# TO MIGRATE OR NOT TO MIGRATE - THAT'S THE QUESTION: WHY DO RUDD (*SCARDINIUS ERYTHROPHTHALMUS*) IN THE STORELVA SYSTEM MIGRATE TO SANDNESFJORDEN?

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# Abstract

Migration is a common behaviour in many species and the duration and migration distance vary among species. The occurrence of migration has been related to a gain in fitness through feeding, refuge and spawning benefits, and is often a trade-off between benefits e.g. gaining high growth rate, and disadvantages, as exposure to predators.

In this study I look at the demography behind the tendency to migrate, and compare growth and survival between Storelva rudd (*Scardinius erythropthalmus*) that migrate to brackish water with those that do not. I test the hypothesis that migratory individuals of rudd experience higher or equal fitness than non-migratory individuals, primarily driven by growth benefits from residing in brackish waters.

A total of 455 individuals were PIT-tagged. Capture-Mark-Recapture-analysis was used to find their survival probabilities and between-habitat migration probabilities under different period-specific and individual-specific covariates. Individual growth rates were compared between the two groups and I used life-table simulations to estimate fitness for the different behaviour options.

The freshwater rudd grew slightly better and growth rate was positively correlated to temperature. Migration to brackish water was driven by river discharge and migration to freshwater by fjord salinity. Survival in brackish water was affected by salinity and fish length and survival in freshwater by water discharge and temperature. Rudd smaller than 12-13 cm had very low survival rates in brackish water. Population mean fitness was lower in migratory individuals than for the freshwater residents.

The ultimate prediction from my study is that the migratory genotypes over time will vanish from the population. I discuss short-comings in the fitness estimates and that the estimates are premature owing to a short study period and lack of information about the maturation pattern. Since the migrants experience no growth-related benefits from migrating into the brackish-water habitat, I suggest that density-dependent factors in the freshwater habitat comprise the main driver of this migration system. In particular, I suggest that the high pike density in Lundevann may motivate the migrants to seek lower predation-pressure in the freshwater habitat. The rudd migrants constitute a threat to spreading of rudd along the

coast and into new water courses. There might be two subpopulation types and they should be managed accordingly.

In conclusion, the driving forces behind rudd migration in the Storelva system remains enigmatic and continuation of the PIT-tag study should be secured.

# Contents

# 1  Introduction

Migration is a common behaviour in many species, both terrestrial and aquatic, where the duration and migration distance vary among species, from long across-seas journeys, to short migration distances within the individual's home range. The occurrence of migration has been related to a gain in fitness through feeding, refuge and spawning benefits (Lucas & Baras 2001).

The migration behaviour often involves trade-offs between benefits and disadvantages. For example in the cases of anadromous migration systems (Harden Jones 1968) where fish migrate from juvenile habitats in freshwater to feeding areas in the sea the migrants experience energy cost of migration per se.  They also become more exposed to predators (Jarvi 1989) both while migrating and due to the higher presence of predators in the sea. By attaining a high growth rate in the resource-rich sea habitat the fish becomes less susceptible to predation by gap- limited predators (Brabrand 2000). By growing bigger in the sea habitat the migrants also experience size-related fitness advantages (females get higher fecundity and males become better fighters) when returning to the spawning grounds. Larger individuals are also more likely to cope with the energy use involved in the bypassing of obstacles and migration barriers (Standen et al. 2002) when ascending the river towards the spawning grounds.

In order to understand the underlying motivation that drives a given migration system one will have to analyse the costs and benefits related to the two behaviour alternatives, i.e., one will have to demonstrate that migratory individuals gain an equal or higher fitness than individuals that do not migrate. This sort of reasoning lies behind optimal habitat-use theory where one of the core predictions is the so-called ideal free distribution (IFD) of animals among habitat patches of indifferent qualities (Fretwell & Lucas 1970). The IFD-theory comprises two phases, where the first phase entails the decision process where the individual assesses habitat qualities (is there an intrinsic quality difference among habitats from which I can benefit from moving?), and the second phase where fitness is realised. The ultimate prediction from the IFD theory is that the animals will distribute so as to equalize fitness over all habitats. The theory as gained support from many experimental systems (Milinski 1988), but until quite recently it had not been tested in a natural system. An

extensive mark-recapture of pike in Lake Windermere demonstrated that pike individuals were ideally-free-distributed between the two lake basins (Haugen et al. 2006). The main drivers of between-basin migration in this system were density-dependent dispersal and density-dependent survival (Haugen et al. 2007). The testing of fitness-consequences of animal behaviour in the wild can only be attained from some sort of tagging experiment, as in the Windermere pike system.

In northern regions, freshwater fish are often restricted by the diet that is available for them in the freshwater habitat and hence the occurrence of anadromy tends to increase with latitude as marine habitats are relatively richer in resources compared to freshwater habitats (Svenning 2000). When the production halts in the winter the growth of freshwater fish is often limited until spring. If there is food available, the restriction for growth is the cold environment. Since the production in the sea is usually greater than in freshwater feeding migrations can be seen as a compensation for the relatively limited growth in freshwater. By moving to another location, either fresh or saltwater, the growth and hence the fitness can be significantly increased. Therefore, systems where fish can move between a more saline habitat with presumably higher potentials for growth compared to stay in freshwater constitute a system for testing optimal habitat use theory.

Cyprinids are freshwater species that thrive in lakes and ponds or slow-running water (Hicks 2003). Migration is known among cyprinids and seasonal movements where they move out of the lake and into a connecting stream has been described (Skov et al. 2008) . In the Skov et al. (2008) study they found that the three species of cyprinids roach *(Rutilus rutilus)*, white bream *(Blicca bjoerkna)* and rudd *(Scardinius erythrophthalmus)* moved into the streams during fall or winter and speculate that the rudd moves to lower its predation risk. Diel migration has also been described, for example in the lower parts in the river Rhine (Heermann & Borcherding 2006). Here carps moved from the lake into a river channel in the morning, and the reversed direction in the evening. Since the predator did not follow them to the channel they suggest that predator avoidance could be a reason why they move into the channel at daytime. The channel had a higher current velocity which could be a reason for the migration to the lake in the evening. Spending nights in the lake would then be time spent energy conserving and an explanation for the observed diel migration pattern. Despite being considered a freshwater species rudd has been observed in brackish waters

and in low salinities between 0.5- 2‰, however, as its abundance was increasing it also started appearing in salinities at 4-6‰ (Vetemaa et al. 2006). Rudd has also been observed in salinities up to 10‰ (Simonsen & Matzow 2000). In a more recent study (Solberg 2012) rudd was found to thrive in salinities up to 12‰.

In the Storelva river system, Aust-Agder County, Norway, there is an ongoing monitoring program on all migratory fish. This project use rotary smolt screw traps to catch descending fish passing through Lundevann and into the fjord during the spring period. In addition to salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolt, rudd and whitefish (*Coregonus lavaretus*) are also caught in the rotary screw trap – presumably on their way towards the brackish water fjord system. This has been recorded to occur every year since 2009 and after implanting PIT-tags in some descending individuals it was registered that at the least some individuals migrate back to the river system later in the season (Kroglund et al. 2010). To date, the extent, demography and ecology behind this migratory rudd population remains enigmatic. However, it has been speculated if the migratory rudd experience fitness advantages from migrating into brackish water for instance in relation to individual growth. Therefore, this study system offers an opportunity to test whether the observed migration can be linked to optimal habitat-choice behaviour.

In this MSc-project, I explore the demography behind tendency to migrate, and I compare growth and survival between Storelva rudd that migrate with those that do not. Finally, I test the hypothesis that migratory individuals of rudd experience higher or equal fitness than non-migratory individuals primarily driven by growth benefits from residing in brackish waters.

## 2 Materials and methods

### 2.1 Study area

This study was carried out in the Storelva river system (Figure 1), Tvedestrand municipality, and in Sandnesfjorden, Risør municipality, in Aust Agder, southern Norway. The river Storelva runs eastward for about 10 km before entering the lake Lundevann (Figure 2), which is 1.1 km long and 20 meters deep(Kroglund et al. 2010). Lundevann exits at Strømmen, a 130 meter long passage that runs into the lake Songevann. Storelva further enters into Nævestadfjorden and Laget, where the river meets the sea in Sandnesfjorden. The river Storelva always consists of freshwater until it exits Strømmen. From Songevann to Laget, the salinity varies depending on Storelva water level, tide cycles and season.

In addition to the study species rudd, pike *(Esox lucius),* perch *(Perca fluviatilis),* tench *(Tinca tinca)* and whitefish (*Coregonus lavaretus*) live in the lake*.* The lake is part of a river system that holds populations of anadromous salmon (*Salmo salar*) and brown trout (*Salmo trutta*)*.* The anadromous salmon/brown trout has been a subject of study since 2005(Kroglund et al. 2010).
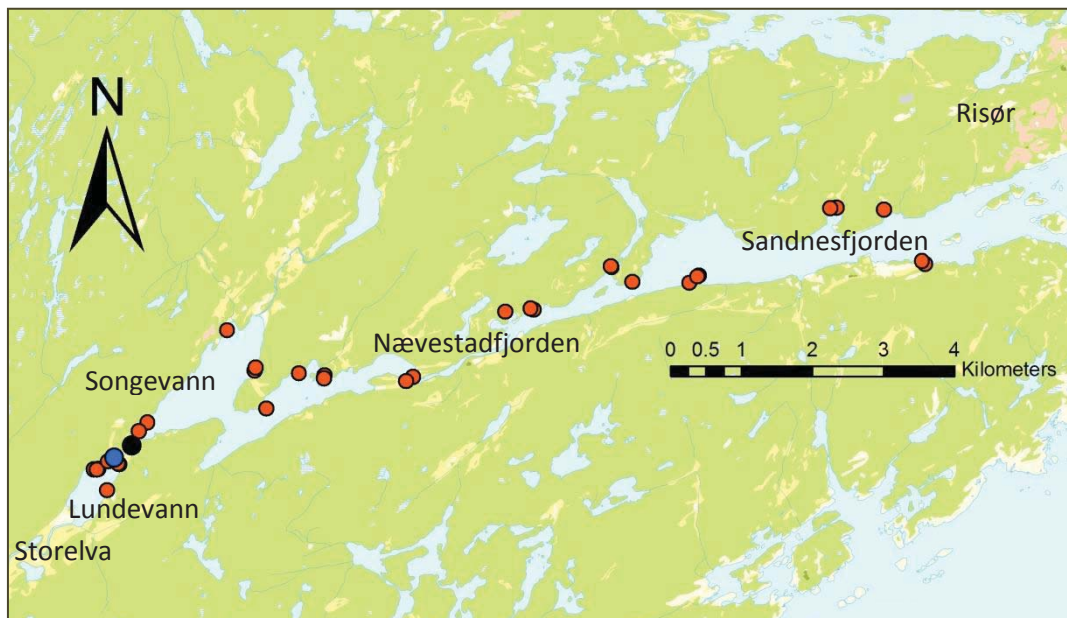


Figure 1: The Storelva river system: Lundevann, Songevann, Nævestadfjorden and Sandnesfjorden. The coloured makings shows trapping methods. Black: rotary screw trap in Strømmen, blue: trap net, red: gill nets.
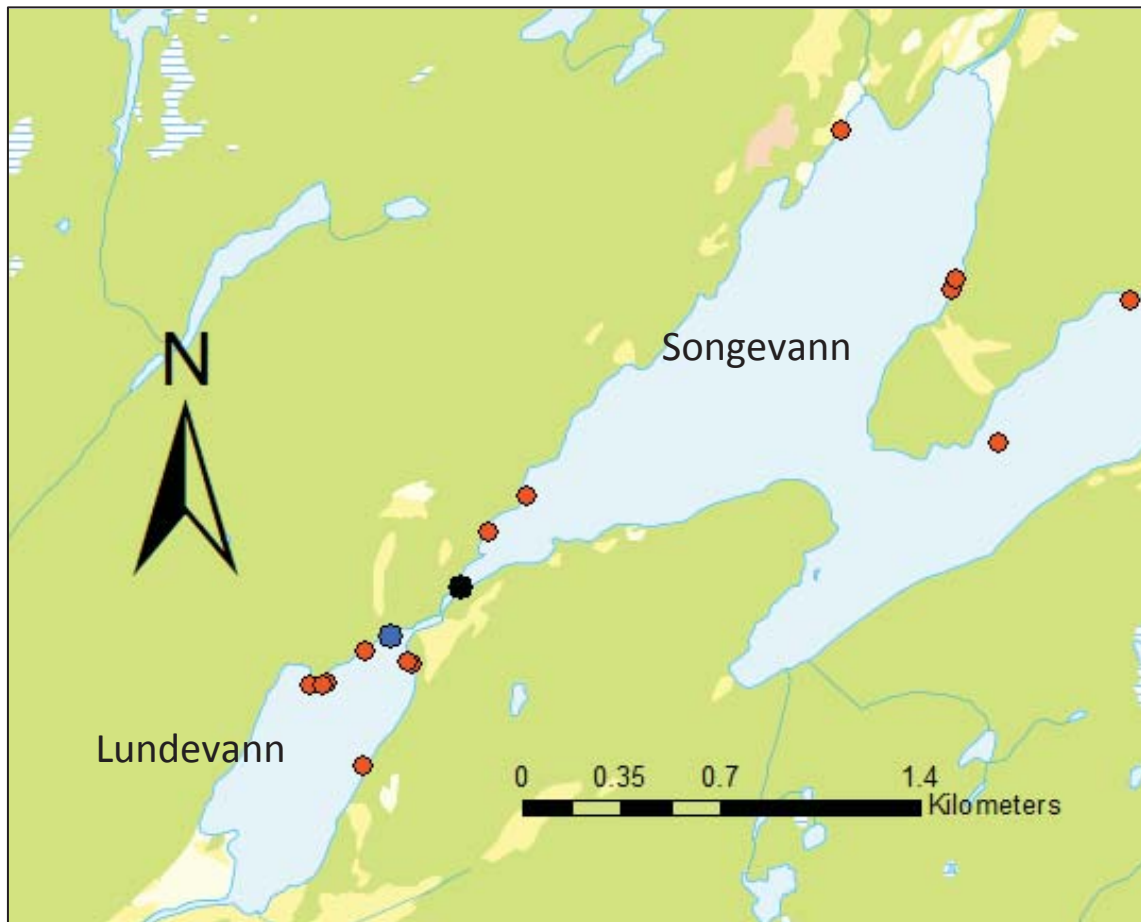
Figure 2: Close up of Lundevann, Songevann and a part of Nævestadfjorden with placement of equipments. Black: rotary screw trap in Strømmen, blue: trap net, red: gill nets.

