, C. (2012b). Partial migration in fishes: definitions, methodologies and taxonomic distribution. *Journal of Fish Biology*, 81(2), pp. 479-499.
- Clark, C.W. (1994). Antipredator Behavior and the Asset-Protection Principle. *Behavioral Ecology*, 5(2), pp. 159-170.
- Dahl, J., Dannewitz, J., Karlsson, L., Petersson, E., Lof, A. & Ragnarsson, B. (2004). The timing of spawning migration: implications of environmental variation, life history, and sex. *Canadian Journal of Zoology*, 82(12), pp. 1864-1870.
- Ecke, F., Levanoni, O., Audet, J., Carlson, P., Eklof, K., Hartman, G., Mckie, B., Ledesma, J., Segersten, J., Truchy, A. & Futter, M. (2017). Meta-analysis

- of environmental effects of beaver in relation to artificial dams. *Environmental Research Letters*, 12(11).
- Elliott, J.M. (1994). *Quantitative ecology and the brown trout*. Oxford: Oxford University Press.
- Elton, C.S. & Nicholson, M. (1942). *The ten-year cycle in numbers of the lynx in Canada*. Oxford: Blackwell Scientific.
- Eva Jablonka & Gal Raz (2009). Transgenerational Epigenetic Inheritance: Prevalence, Mechanisms, and Implications for the Study of Heredity and Evolution. *The Quarterly Review of Biology*, 84(2), pp. 131-176.
- Fleming, I.A. (1996). Reproductive strategies of Atlantic salmon: Ecology and evolution. *Reviews in Fish Biology and Fisheries*, 6(4), pp. 379-416.
- Fleming, I.A., Jonsson, B., Gross, M.R. & Lamberg, A. (1996). An experimental study of the reproductive behaviour and success of farmed and wild Atlantic salmon (*Salmo salar*). *Journal of Applied Ecology*, 33(4), pp. 893-905.
- Granath, B. & Norman, L. (2006). *Bevarandeplan för Natura 2000-område - Dammån SE0720360, Dammån-Storån SE0720288*. Östersund: Miljö & Fiske.
- Gross, M.R., Coleman, R.M. & McDowall, R.M. (1988). Aquatic Productivity and the Evolution of Diadromous Fish Migration. *Science*, 239(4845), pp. 1291-1293.
- Gutowsky, L.F.G., Harrison, P.M., Martins, E.G., Leake, A., Patterson, D.A., Power, M. & Cooke, S.J. (2013). Diel vertical migration hypotheses explain size-dependent behaviour in a freshwater piscivore. *Animal Behaviour*, 86(2), pp. 365-373.
- Hansen, L.P. & Jonsson, B. (1991). Evidence of a genetic component in the seasonal return pattern of Atlantic Salmon, *Salmo-salar* L. *Journal of Fish Biology*, 38(2), pp. 251-258.
- Haraldstad, O. & Jonsson, B. (1983). Age and Sex Segregation in Habitat Utilization by Brown Trout in a Norwegian Lake. *Transactions of the American Fisheries Society*, 112(1), pp. 27-37.
- Haraldstad, T., Kroglund, F., Kristensen, T., Jonsson, B. & Haugen, T.O. (2017). Diel migration pattern of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) smolts: an assessment of environmental cues. *Ecology of Freshwater Fish*, 26(4), pp. 541-551.
- Harris, G. & Milner, N. (2006). *Sea trout : biology, conservation and management : proceedings of the First International Sea Trout Symposium, Cardiff, July 2004*. Oxford: Blackwell.
- Hindar, K., Jonsson, B., Ryman, N. & Stahl, G. (1991). Genetic-Relationships among Landlocked, Resident, and Anadromous Brown Trout, *Salmo-Trutta* L. *Heredity*, 66, pp. 83-91.
- Hixon, M.A., Johnson, D.W. & Sogard, S.M. (2013). BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *Ices Journal of Marine Science*, 71, pp. 2171-2185.
- Hudson, P.J., Dobson, A.P. & Newborn, D. (1998). Prevention of Population Cycles by Parasite Removal. *Science*, 282, pp. 2256-2258.