## 2.2 Capture and tagging

### 2.2.1 Rotary screw trap

A rotary screw trap was placed at the outlet of Strømmen in the middle of the current to catch descending rudd. The trap consists of a wheel that rotates when the water current enters. Fish entering the rotary screw get trapped and forced into the capture chamber. The chamber was checked and emptied twice a day, in the morning and evening until 27th of May, and only in the morning from the 28th of May to the 7th of June 2011. All fish were determined to species and counted. Due to low numbers of captured rudd the first days of the field work, the rudd were kept in a barrel in the water next to the rotary screw awaiting a collective tagging later on. The rotary screw trap was operational from the 26th of April to the 7th of June 2011.

### 2.2.2  Trap net

A trap net was placed in Lake Lundevann at the 6th of May until the 6th of June to catch Rudd. The trap net was placed with the entrance facing towards the exit of the lake (Figure 3). One wing let from one side of the shore toward the other, leaving a passage on the other side of the lake. The trap net was checked and emptied at least once a week. The rudd caught were checked for PIT- tags and tagged fish were released back into the lake. Non-tagged rudd caught were kept in a keep net in the lake for PIT-tagging on the 11th, 16th and 31st of May. The PIT-tagged rudd were released back into Lundevann.



Figure 3: Position of the trap net in Lundevann with entrance facing towards the exit of the lake. The PIT-antenna was placed at the entrance of Strømmen and the rotary screw trap at the exit.

### 2.2.3  Gill net fishing

Gill net fishing was conducted in Lundevann to get information both about rudd that do not leave the lake and migrating individuals. The gill nets used in Lake Lundevann were 25 meters long and 1.5 meter deep. Three different mesh sizes were used: 21.5; 23 and 26 mm, and placed randomly along the littoral zone of Lundevann between 26th and 28th of May. The gill nets were set out 7:30 in the morning and checked at 12:00. If no Rudd were caught the

gill nets were either left alone at the site or moved to another location in the lake and checked every 2 to 3 hours. The rudd caught in Lundevann were kept in a keep net in the lake until PIT- tagging on the 31$^{st}$ of May. After tagging they were released at the same site.

Table 1: Number of rudd caught and PIT-tagged by the different methods.

|  | PIT-tagged | Total |
|---|---|---|
| **Gill net** | 43 | 43 |
| **Trap net** | 77 | 77 |
| **Rotary screw** | 335 | 1352 |

## 2.3 The samples

A total of 1352 rudd were caught from the 26$^{th}$ of April to the 7$^{th}$ of June 2011 in the rotary screw trap. 455 rudd above 115 mm (total length) were pit-tagged. 335 of these were caught in the rotary screw in Strømmen and 77 in the trap net in Lundevann. The catches in the rotary screw trap had the widest length-distribution of rudd whereas the catches in gillnets and trap net the length of the rudd were distributed around 200 mm (Figure 4).
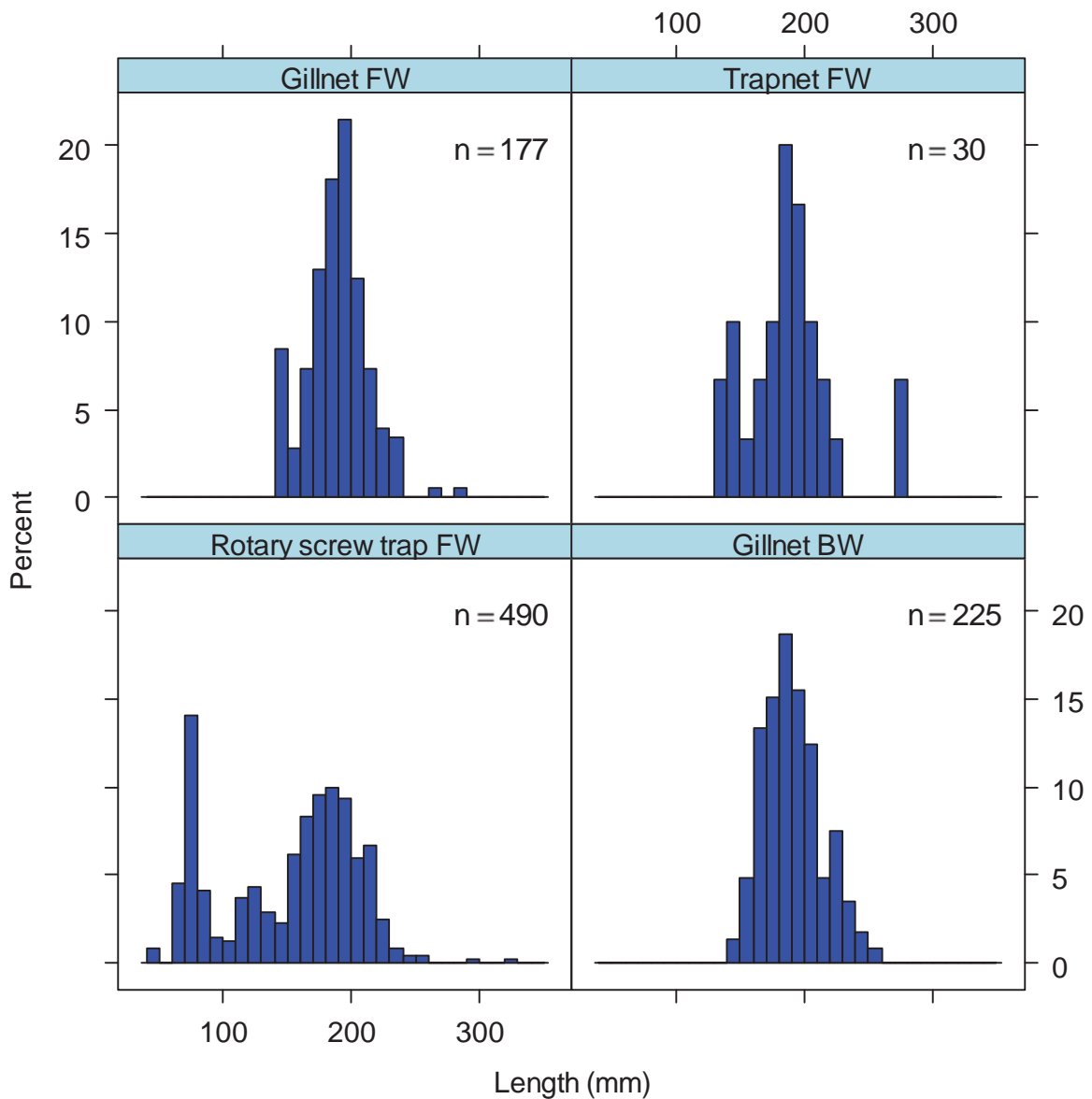
Figure 4: Distribution and percentage of the sizes of rudd caught with gill net, trap net and rotary screw trap in freshwater (fw) and gill net in brackish water (bw).

## 2.4 PIT antenna and PIT-tags

A PIT antenna was mounted at the entrance of Strømmen, from shore to shore, on the 26th of April. The PIT antenna consists of two antenna loops with one part along the riverbed and one along the water surface. One antenna (A2) was placed about 2.5 meters upstream from the other (A1) and the lengths were 8.3 meters and 8.0 meters. By looking at the time difference a PIT-tag was registered between the two antennas this set-up enabled

determination of swimming direction.

The PIT-registration system consisted of commercially available Radio-frequency identification (RFID) produced by Texas Instruments (TIRIS S-2000) connected to a control unit (TIRIS RI-CTL_MB2A). Mounted in a loop, the antennas produces a low frequent (134. 2 kHz) electromagnetic field that activates the PIT-tags and enables them to transfer data to the two antenna readers. The antenna readers and a data logger were kept in a box at the shore protected from the weather. The readers are connected to two tuning boxes (TIRIS RI-RFM-008) that is connected to the two antennas. The system was powered by a 110 Ah 12 V battery.

The PIT-tags contains a unique number and help us indentify each tagged fish. The pit- marks were 23.1 mm long, 3.9 mm in diameter and weighed 0.6 g (Texas Instruments, TIRIS).



Figure 5:  Insertion of a PIT-tag into the body cavity of a fish. Photo: Bernhard Nerland.


## 2.5  PIT- tagging

PIT- tagging of rudd was done at the 11th, 12th and 16th of May, and 1st of June at Strømmen, and at the 11th, 16th and 31st of May at Lake Lundevann. Before PIT- marking the Rudd was anesthetized with Benzokaine (100 mg/ ml). 5 ml of Benzokaine was dissolved in 10 litres of water from the river. About five rudd were kept in the tank to be anesthetized at a time. The

rudd was considered anesthetized when their swimming movements ceased and they sank belly-up to the bottom of the tank. After removal of a few scales the PIT- tags were surgically inserted into the body cavity by making a small incision in the abdominal area behind the pelvic fins (Figure 5). The incision marks were 5-6 mm in length and left to heal without any stitching. After the PIT- tagging the rudd were moved to a tank holding river water, and left until recovering consciousness and swimming activity. The recovery water was changed regularly to prevent oxygen depletion. The rudd was then released back into the water. Individuals caught in Lundevann were released into Lundevann, and individuals caught in the rotary screw were released in the middle section of Strømmen. All PIT-tagged Rudd were weighted and length measured (total length), and scale samples were taken.

## 2.6  Recaptures

In order to monitor fjord movements and habitat use, three periods of gill-net fishing were done in the summer; at the 7th of July, 18th and 19th of August, 27th of September and 13th of October. The sites were in Lundevann, Songevann, Nævestadfjorden and Sandnesfjorden. The gill nets used had mesh sizes of 21.5; 23 and 26 mm. The number of nets at each site and placing at the sites changed between the periods. In Sandnesfjorden the same gill nets sites were used each period, but not all of the sites were used every period. The gill nets were placed along the littoral zone close to the vegetated area, or near the shore when there was no vegetation. All gill nets were set in the evening and left until the morning. The numbers of Rudd caught at each site were counted, and a total of 30 individuals from each location taken scale sample of, weighted and length measured. Blood samples were taken from 3-4 individuals from each site, from fish alive with little or no damage from the gill nets.

## 2.7  Scale samples

The scale samples (Figure 6) were used for age determination and back-calculation of length using a microfilm machine. The lengths were back-calculated according to the equation $L_i = (R_i/R_c) \times L_c$, were $L_i$ = total length of the fish at age i, $L_c$ = total length of the fish at capture, $R_i$ = radius of the scale at age i, and $R_c$ = radius of the scale at capture. The 2011 growth rate

was calculated by the equation (ln($R_c$) – ln(Rmax))/ growth period, were Rmax is the radius of the scale to the outermost annular mark, and growth period is number of days from the growth season started to the day it was captured. The start of the growth season was set to be the 15th of May. I also estimated annual age-specific back-calculated growth rates for each individual. For age1 growth rates I assumed size at initial feeding (i.e., when the yolk is resorbed) to be 6 mm (Wolnicki et al. 2009).
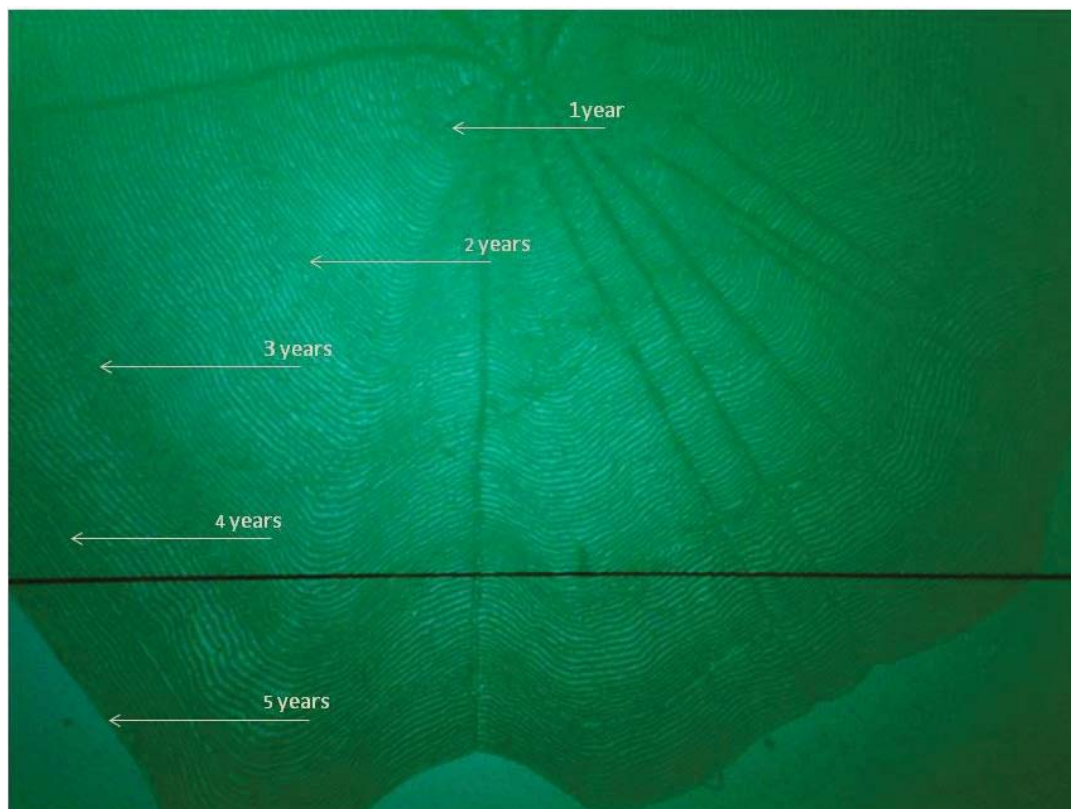


Figure 6: Scale of a 5-year old rudd caught in May 2011 showing the winter-zones.

## 2.8 Quantitative analyses

### 2.8.1 Statistics

All statistics (apart from mark-recapture analyses) was undertaken using R version 2.15.2 (R Development Core Team 2010).

Differences in age distribution between the two migration groups were explored using $\chi^2$-test.

In order to analyse factors affecting individual back-calculated growth rates (e.g., age, habitat, temperature, salinity a s o), I used generalized linear models (GLM). This applied to both 2011 growth rates as well as pre-2011 growth rate analyses. The most supported model was selected using Akaike's Information Criterion (AIC), which is a metric that quantify the balance between model bias and model precision (Burnham & Anderson 1998).

In order to explore differences in individual growth trajectories between the two migration groups von Bertalanffy growth functions were fitted the back-calculated growth data. The von Bertalanffy growth function predicts length at age ($L_t$) and contains three parameters: $L_\infty$ = the asymptotic length; $K$ = the growth coefficient; and $t0$ = the theoretical time at size = 0. I fitted models that included separate parameter values for the two migration groups as well as models with similar parameter values. The most supported model structure was selected using AIC and between model ANOVAs. The full model looked like this:

$$L_t = L_\infty[group]\left(1 - e^{-K[group](t-t_0[group])}\right)$$

The model was fitted the data using the nls, nlstools and FSA packages in R.

Whenever I compared the two migration groups and heterogeneous variance existed between them (e.g., 2011 growth rate), Welsh ANOVA was undertaken using the oneway.test procedure in R (Sokal & Rohlf 1995).

All statistical models were validated and explored for deviations from model assumptions (residual homogeneity) using residual plots and qq-plot tools.

### 2.8.2 Capture-Mark-Recapture analyses

The mark-recapture data was analyzed using the software MARK version 6.1 (White & Burnham 1999). The data was discretized into 12 sampling occasions, corresponding to monthly periods over which survival and dispersal probabilities could be estimated. A multi-strata approach was used, where individual capture histories comprised of a 12-digit array of either "0", "1" or "2" depending on whether the individual was encountered during a sampling occasion or not ("0" if not) – and if encountered, in what habitat the encounter took place ("1"=freshwater, "2" = brackish water). A capture history like

"100220000000"would mean that the individual was captured and tagged in freshwater at first occasion, not recaptured during the second and third occasion, but recaptured in brackish water at fourth and fifth occasions. After that, the individual was never encountered, which normally would be interpreted as the individual being dead after occasion 5.

The parameterization of multi-state mark-recapture models is visualized in a fate diagram in Figure 7. From the fate diagram, we can follow individuals tagged at occasion **k** that are captured (and tagged and released) in freshwater. In the diagram, we follow the Markovian steps describing survival and dispersal process involved over two capture occasions. Following the conditional Arnason-Schwarz parameterization (Arnason 1973), $s_k^1$ is the survival probability over the **k** to the **k+1** period for individuals that stayed in freshwater at occasion **k**, $\psi_k^{12}$ is the probability of dispersing from freshwater to brackish water during the **k** to **k+1** period ($\psi_k^{11}$ is the probability of staying), and $p_k^1$ is the probability of being captured in freshwater at occasion **k**. Capture histories for some example fates (corresponding to fates on the same line in figure) are provided in curly brackets to the right; 0, not caught; 1 caught in freshwater; 2 caught in brackish water; -1 caught in freshwater, and died during capture process (i.e., right censored). In Figure 8, there is a full overview of the parameters for my study system, apart from the $\psi$-parameter for which just a couple of examples are provided to ease readability.

Parameters were fitted using the maximum log likelihood method. All parameters can in theory be estimated as being constant over all occasions/periods, or to be time dependent. In addition, and more ecological relevant, the parameters can be estimated as functions of covariates of interest. These covariates can both be occasion-specific (e.g., temperature and salinity), and individual-specific (e.g., size).
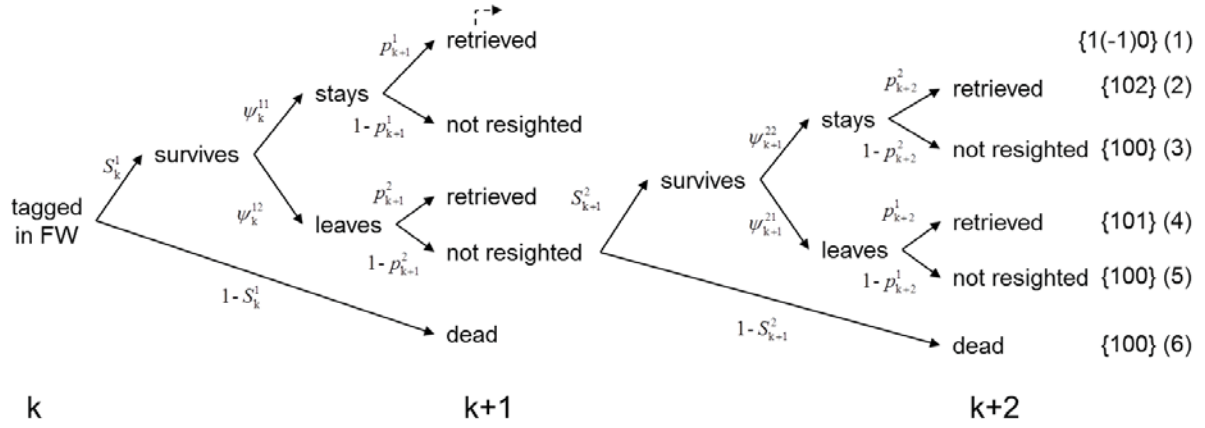
Figure 7: Fate diagram with corresponding Conditional Arnason-Schwarz (CAS) parameterization for a three-occasion study system (see text for a detailed description).
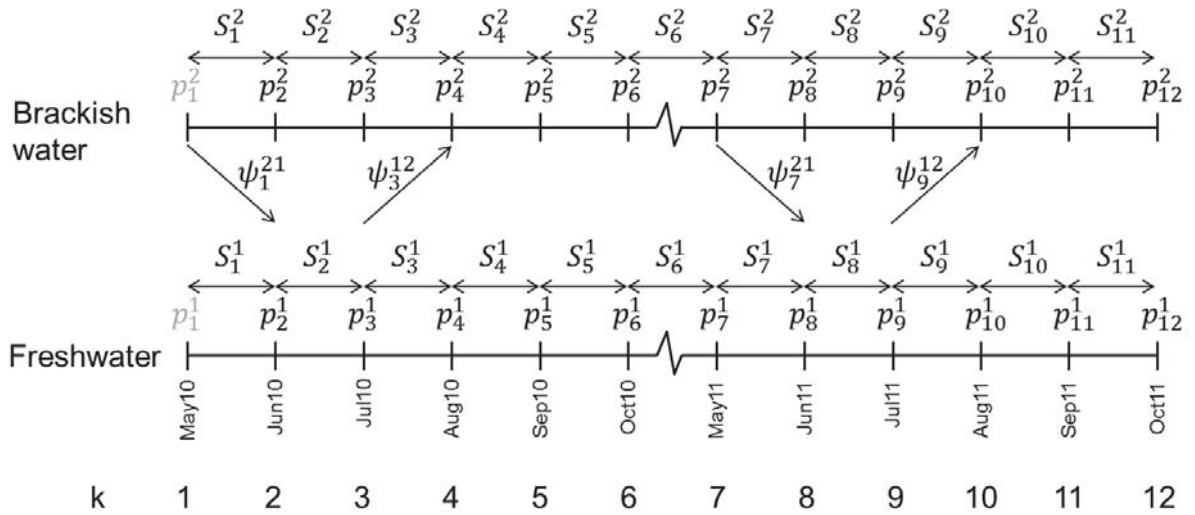


Figure 8: Overview of the CAS parameters fitted for this study system. k = occasion number; $S_k^h$ represents survival over the $k$ to $k+1$ period in habitat $h$ (1 or 2, where 1= freshwater and 2 = brackish water); $p_k^h$ represents (re)capture probability at occasion $k$ in habitat $h$ (p1 are indicated in grey as these are not estimable); $\psi_k^{h1h2}$ represents the dispersal probability from habitat h1 to h2 over the $k$ to $k+1$ period.

### 2.8.3 Life-table simulations

In order to estimate fitness for the different behaviour options (migrate vs not migrate), I undertook life-table simulations (e.g.,(Caswell 2001)). This was done by simulating population size development over a 100-year period for three migration strategies populations under influence of climate. The three strategies were: 1) freshwater residents, 2) not-returning brackish-water migrants and 3) returning brackish-water migrants. The difference between group 2 and 3 is that group 2 individuals never return to freshwater (apart from when spawning) after having migrated to brackish water whereas group 3 individuals do. The three groups can be viewed as three different genotypes and by comparing the estimated mean fitness of the three I can infer which one(s) of them will increase in frequency in the Lundevann-Sandnesfjorden system sensu Stearns(1992). Changes in the age structure and population size was modelled from $N_{t+1}=K(E,t)N_t$ or rather:

$$
\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_{a_{max}} \end{bmatrix}_{t+1} =
\begin{bmatrix}
f_1(E_t)m_1 & f_2(E_t)m_2 & \cdots & \cdots & f_{a_{max}}(E_t)m_{a_{max}} \\
s_1(E_t) & 0 & \cdots & \cdots & 0 \\
0 & s_2(E_t) & \cdots & \cdots & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots \\
0 & 0 & 0 \ \ s_{a_{max}-1}(E_t) & 0
\end{bmatrix}
\begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ \vdots \\ N_{a_{max}} \end{bmatrix}_t \quad \text{(Eq 1)}
$$

where $N_t$ is the abundance of rudd across all age classes $a=1,…, a_{max}$ at year $t$. Census time is chosen so that reproduction occurs at the beginning of each annual season. $f_a$ is the fecundity at age $a$ (i.e., the number of offspring produced per individual of age a during a year). The fecundity was estimated from: Fecundity = $562.37e^{(0.1301*Length)}$ (Tarkan 2006); $m_a$ is the age-specific probability for spawning (0 for a<3, 0.5 for a=3 and 1 for a>3); $s_a$ is the survival probability of individuals from age $a$ to age $a + 1$, and $a_{max}$ is the maximum age considered in the model (set to 9 in this study). The vital rates $f_a$ and $s_a$ differ from year to year depending on the age-specific individual growth rate $g_{a,t}$ and direct effects of the environment $E$ and vary with time. Accordingly, $K(E,t)$, the Leslie projection matrix, is a function of $E$ – and thus vary with time. At each time step, a random climate was drawn from a set of observed conditions during the 2002–2012 period. A salinity regime was estimated from the drawn discharge regime using a generalized additive model (GAM) that was previously fitted to 2002-2012 data (Solberg 2012). For each time step, the survival of individuals in age class $a_{max}$ was set to 0, whereas individuals at all other ages spawn if

mature and experience natural mortality (i.e., harvest is considered negligible) as defined below. From the annual projection matrices (Figure 9), I extracted the population's long term rate of increase, λ, from the dominant eigenvector of the matrix (Caswell 2001). The geometric mean values from the 100-year time series were compared among the three migration-behaviour "genotypes" to evaluate which one(s) would increase in frequency in a population comprised of all three of them sensu Stearns (1992).
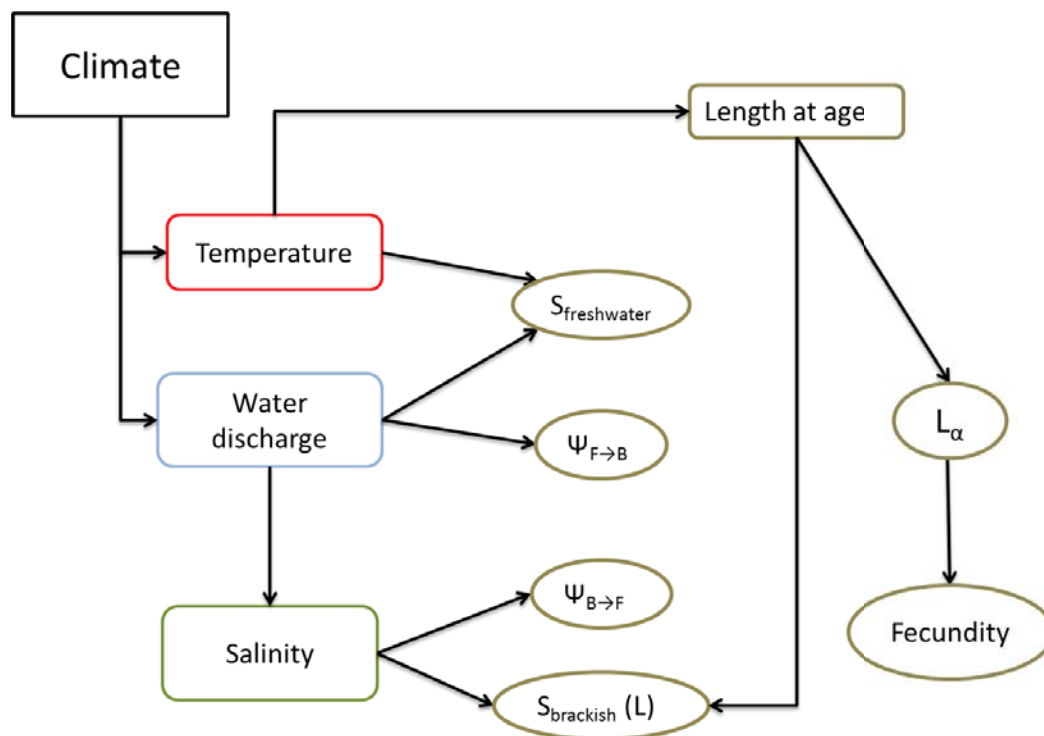


Figure 9: Flow diagram showing the climate forcing of vital rates included in the projection matrix used to model population trajectories.
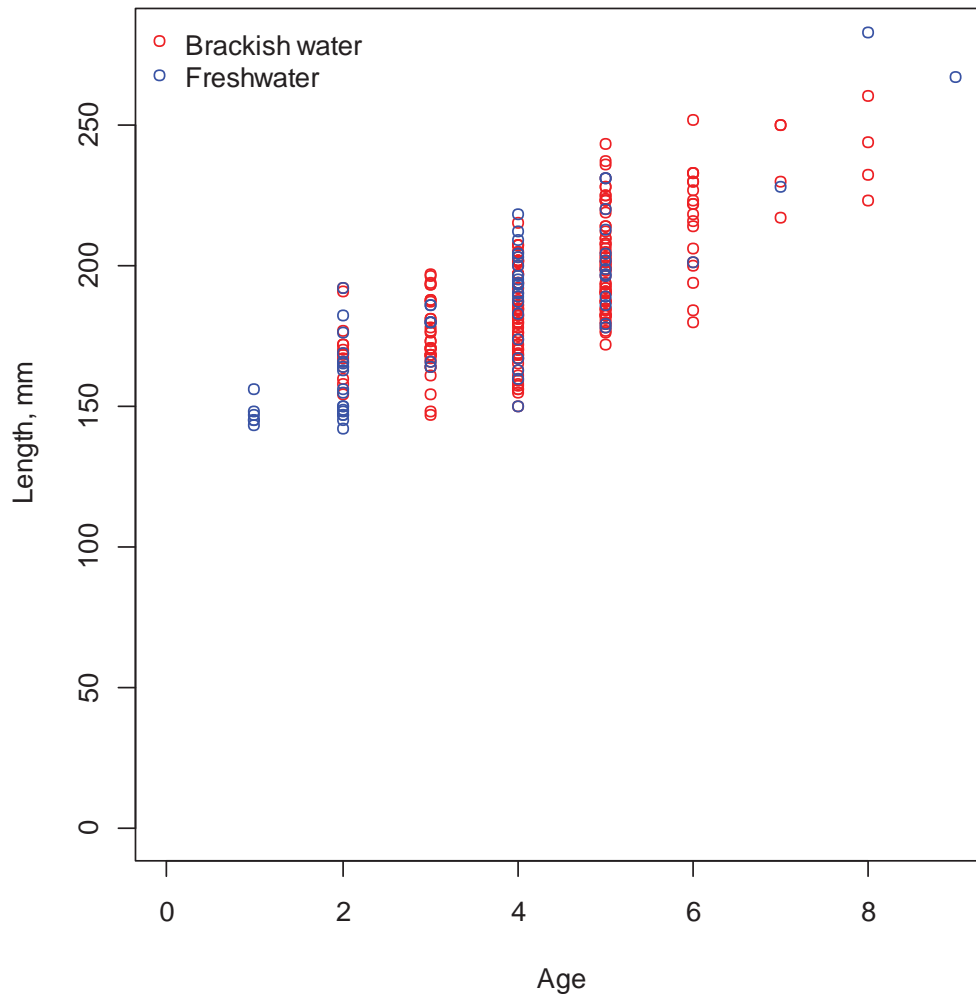
# 3 Results

## 3.1 Age distribution

There were significantly different age distributions between rudd caught in brackish water compared to those caught in freshwater ($\chi^2$= 48.09, df = 8, p<0.0001). The same result was also found between the two groups for tagged individuals ($\chi^2$= 14.3915, df = 5, p = 0.0133). The main difference of age distribution is that freshwater individuals are younger than brackish individuals (Table 2).