- Jonsson, B. (1985). Life-History Patterns of Fresh-Water Resident and Sea-Run Migrant Brown Trout in Norway. *Transactions of the American Fisheries Society*, 114(2), pp. 182-194.
- Jonsson, B. & Gravem, F.R. (1985). Use of Space and Food by Resident and Migrant Brown Trout, *Salmo-Trutta*. *Environmental Biology of Fishes*, 14(4), pp. 281-293.
- Jonsson, B. & Jonsson, N. (2006). Life-history effects of migratory costs in anadromous brown trout. *Journal of Fish Biology*, 69(3), pp. 860-869.
- Jonsson, B. & Jonsson, N. (2011). *Ecology of Atlantic salmon and brown trout : habitat as a template for life histories*. (Fish & fisheries series. Dordrecht ; New York: Springer.
- Jonsson, B., Jonsson, N., Brodtkorb, E. & Ingebrigtsen, P.J. (2001). Life-history traits of Brown Trout vary with the size of small streams. *Functional Ecology*, 15(3), pp. 310-317.
- Jonsson, N. (1991). Influence of water flow, water temperature and light on fish migration in rivers. *Nordic journal of freshwater research*, 66(1991), pp. 20-35.
- Jonsson, N. & Jonsson, B. (2002). Migration of anadromous brown trout *Salmo trutta* in a Norwegian river. *Freshwater Biology*, 47(8), pp. 1391-1401.
- Labeelund, J.H. (1991). Variation within and between Rivers in Adult Size and Sea Age at Maturity of Anadromous Brown Trout, *Salmo-Trutta*. *Canadian Journal of Fisheries and Aquatic Sciences*, 48(6), pp. 1015-1021.
- Lansstyrelsen Jamtlands lan (2015). *Storsjöns vattensystem - en samlad beskrivning och prioriterade miljöåtgärder*.
- Lepori, F., Palm, D., Brannas, E. & Malmqvist, B. (2005). Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? *Ecological Applications*, 15(6), pp. 2060-2071.
- Lucas, M.C. & Baras, E. (2001). *Migration of freshwater fishes*. Oxford ; Malden, MA: Blackwell Science.
- Madsen, B.L. & Denmark. Miljøstyrelsen. (1995). *Danish watercourses : ten years with the New Watercourse Act : collected examples of maintenance and restoration*. (Miljønyt. Copenhagen: Ministry of Environment and Energy Danish Environmental Protection Agency. Available from: Table of contents only <http://www.loc.gov/catdir/toc/fy0612/2006436071.html>.
- McDowall, R.M. (2008). Why are so many boreal freshwater fishes anadromous? Confronting 'conventional wisdom'. *Fish and Fisheries*, 9(2), pp. 208-213.
- Migaud, H., Davie, A. & Taylor, J.F. (2010). Current knowledge on the photoneuroendocrine regulation of reproduction in temperate fish species. *Journal of Fish Biology*, 76(1), pp. 27-68.
- Morbey, Y.E. (2002). Protandry models and their application to salmon. *Behavioral Ecology*, 13(3), pp. 337-343.
- Ohlberger, J., Ward, E.J., Schindler, D.E. & Lewis, B. (2018). Demographic changes in Chinook salmon across the Northeast Pacific Ocean. *Fish and Fisheries*, 19(3), pp. 533-546.

- Palmer, M.A., Menninger, H.L. & Bernhardt, E. (2010). River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? *Freshwater Biology*, 55, pp. 205-222.
- Quinn, T.P. & Adams, D.J. (1996). Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology*, 77(4), pp. 1151-1162.
- Ros, T. (1981). Salmonids in the Lake Vanern Area. *Ecological Bulletins*(34), pp. 21-31.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000). Biodiversity - Global biodiversity scenarios for the year 2100. *Science*, 287(5459), pp. 1770-1774.
- Subbey, S., Devine, J.A., Schaarschmidt, U. & Nash, R.D.M. (2014). Modelling and forecasting stock-recruitment: current and future perspectives. *Ices Journal of Marine Science*, 71(8), pp. 2307-2322.
- Sundberg, U. (1978). Teknik i Skog. In: Fries, J. & Zimmerman, J. (eds) *Skogshögskolan 150 år*. Uppsala: LiberTryck Stockholm, p. 131.
- Szuwalski, C.S. & Hollowed, A.B. (2016). Climate change and non-stationary population processes in fisheries management. *Ices Journal of Marine Science*, 73(5), pp. 1297-1305.
- Tesch, F.W. (1978). Methods for assessment of fish production in fresh waters. In: Bagenal, T.B. & Ricker, W.E. (eds) *IBP handbook no 3*. 3d. ed. Oxford Eng. Philadelphia: Blackwell Scientific ; distributed by J. B. Lippincott, p. p. 118.
- Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31(1), pp. 79-92.
- Wright, S. (1932). *The roles of mutation, inbreeding, crossbreeding, and selection in evolution*1): na.
- Zuur, A.F., Saveliev, A.A. & Ieno, E.N. (2012). *Zero inflated models and generalized linear mixed models with R*. Newburgh, U.K.: Highland Statistics Ltd.

SENASTE UTGIVNA NUMMER

- 2018:4 Grazing impacts on savanna vegetation states and its role in albedo changes
Författare: Joana Fernandes
- 2018:5 Factors affecting damage to Scots Pine in a multiple ungulate species system
Författare: Matthew Knibb
- 2018:6 Supplementary feeding of game; an attitude survey of hunters, forest owners and farmers
Författare: Micaela Johansson
- 2018:7 The effect of nest box temperature on the breeding success of Pied Flycatchers (*Ficedula hypoleuca*) in northern Sweden
Författare: Jorina Boer
- 2018:8 Resource distribution in disturbed landscapes – the effect of clearcutting on berry abundance and their use by brown bears
Författare: Matej Domevšič
- 2018:9 Presence and habitat use of the endangered Bornean elephant (*Elephas maximus borneensis*) in the INIKEA Rehabilitation project site (Sabah, Malaysia) - A pilot study -
Författare: Laia Crespo Minguenza
- 2018:10 Why have the eggs in Baltic salmon (*Salmo salar* L.) become larger?
Författare: Shoumo Khondoker
- 2018:11 Consequences of White Rhinoceros (*Ceratotherium simum*) Poaching on Grassland Structure in Hluhluwe-iMfolozi Park in South Africa
Författare: Emy Vu
- 2018:12 Effects of Body Condition on Facultative Anadromy in Brown Trout (*Salmo trutta*)
Författare: Samuel Shry
- 2018:13 Biodiversity in assisted migration trials – A study comparing the arthropod diversity between different populations of cottonwood (*Populus Fremontii*) translocated to new areas
Författare: Maria Noro-Larsson
- 2018:14 Nutrient distribution by mammalian herbivores in Hluhluwe-Imfolozi Park (South Africa)
Författare: Laura van Veenhuisen
- 2018:15 Status of supplementary feeding of reindeer in Sweden and its consequences
Författare: Anna-Marja Persson
- 2018:16 Effects of wolf predation risk on community weighted mean plant traits in Białowieża Primeval Forest, Poland
Författare: Jone Lescinskaite