Table 2: The age distribution of rudd caught in 2011 separated into habitat and capture method.

| Data source | Habitat | Age | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| Captured individuals | | | | | | | | | | |
| Gill net | Brackish | | 14 | 32 | 82 | 66 | 19 | 4 | 4 | |
| Gill net | Freshwater | 6 | 18 | 7 | 22 | 13 | 1 | 1 | 1 | 1 |
| Tagged individuals | | | | | | | | | | |
| Screw trap | Brackish | | 15 | 4 | 11 | 6 | 2 | | | |
| Trap net/gill net | Freshwater | | 1 | 2 | 13 | 5 | 4 | 2 | | |

## 3.2 Growth

There were no obvious growth differences between the two habitat groups in the empirical growth data (Figure 10).



Figure 10: Length-at-age plot for rudd caught in gillnet in the Lundevann-Sandnesfjorden system during July-October 2011. The youngest individuals were all caught beyond mid August.

The overall back-calculated lengths for rudd in 2011 showed large variation within the different ages (Figure A 2). The overall back-calculated length at first winter shows that there was a general trend that younger age groups at capture were larger early in life than older age groups (Figure A 3).

The back-calculated length for the different age groups showed that the freshwater rudd grows better at all ages except at age one where the brackish water rudd grows slightly better. The within-age size variation seems larger in freshwater individuals for the 1-4 age groups (Figure 11).
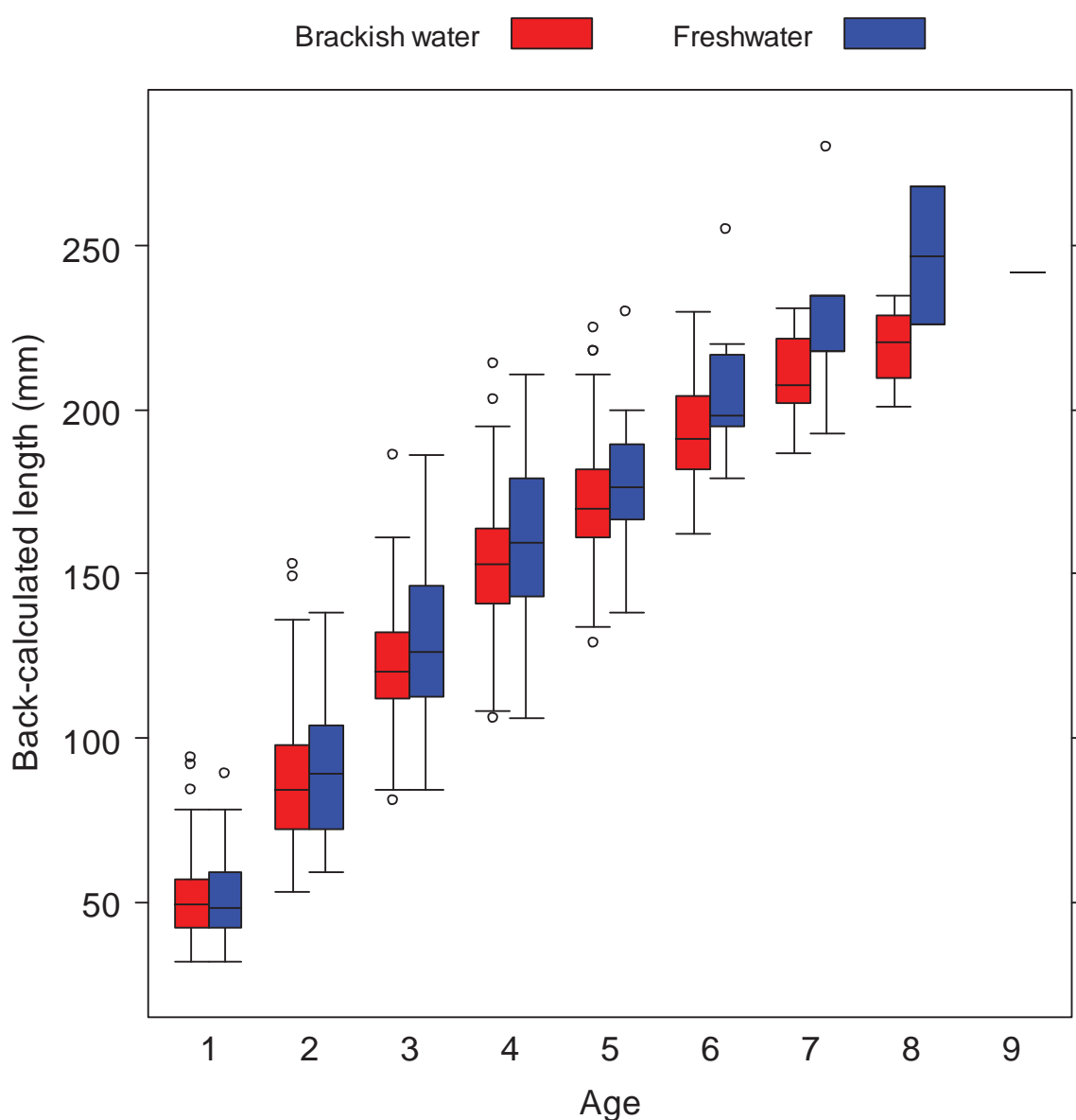


Figure 11: Box plot of back-calculated length for the different age groups in the two habitat types.

When fitting von Bertalanffy growth functions to the back-calculated size data the most supported model (based on AIC) included different parameter values for Linf, but similar values for the K and t0 parameters for the two habitat groups (Table 3, Figure 12). This selected model had significantly better fit to the data than a model with same parameter values for both habitat groups ($F_{1,1439} = 19.926$, p<0.0001), and did not explain significantly less of the back-calculated size variation than a model where the two habitat groups had different parameter values for all three parameters ($F_{2,1438} = 0.838$, p=0.433). The most supported model predicts that freshwater-residing individuals grow better than brackish-water individuals for ages beyond 4 years (Figure 12, right panel).

Table 3: von Bertalanffy parameter estimates for rudd from Lundevann and Sandnesfjorden back-calculated size-at-age-data. 95% confidence limits (lower (LCL) and upper (UCL)) were derived from parametric boostrapping (1000 iterations). FW = freshwater; BW = brackish water.

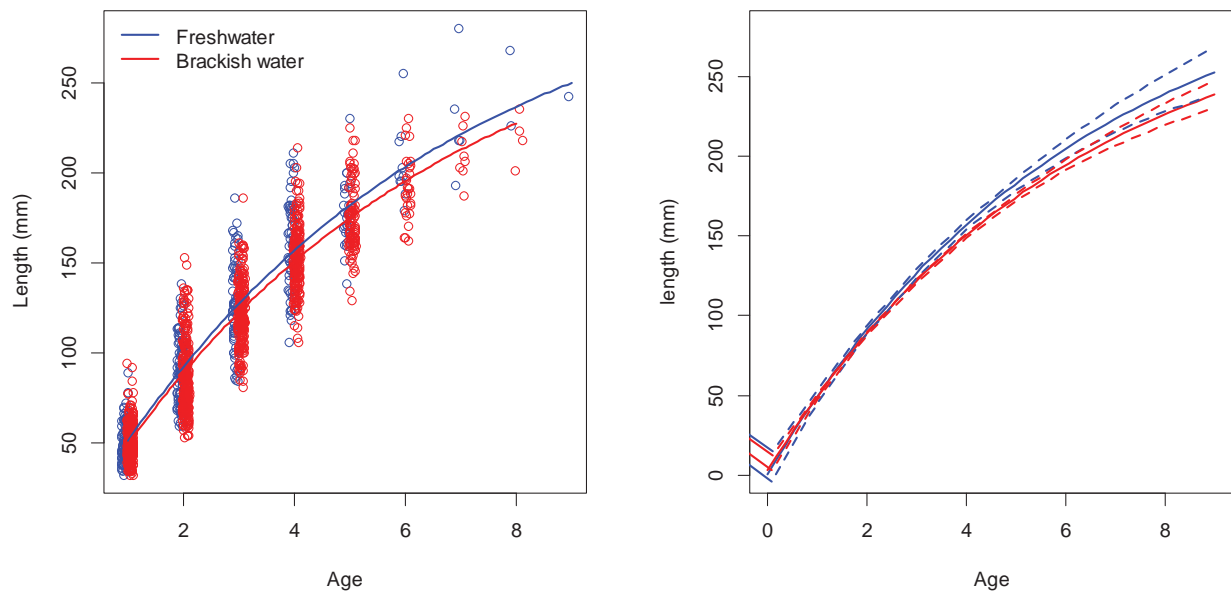| Parameter | Estimate | SE | LCL | UCL |
|---|---|---|---|---|
| Linf[FW] | 323.029 | 15.485 | 292.654 | 353.405 |
| Linf[BW] | 310.379 | 14.907 | 281.138 | 339.621 |
| K | 0.164 | 0.013 | 0.139 | 0.189 |
| t0 | -0.049 | 0.045 | -0.137 | 0.038 |

Figure 12: Left panel: Scatter plot of back-calculated lengths for individuals caught in brackish water and freshwater during 2011 in the Lundevann-Sandnesfjorden system. Lines correspond to fitted von-Bertalanffy growth functions as provided in (Table 3). Right panel: Fitted von-Bertalanffy growth functions with corresponding 95% confidence bounds retrieved from parametric bootstrapping.

The AIC-selected GLM-model fitted to back-calculated growth data showed that individual growth rates were in general higher for freshwater rudd than for brackish water rudd for all ages (Table 4). There was also evidence that water temperature had an additive positive effect on specific growth rate.

Table 4: Parameter estimates and corresponding test statistics for the GLM-model fitted to predict back-calculated specific growth rate as function of growth age, habitat and water temperature. The model explained 95% of the variance (model fit statistics: $F_{10,1432} = 2586$, $p < 0.00001$).

Parameter estimates

| term | Estimate | s.e |
|---|---|---|
| Intercept | 1.542 | 0.160 |
| Habitat[Freshwater] | 0.012 | 0.009 |
| Growth age 2 | -1.263 | 0.011 |
| Growth age 3 | -1.425 | 0.012 |
| Growth age 4 | -1.573 | 0.012 |
| Growth age 5 | -1.657 | 0.016 |
| Growth age 6 | -1.684 | 0.026 |
| Growth age 7 | -1.696 | 0.043 |
| Growth age 8 | -1.729 | 0.062 |
| Growth age 9 | -1.766 | 0.151 |
| Water temperature | 0.018 | 0.011 |

Effect test

| | Df | Deviance | Resid. Df | Resid. Dev | F | P |
|---|---|---|---|---|---|---|
| Habitat | 1 | 0.67 | 1441 | 619.92 | 29.627 | <0.0001 |
| Growth age | 8 | 586.65 | 1433 | 32.59 | 3224.107 | <0.0001 |
| Water temperature | 1 | 0.07 | 1432 | 32.53 | 2.9356 | 0.087 |

The 2011 specific growth rate was significantly higher for rudd in the freshwater habitat than in brackish habitat (Welsh anova: Welsh anova: $F_{1,\,73.09}$=13.089, p=0.0005). The rudd in freshwater also had more variation in the 2011 specific growth- rate.

The back calculations show that the freshwater rudd at a small length has a better growth rate than brackish water rudd. The specific growth rates are however descending for both groups as they get longer. At age three (Table 5, Figure 13) the growth rate for the brackish water rudd is larger than for the freshwater rudd.
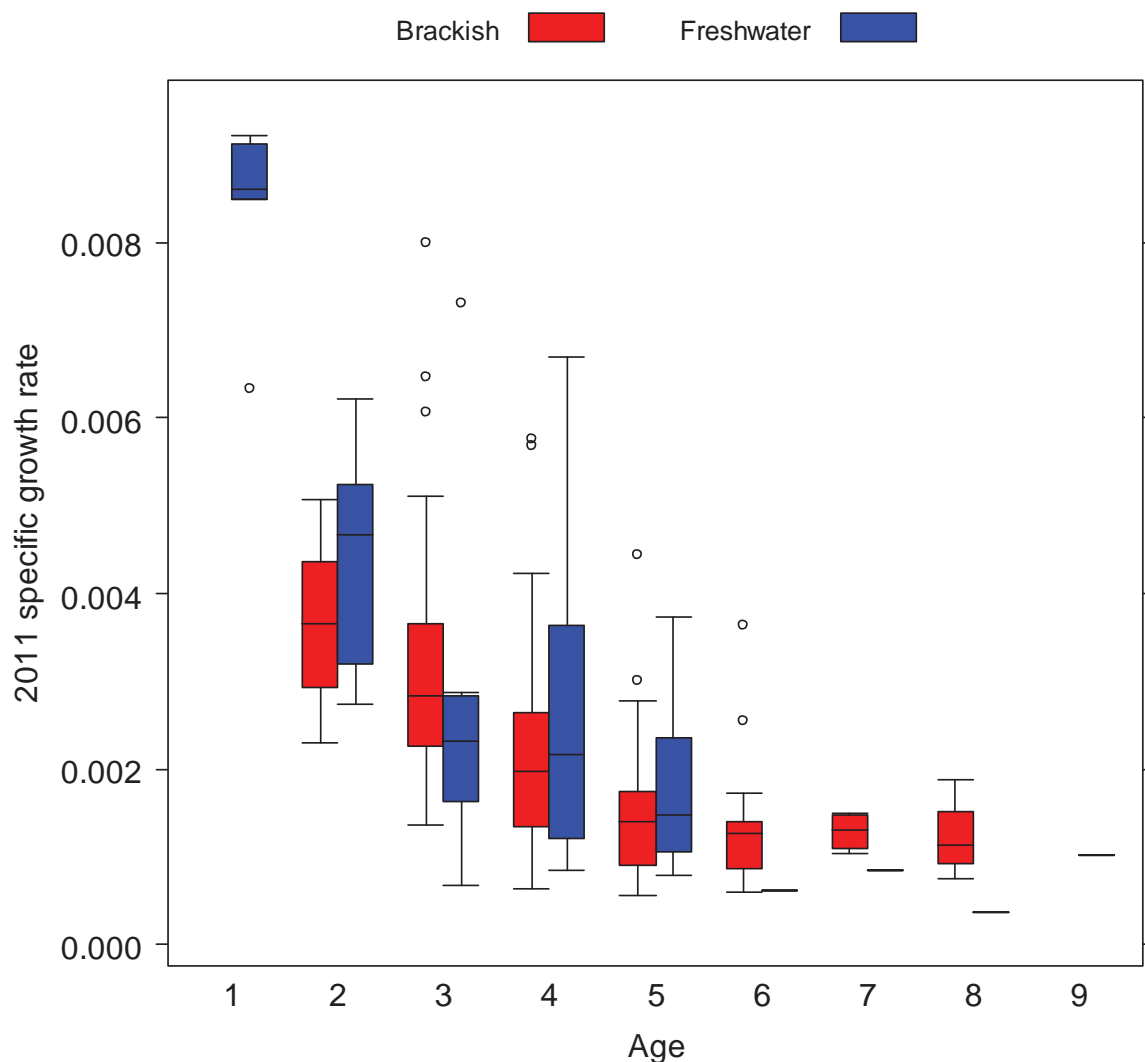


Figure 13: Age-specific box-plots of 2011 specific growth rate for individuals caught in gill net in freshwater and brackish water. The boxes cover 50% of the observations, the solid line inside gives the median while the vertical lines (whiskers) show 90 % of the observations

As for the back-calculated analyses the 2011-growth rate data shows that younger individuals grows better than older ones and that individuals caught in freshwater grows better than brackish water individuals –except for age three individuals (Figure 13). A GLM fitted to explore size effect on 2011 growth rate shows that the length effect differs between habitats (GLM: $p_{habitat*L^2} < 0.0001$, Table 5, Figure 14).

Table 5: Parameter estimates and corresponding test statistics for the GLM-model fitted to predict 2011 specific growth rate as function of habitat and size at capture. The model explained 39% of the variance (model fit statistics: $F_{5,284} = 35.72$, $p < 0.00001$)

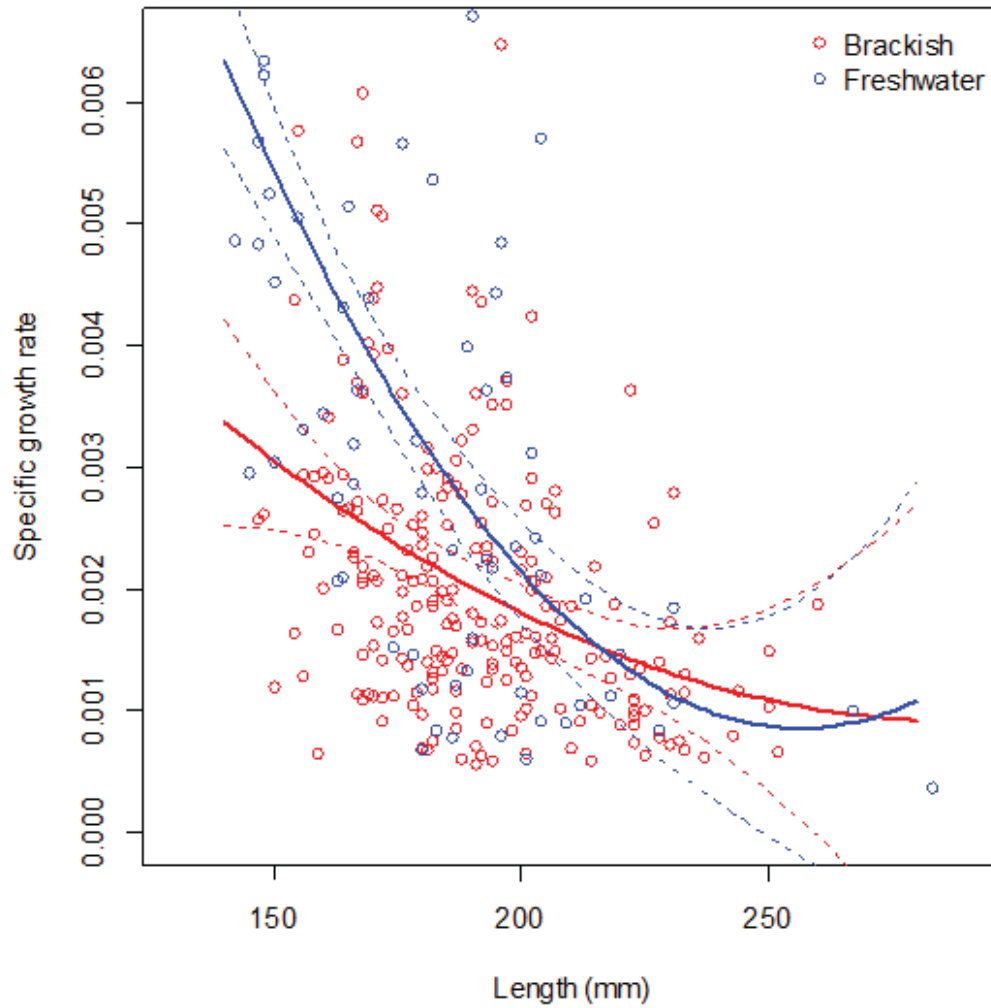| Parameter estimates | | | Effect test | | | | |
|---|---|---|---|---|---|---|---|
| term | coef | s.e. | Effect | df | SS | F | p |
| Intercept | 0.00210 | 0.00009 | Habitat | 1 | 0.00009 | 55.956 | <0.0001 |
| Habitat[FW] | 0.00084 | 0.00019 | $length^2$ | 2 | 0.00017 | 51.111 | <0.0001 |
| length | -0.00843 | 0.00160 | $Habitat*length^2$ | 2 | 0.00003 | 10.216 | <0.0001 |
| $length^2$ | 0.00159 | 0.00200 | | | | | |
| length*Habitat[FW] | -0.01165 | 0.00275 | | | | | |
| $length^2*Habitat[FW]$ | 0.00443 | 0.00266 | | | | | |

Figure 14: The 2011 specific growth rate versus length for rudd caught in freshwater (blue) and brackish water (red). Lines show model predictions for the GLM-model provided in Table 5. The stippled line shows the 95% confidence intervals.

## 3.3 Migration

The registration of rudd in the rotary screw started at the 26th of April. In the beginning the catch of rudd was low but it increased towards the mid of May. The peak of catches was at the 11th of May, with 188 rudd caught. By comparing the rudd captures to the salmon captures it shows that the peak migration of rudd happens later than for salmon and that rudd has two main migration bursts. The catches are also compared to water temperature and water discharge (Figure 15).
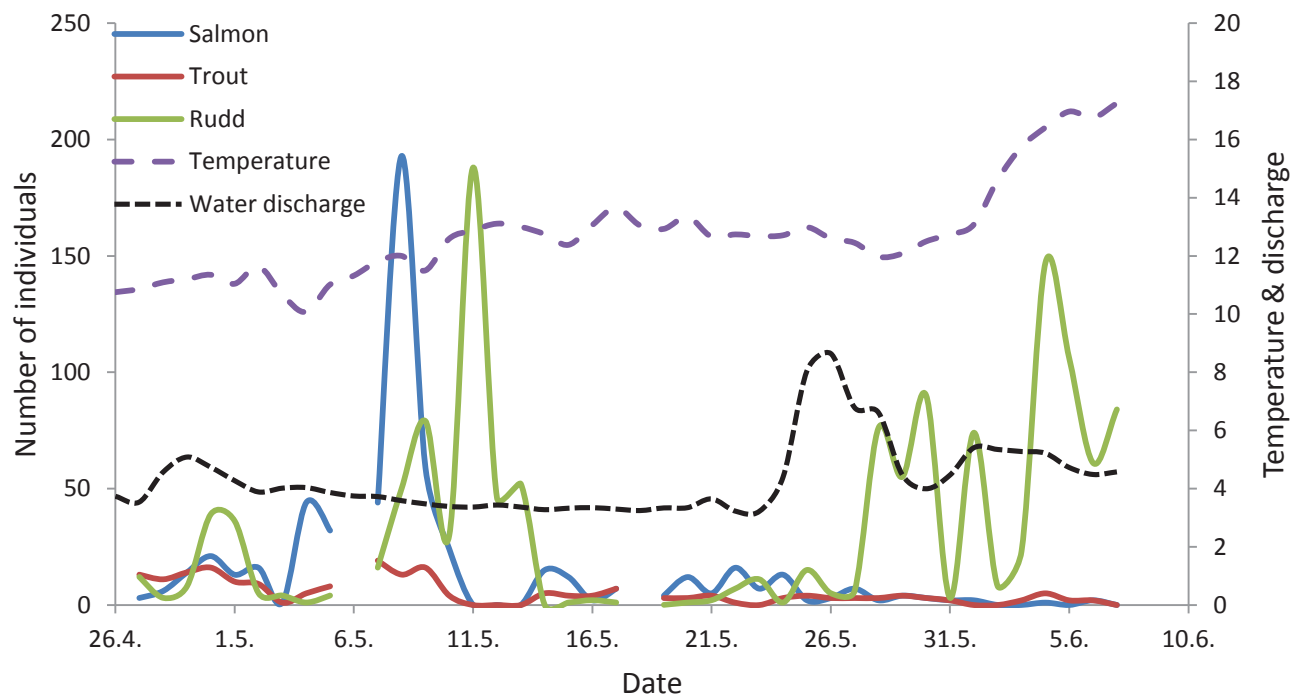
Figure 15: Daily catches of rudd, salmon and trout in the Strømmen rotary screw trap during 2011 descent period compared to water temperature at 1 m in Lundevann and water discharge (m³/sec). Gaps in the species curves are days when the rotary trap was not sampled.

## 3.4 Migration groups

Of the individuals caught in Strømmen the rudd migrating prior to 17th of May and after the 17th of May were assigned the notations "early" and "late" group, respectively. The mean length of rudd in the data was 145.1 mm, the smallest and largest was 46 and 280 mm. The mean lengths of 180 rudd in the early group (127 mm) and 219 in the late group (160 mm) were tested using one-way anova. The results showed a weak difference between the two (Welsh anova: $F_{1,210.9}=3.900$, p=0.0496), where late migrants were the largest on average (Figure 16).
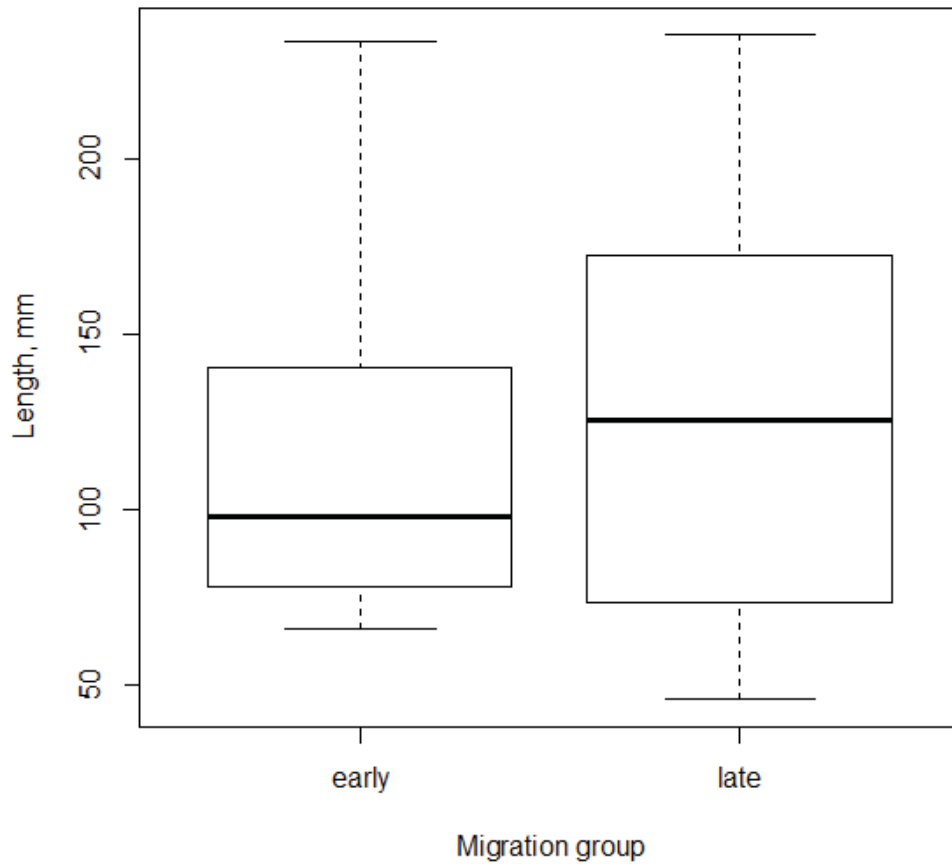
Figure 16: Box plot of length distribution for the two migration groups of rudd. The "early" group was assigned to individuals migrating prior to May 17, "late" for individuals that migrated beyond this date.

## 3.5 Capture-mark-recapture analysis

Three models had a ΔAICc below 2 (Table 6). The difference between these models was the survival structure in freshwater but all the three models included water discharge and water temperature as predictor variables. All three top models had similar p and ψ model structures. There was just slight support (AICc weight = 0.30) for interaction effect between the two predictor variables and even less support for a length effect (AICc weight = 0.17, Table 6).

### 3.5.1 Between-habitat migration

The most supported CAS-model (Table 7) showed that the probability for migrating from brackish water to freshwater was found to be a function of salinity. As the salinity rises the probability of migrating to freshwater increases. At salinity 12.0 the probability is about 0.3 and it increases to 0.9 at salinity 14.5 (Figure 17). The probability for migrating from freshwater to brackish water was a function of water discharge ($m^3$/s), and increased with increasing water discharge (Figure 17).
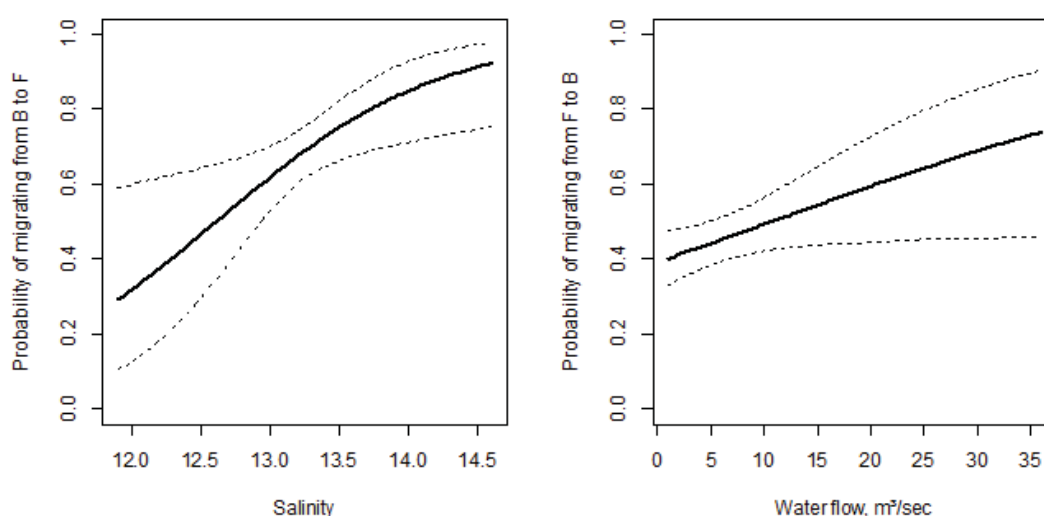


Figure 17: Predicted between-habitat migration probabilities as function of salinity (B→ F) and water discharge (F→ B). Predictions were derived from the most supported CAS-model (Table 7). B = brackish water and F = freshwater.

### 3.5.2 Survival

Survival in brackish water was predicted to be a function of salinity and length. The survival was low for sizes between 10-12 cm and survival decrease with increasing salinities (Table 7, Figure 18).

The survival in freshwater was a function of water discharge ($m^3$/sec) and temperature. The survival decreases quickly with temperatures above 15 °C and survival decrease with increasing discharge (Figure 19). The difference in freshwater survival indicated that survival was affected by water discharge and temperature in an additive fashion where both predictors had a negative effect on survival (Table 7, Figure 19).

Table 6: Model selection parameters for the 10 most supported CAS models fitted rudd CMR-data from Storelva system 2010-2011. AICc is the corrected AIC value, Delta AIC, AICWeights, Num par = number of estimated parameters. S=survival, p=recapture probability, Ψ=migration probability, F=freshwater, B=brackish water, temp=temperature, vf=water discharge.

| Model structure | AICc | Delta AICc | AICc Weights | Model Likelihood | Num. Par | Deviance |
|---|---|---|---|---|---|---|
| S[F(temp+vf),B(salt+length)]; p[F(temp),B(t)]; Ψ[F→B(vf), B→F(sal)] | 2722.394 | 0 | 0.41154 | 1 | 21 | 2679.393 |
| S[F(temp*vf), B(salt+length)]; p[F(temp), B (t)] Ψ[F→B(vf), B→F(sal)] | 2723.039 | 0.6445 | 0.29817 | 0.7245 | 22 | 2677.941 |
| S[F(temp+vf+Length), B(salt+length)]; p [F(temp), B(t)]; Ψ[F→B(vf) Ψ B→F(sal)] | 2724.254 | 1.8595 | 0.16242 | 0.3947 | 22 | 2679.156 |
| S[F(temp*vf+Length),B(salt+length)]; p[F(temp),B(t)]; Ψ[F→B(vf),B→F(sal)] | 2724.732 | 2.3377 | 0.12788 | 0.3107 | 23 | 2677.533 |
| S[F(t), B(salt+length)]; p[F(temp), B(t)]; Ψ[F→B(vf), B→F(sal)] | 2749.958 | 27.5634 | 0 | 0 | 25 | 2698.543 |
| S[F(t), B(salt+length)]; p[F(temp), B(t)]; Ψ [F→ B(temp), B→F(sal)] | 2750.625 | 28.2306 | 0 | 0 | 25 | 2699.21 |
| S[F(temp+vf), B(salt)]; p [F(effort), B(t,t5=0)]; Ψ[F→B(vf), B→F(sal)] | 2759.863 | 37.4684 | 0 | 0 | 20 | 2718.954 |
| S[F(temp*vf), B(salt)]; p [F(effort), B(t,t5=0)]; Ψ [F→B(vf), B→F(sal)] | 2760.292 | 37.8978 | 0 | 0 | 21 | 2717.291 |
| S[F(temp+vf+length), B(salt)]; p [F(effort), B(t,t5=0)]; Ψ[F→B(vf), B→F(sal)] | 2760.919 | 38.5247 | 0 | 0 | 21 | 2717.918 |
| S[F(temp*vf+length),B(salt)]; p [F(effort), B(t,t5=0)]; Ψ [F→B(vf), B→F(sal)] | 2761.811 | 39.4169 | 0 | 0 | 22 | 2716.714 |

p(B(t)) where t=5 was fixed to 0 since there was no sampling in the brackish habitat at this occasion.

Table 7: Logit parameter estimates with corresponding standard error (SE) and 95% confidence limits for the most supported CAS model fitted rudd CMR-data from Storelva system 2010-2011. Abbreviation key is provided in Table 6. t1, t2 etc indicate occasion 1, occasion 2 etc.

| Parameter type | Habitat | Parameter | Est | SE | LCL | UCL |
|---|---|---|---|---|---|---|
| S | F | Intercept | 8.325 | 1.155 | 6.062 | 10.588 |
| S | F | Discharge | -0.127 | 0.015 | -0.157 | -0.098 |
| S | F | Temperature | -0.380 | 0.061 | -0.499 | -0.261 |
| S | B | Intercept | 4.702 | 10.115 | -15.124 | 24.528 |
| S | B | Length | 2.199 | 0.853 | 0.527 | 3.871 |
| S | B | Salinity | 0.005 | 0.704 | -1.375 | 1.385 |
| | | | | | | |
| p | F | Intercept | -2.597 | 0.406 | -3.393 | -1.800 |
| p | F | Temperature | 0.141 | 0.024 | 0.095 | 0.188 |
| p | B | Intercept | -2.004 | 1.137 | -4.233 | 0.225 |
| p | B | t1 | 0.332 | 1.213 | -2.045 | 2.710 |
| p | B | t2 | 0.585 | 1.195 | -1.757 | 2.926 |
| p | B | t3 | 18.608 | NA | NA | NA |
| p | B | t4 | -0.328 | 1.256 | -2.790 | 2.133 |
| p | B | t5 | 0.000 | fixed | | |
| p | B | t6 | 0.276 | 1.318 | -2.308 | 2.860 |
| p | B | t7 | 0.789 | 1.173 | -1.509 | 3.087 |
| p | B | t8 | 2.527 | 1.303 | -0.028 | 5.081 |
| p | B | t9 | 3.325 | 1.374 | 0.631 | 6.019 |
| p | B | t10 | 0.489 | 1.702 | -2.847 | 3.825 |
| | | | | | | |
| Ψ | F→ B | Intercept | -0.341 | 0.257 | -0.845 | 0.162 |
| Ψ | F→ B | Discharge | 0.002 | 0.029 | -0.056 | 0.059 |
| Ψ | B→ F | Intercept | -15.692 | 6.329 | -3.823 | 14.194 |
| Ψ | B→ F | Salinity | 1.245 | 0.480 | -0.900 | 0.402 |
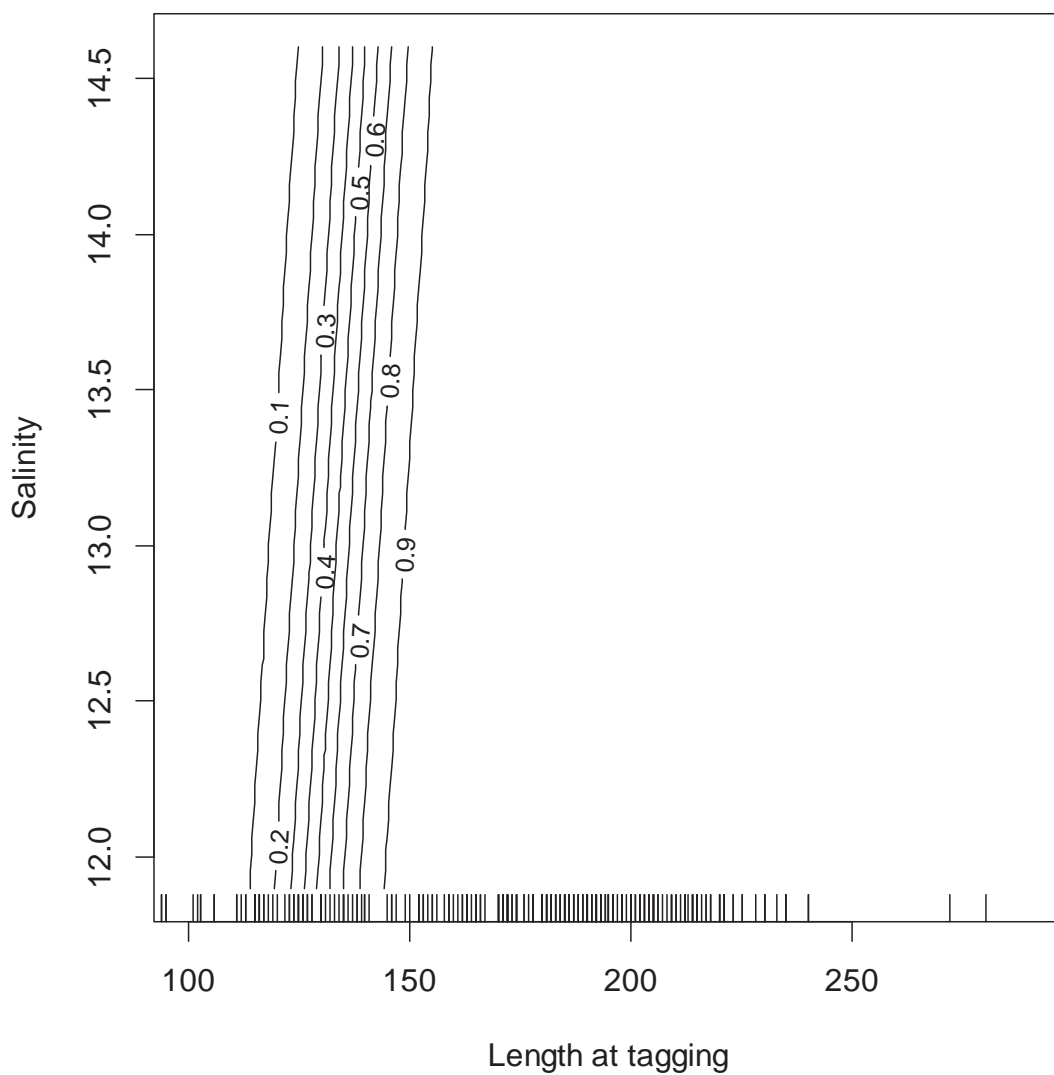
Figure 18: Graph shows the predicted monthly survival probability in brackish water habitat as a function of length and salinity. Predictions were derived from the most supported CAS-model (Table 7). Isoclines represent monthly survival probabilities.
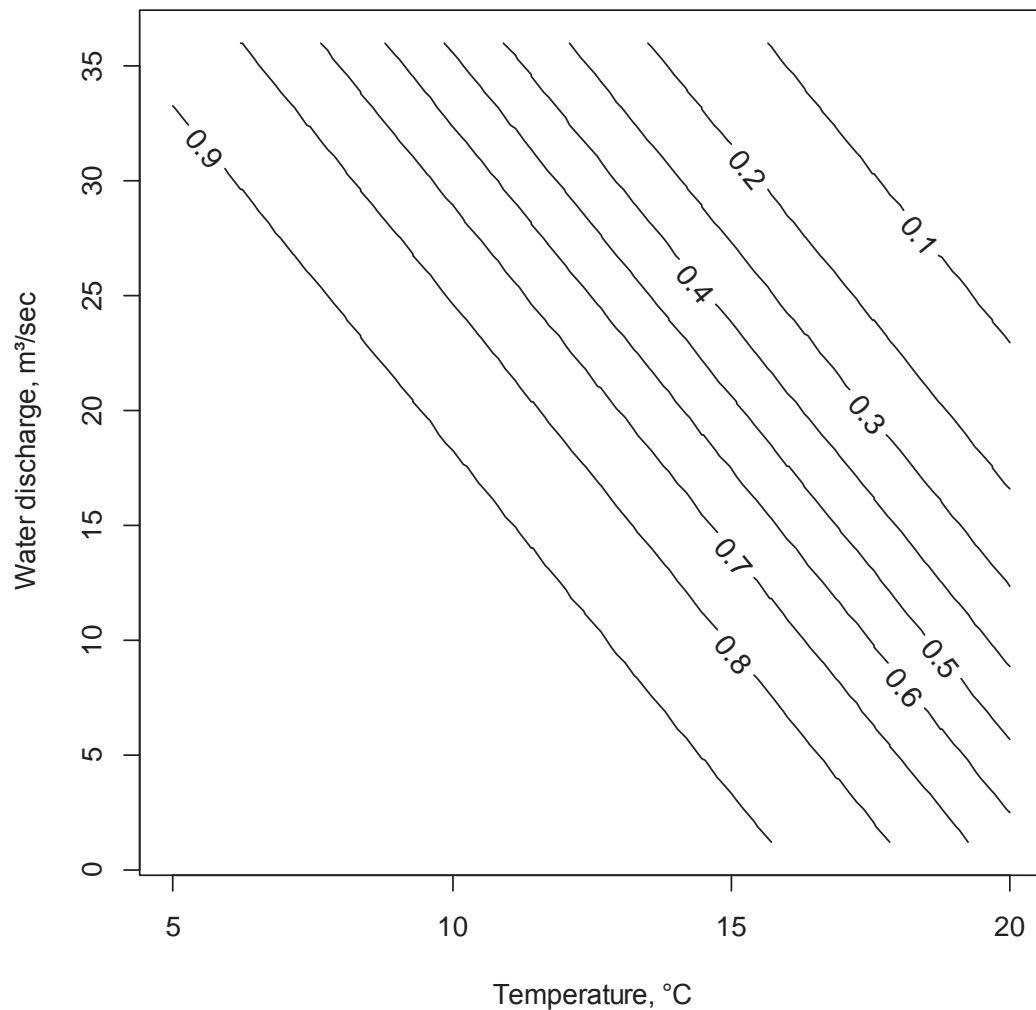
Figure 19: The graph shows predicted monthly survival probability in freshwater habitat as function of water temperature and water discharge in the Lundevann outlet area. Predictions were derived from the most supported CAS-model. Isoclines represent survival probabilities.

### 3.5.3 Recapture probability

Recapture probability in freshwater was positively affected by water temperature (0.141±0.024 (SE), Table 7), whereas the recapture probability in brackish water was time dependent (i.e., I did not succeed in finding evidence for a relevant covariate for this parameter).

## 3.6 Fitness consequences

The life-table simulations revealed that overall fitness was larger in the freshwater-residing group (geometric mean $\lambda$ =1.014 ± 0.071 (SD)) than in both the non-returning brackish-water group (GM $\lambda$ =0.913 ± 0.002, one-way anova: $F_{1,198}$=302.04, p<0.0001) and the returning brackish-water group (GM $\lambda$ =0.967 ± 0.040, one-way anova: $F_{1,198}$=33.14, p<0.0001). Consequently, simulated population trajectories revealed a population decline for both brackish-water strategies, whereas the stationary freshwater population remained fairly stable (Figure 20 and Figure 21). For the non-returning brackish-water strategy, the beyond-age 3 age groups rapidly go extinct and the entire strategy prevails throughout the simulated 100 years by recruitment from maturing 3-year olds only. As a consequence, a generation-time cycle, peaking every three years, arise (Figure 20, lower panel). However, as the population declines throughout the 100-year simulation period, extinction is inevitable.
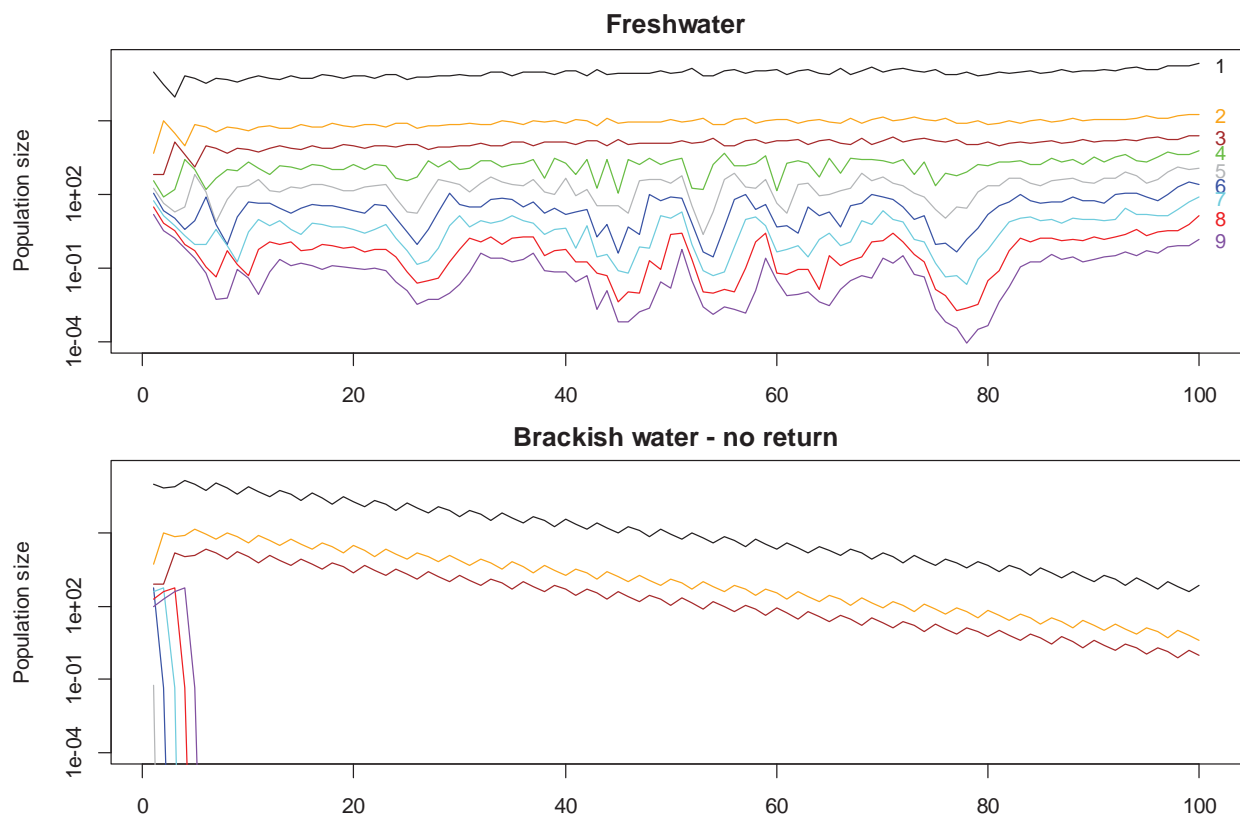


Figure 20: Population-size trajectories as predicted over 100 years (x-axis) using life-table simulations. In this simulation the brackish water strategy did not allow for return-to-freshwater migration (lower panel). Age classes are drawn with unique colours and the respective ages are provided to the right in the top panel. The y-axis is on log scale.
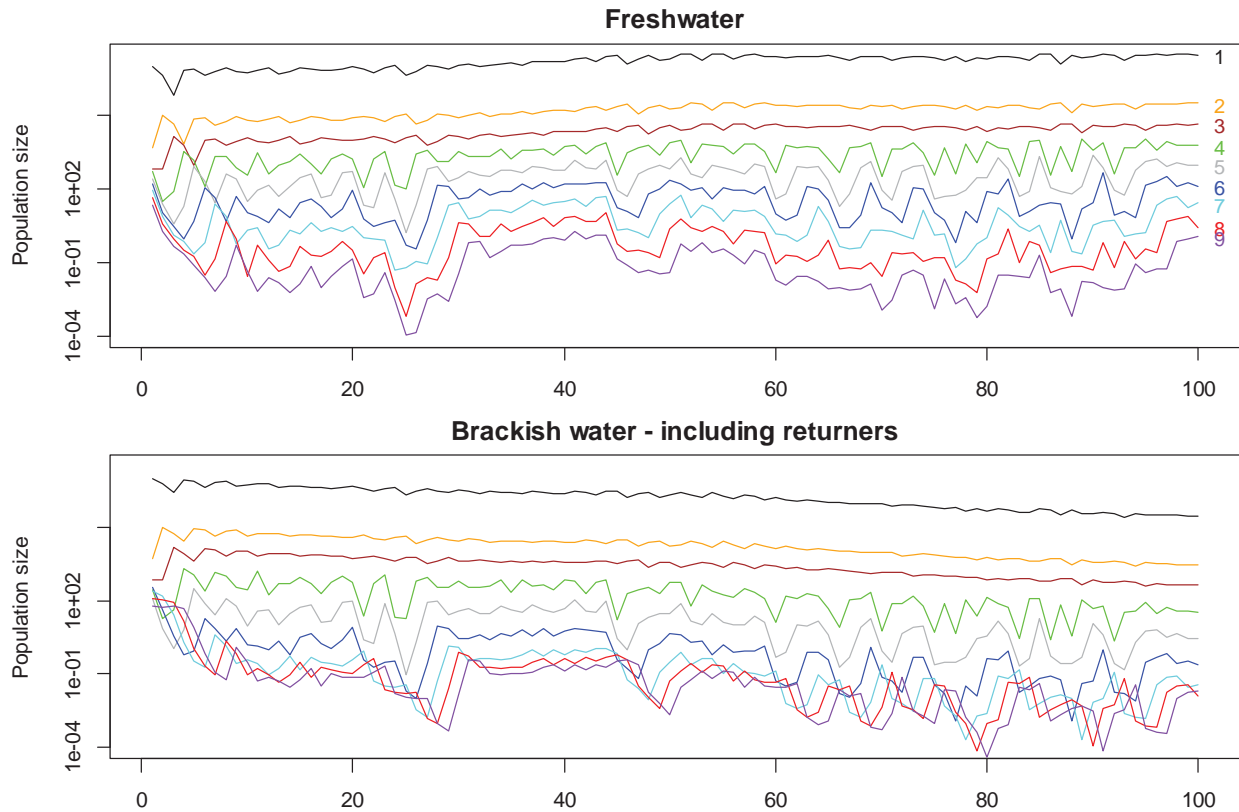
Figure 21: Population-size trajectories as predicted over 100 years (x-axis) using life-table simulations. In this simulation the brackish water strategy allowed for return-to-freshwater migration. Age classes are drawn with unique colours and the respective ages are provided to the right in the top panel. The y-axis is on log scale.

# 4 Discussion

## 4.1 Between-habitat migration

I found no individual-related characteristics that could predict brackish-water migration probability in a robust fashion for the rudd in my study system. Hence, external factors seem to be the key predictors for between-habitat migration. The probability of migrating to brackish water increased with increasing water discharge. Discharge has been shown to be a relevant cue for down-stream migration in other fish systems (Heggenes & Traaen 1988). To my knowledge this has not been shown for other rudd systems before. One should keep in mind that water discharge might be correlated with other environmental variables (e.g., predation risk or food availability) that have an important influence on migration probability.

This potential source of confounding can be resolved by either conducting controlled experiments or via long-term mark-recapture studies.

The rotary screw trap caught rudd of all sizes, but the largest group of rudd (15%) was less than 10 cm in length (Figure 4). Skov et al. (2008) and Borcherding (2002) found that small rudd individuals migrated more than larger ones. Although there was little support for size-specific migration probability in my data (not among the 10 most supported CAS models provided in Table 6) there was indeed a high number of ca. 5 cm rudd in the fish trap. This may indicate that the small ones are more prone to migrate, but may just as well reflect the fact that small individuals are more numerous in the general population. Unfortunately, I do not have representative samples from the total population for individuals smaller than some 15 cm, but from the size distribution in the rotary screw trap the smallest size peak seems to reflect the 1+ age group and as expected this age group should be more numerous than older age groups, as is normal in most fish populations (Wootton 1990). If one has access to the background age distribution one can compare with the migration population size distribution and from that derive if smaller ones has a higher migration probability than larger ones. Mark-recapture can also resolve this issue, but then smaller PIT-tags will need to be used (see under Methodological issues further down). In Skov et al. (2008), the migration coincided with the spawning period of pike and they speculate that migration is triggered by habitat overlap with the predator. Pike spawns in vegetated habitat in spring (Bry 1996). During the migration of salmon smolt through Lundevann rudd is the second most important prey species (Kristensen et al. 2010), suggesting it may be an overall important food resource for pike. There seems to be a lower predation pressure in the brackish water habitat (Kroglund et al. 2010) – and therefore this might be a reason for the observed brackish water migration. Borcherding (2002) suggest that the higher migration rate by small fish (0+) is linked to predation risk by avian predators.

Thus far I have only discussed migration in relation to resource use and anti-predation. An alternative reason for migrating could be related to reproduction (Harden Jones 1968). I am confident that this is not a likely reason for migration of rudd in my study system as the egg salinity tolerance is very low in cyprinid species like the rudd (Jager et al. 1981). Hence, I conclude that migration of rudd in the Lundevann-Sandnesfjorden system is not likely to be motivated by reproduction.

## 4.2  Survival

The survival in brackish water was dependent on salinity and individual length where rudd smaller than c 12cm had very low probability of surviving. The water downstream the rotary screw trap was fluctuating (tidal cycles) and at times hold quite high salinity (Solberg 2012). Despite this many small fish were caught in the rotary screw trap migrating towards the brackish water. Salinity will affect small fish more negatively than larger ones (James et al. 2003), and with the high mortality probability at high salinities one would think that the rudd would move away from that environment when the salinity rises. Since no rudd smaller than 11.5 cm were tagged it is not known if they went back to freshwater habitat in Lundevann, or alternatively, if they stayed in brackish water throughout the winter or died. Hence, the size-dependency on brackish-water survival may be flawed by these circumstances.

In an experimental study by Solberg (2012) with rudd from the same water system she found the mortality was high in salinities between 12-15 ppt and that size had a positive effect on survival at salinity 15. Hence, smaller individuals have lower salinity tolerance than larger individuals. As a consequence, these smaller individuals may display adverse behaviour as the salinity increases and thus make them more susceptible towards predation. In general, small individuals are more at risk than larger individuals in gap-limited predators systems (Nilsson & Brönmark 2000). So, I hypothesize that the combined effect from salinity stress and predation make smaller individuals easy targets for predators (both avian and fish) in the brackish-water habitat.

Survival in freshwater was dependent on water discharge and temperature in an additive fashion. A temperature of 15°C seems to be a threshold where by increasing water discharge will decrease the survival even further. Rudd has a preference for warmer habitats and swimming capacity often increase with temperature (Souchon & Tissot 2012). Large individuals have better swimming capacity (Nunn et al. 2010). Lower survival due to discharge and temperature could be expected for the smallest rudd. Discharge has been reported to decrease survival in fry of trout and salmon (Jensen & Johnsen 1999), but had no significant effect on age 1 or older fish. Compared to my study the discharge was much higher in Jensen & Johnsen (1999) which could be of importance for the result, along with species differences. Rudd lives and spawns in the vegetation close to the shore and might therefore be protected from negative effects of water discharge in Lundevann. Cyprinids are,

however, sensitive to weak water velocities (Mann & Bass 1997). Potential negative effects of discharge might be displacement of egg or juveniles to less fortunate habitats, for example leaving them more exposed to predation or flushing them to brackish water.

It is surprising to find that temperature is negatively correlated with freshwater temperature as rudd is generally considered a warm-water species (Souchon & Tissot 2012). I can think of two reasons for the observed temperature effect: food limitation and predator activity level. Under limited food conditions fish will experience starvation to a larger extent as temperature rises. This phenomena arise as the general metabolism will increase as temperature rises and thus food demand increase (Jobling 1994). I do not have the data required to test for this effect in my study system. The main predator in Lundevann is pike and pike activity level as well as food demands increase with temperature, peaking at 14-20 °C (Armstrong et al. 1992). Due to this thermal-related behaviour, predation risk will increase with temperature and thus may explain why survival in rudd decreases with increasing temperature.


## 4.3 Growth

The specific growth-rate was higher for rudd caught in freshwater than in brackish water which might not be what is expected of fish migrating to brackish water ((Bohlen 1999; Jobling 1995) and references therein). Having been observed in salinities up to 12‰ (e.g. (Solberg 2012; Vetemaa et al. 2006) the rudd might be categorized as a euryhaline species. In Altinok & Grizzle (2001), the euryhaline species had a better growth rate in salinity 3 and 9‰. By comparison, the freshwater stenohaline species had the highest specific growth rate in freshwater, and were negatively affected even at 1‰. However, the two groups compared were different both in phylogeny and tolerance, and also size, age and physical condition. A comparison of two forms of perch *(Perca fluviatilis)* in the Baltic Sea, one resident that spawns in brackish water, and one migratory that spawns in freshwater showed that the juvenile brackish water perch weight decreased with 37% in salinity 7‰ (Tibblin et al. 2012). This study also suggests that the reduced growth is connected to reduced food consumption or/ and reduction in food conversion efficiency.

It is suggested that small fish are more negatively affected by salinity (James et al. 2003). In the study by Tibblin et al. (2012), they suggest that a migratory life strategy can be favoured because it will be beneficial in later life stages as of higher recourse levels in brackish water, even though salinity has a negative effect on juveniles. Results from my study show that freshwater rudd grow better until they reach c 22 cm after which they have approximately similar growth. Hence, there seems not to be any growth benefits from migrating to the brackish-water habitat. These growth-related findings indicate that rudd, at least in the Storelva system, are not well-adapted to the brackish-water habitat, and thus that they migrate into this habitat for other reasons than growth maximization.

## 4.4 Fitness consequences for migration

This study estimated that fitness tended to be lower in migratory individuals compared to freshwater-residing individuals. Because of this, and by assuming there is a genetic component related to the migration behaviour (Liedvogel et al. 2011), the migratory behaviour genotypes seems maladapted and will be selected against, become less frequent in the population and as time goes by eventually go extinct. However, since my study entails two years only, this might be a hasty conclusion. Since the study period just covers two years, this is too short for estimating life-time fitness. As mentioned earlier, the survival estimates may be flawed for smaller individuals as I did not tag the smallest ones and if the smaller ones over-winter in the brackish habitat. Further, the short study period has not opened for fitness estimation under very different environmental conditions (the projection matrix parameters are based on survival and growth responses estimated for just 2010 and 2011 conditions). Finally, there might be benefits not accounted for in relation to migration – like colonizing new areas (e.g., Solberg 2012). One way to overcome these shortcomings in the fitness estimates will be to continue the on-going tagging program to further improve the estimates of the fitness components.

Since migration to brackish water seems to be a common behaviour in my study population I wanted to look deeper into the factors driving this behaviour. Initially, I hypothesized that there should be some growth advantages behind, like in anadromous salmonid systems (Hembre et al. 2001), where the migrants benefits from feeding in a richer habitat and also

with low physiological costs from osmoregulation (Harden Jones 1968). As such, this will be like testing the ideal free distribution hypothesis where fitness is equalised over time over the two habitats (Fretwell & Lucas 1970). However, as seen from the growth rate analyses (Figure 12 and Figure 14) there seem to be no or rather a disadvantage for the rudd that migrate as growth is slower in brackish water. It therefore seems more likely that migration is motivated by density-dependent pushing factors – within Lake Lundevann, rather than pulling factors in the brackish-water habitat. I can think of two such pushing factors: predation from pike and intraspecific competition. The migration of rudd seems to start just after the pike spawning period – a period of high feeding activity and movement in the ripe pike individuals (Kobler et al. 2008). At the same time the water level drops in Lundevann decreasing habitat availability and potentially increasing interspecific competition over resources. As a consequence, the rudd may become squeezed between predators and competitors and start searching for alternative habitats. Unfortunately, I do not hold data on neither pike activity/feeding levels nor rudd densities required to enlighten the role of these potential density-dependent drivers of migration.

## 4.5  Methodological issues

There are two short-comings in this study that both potentially may affect the general conclusions drawn. 1) I have little control on the smaller individuals due to the tag size used were too large to tag individuals smaller than c 11 cm, but also because from the large mesh sizes applied when sampling in the fjord and lake. Finally, the younger individuals that were caught probably comprised a biased sample from the true population – i.e., the fastest growing individuals (see Figure A 3). In the future, Nordic multi-mesh gillnets should be used to secure a more representative sampling regime (Appelberg et al. 1995). Also, by using smaller PIT-tags one can tag individuals that are even smaller than 5 cm. These tags have a smaller probability of getting detected by the PIT-antennas, but the CMR-analysis tools enable modelling this recapture (or detection) heterogeneity (Lebreton et al. 1992).

The second short-coming is related to the short study period (also mentioned elsewhere) that may influence the relevance of the fitness estimates.  Since such a short study period was involved one should be cautious when drawing general inferences from the results as

one might risk that the results attained just are relevant to the study-period conditions. Hence, a continuation of the on-going tagging program (with some sampling improvements) is necessary to resolve these challenges.

## 4.6   Management implications

The most serious management implication relevant to the results of this study is the risk of spreading of rudd to novel watercourses via coastal brackish water. This topic has been extensively studied in a recent MSc-thesis at UMB-INA (Solberg 2012) and I will therefore not go deeper into this other than stating that there is indeed a significant risk of horizontal spreading to neighbouring watercourses to the Storelva-Sandnesfjorden system. Interestingly, if predation risk from the pike in Lundevann is the main driving factor of this migration system, culling of pike in the lake will constitute a relevant measure to lower the rudd spreading risk. Such a pike culling operation will also benefit smolt survival as pike impose up to 50% mortality to the descending salmon smolt in Storelva (Kroglund et al. 2010).

An additional management aspect of this rudd migratory system is whether or not the migratory behaviour is randomly distributed within the Lundevann rudd population or not. My study cannot say whether the migratory individuals constitute a sub-population or not. However, if they do, this will potentially call for a differentiated management strategy, with different measures for the resident and migratory sub-populations. This applies regardless of the management goal – whether it is to protect the rudd population or whether it is to cull it.

## 5   Conclusion

Due to the short study period, I cannot draw general conclusions about the ultimate reason for why rudd performs migrations to brackish-water habitat in the Storelva-Sandnesfjorden system, but my data indicate that predation risk and/or intraspecific competition within Lundevann push the rudd towards the fjord. There is no indication of growth benefits from staying in brackish water, but larger individuals may experience lower predation risk in the

brackish fjord system. The fitness of migrating individuals is lower than for freshwater

residents. Ultimately, migrating genotypes will eventually be extirpated from the population.

# 6 References

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# 7   Appendix

## 7.1   Figures



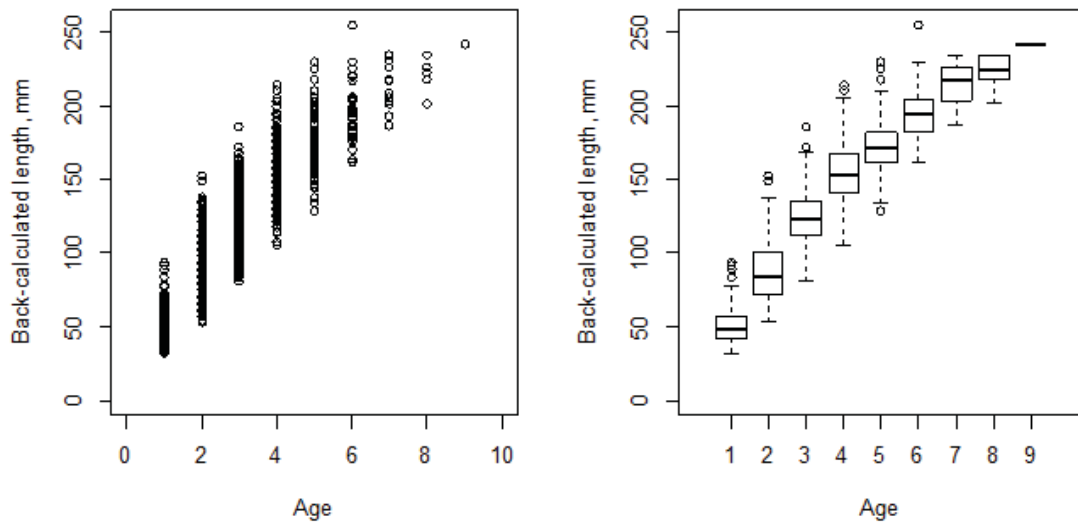Figure A 1: Screen dump of the CAS-input file.



Figure A 2: Back-calculated growth for 2011 rudd. The one on the left shows the back-calculated lengths at the different ages for individuals. On the right the boxes covers 50% of the observations, the solid line inside gives the median while the stippled vertical lines shows 90 % of the observations.
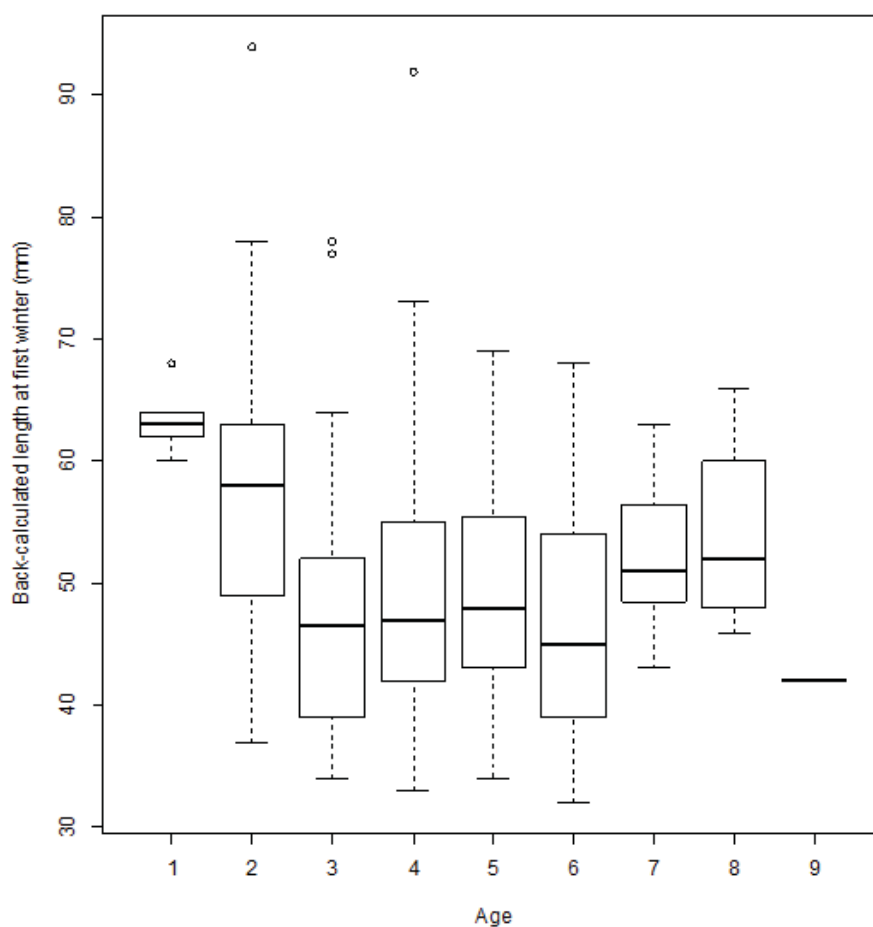
Figure A 3:  Back-calculated length at first winter. The boxes covers 50% of the observations, the solid line inside gives the median while the stippled vertical lines shows 90 % of the observations.

## 7.2   Tables

Table A 1. . Environmental variable values used in the life-table simulations. Temperatures are from Lundevannet at 1 m depth and discharge values are from outlet area in the same lake.

| Year | Month | Temperature (°C) | Discharge (m$^3$ sec$^{-1}$) |
|------|-------|------------------|------------------------------|
| **2002** | May | 12.47 | |
| **2002** | June | 17.44 | |
| **2002** | July | 18.54 | |
| **2002** | August | 17.66 | |
| **2002** | September | 13.32 | |
| **2002** | October | 4.49 | |

| | | | |
|---|---|---|---|
| **2003** | May | 9.87 | 23.31 |
| **2003** | June | 17.68 | 5.71 |
| **2003** | July | 20.47 | 8.64 |
| **2003** | August | 19.33 | 3.52 |
| **2003** | September | 14.65 | 5.54 |
| **2003** | October | 7.39 | 1.86 |
| **2004** | May | 12.90 | 14.84 |
| **2004** | June | 16.81 | 4.77 |
| **2004** | July | 17.78 | 5.41 |
| **2004** | August | 19.15 | 9.18 |
| **2004** | September | 13.93 | 15.34 |
| **2004** | October | 8.92 | 25.64 |
| **2005** | May | 11.55 | 3.72 |
| **2005** | June | 15.70 | 12.39 |
| **2005** | July | 20.21 | 5.41 |
| **2005** | August | 18.18 | 3.48 |
| **2005** | September | 14.22 | 3.74 |
| **2005** | October | 9.28 | 4.00 |
| **2006** | May | 8.84 | 36.30 |
| **2006** | June | 17.29 | 6.51 |
| **2006** | July | 21.09 | 2.32 |
| **2006** | August | 19.42 | 7.79 |
| **2006** | September | 15.74 | 15.52 |
| **2006** | October | 11.57 | 22.60 |
| **2007** | May | 12.34 | 4.67 |
| **2007** | June | 17.40 | 4.31 |
| **2007** | July | 17.03 | 13.02 |
| **2007** | August | 17.69 | 12.69 |
| **2007** | September | 12.96 | 3.36 |
| **2007** | October | 8.92 | 5.63 |
| **2008** | May | 13.64 | 5.82 |

| | | | |
|---|---|---|---|
| **2008** | June | 17.33 | 1.91 |
| **2008** | July | 19.28 | 1.53 |
| **2008** | August | 17.64 | 9.94 |
| **2008** | September | 13.27 | 11.09 |
| **2008** | October | 8.81 | 8.21 |
| **2009** | May | 12.46 | 4.72 |
| **2009** | June | 17.13 | 3.39 |
| **2009** | July | 19.45 | 9.43 |
| **2009** | August | 17.61 | 11.87 |
| **2009** | September | 14.15 | 9.12 |
| **2009** | October | 7.48 | 8.03 |
| **2010** | May | 12.30 | 4.22 |
| **2010** | June | 17.92 | 1.75 |
| **2010** | July | 19.86 | 1.19 |
| **2010** | August | 18.23 | 5.68 |
| **2010** | September | 13.75 | 6.33 |
| **2010** | October | 9.69 | 23.92 |
| **2011** | May | 12.32 | 4.15 |
| **2011** | June | 17.14 | 7.55 |
| **2011** | July | 18.18 | 21.63 |
| **2011** | August | 18.22 | 11.44 |
| **2011** | September | 13.74 | 36.12 |
| **2011** | October | 11.05 | 8.05 |