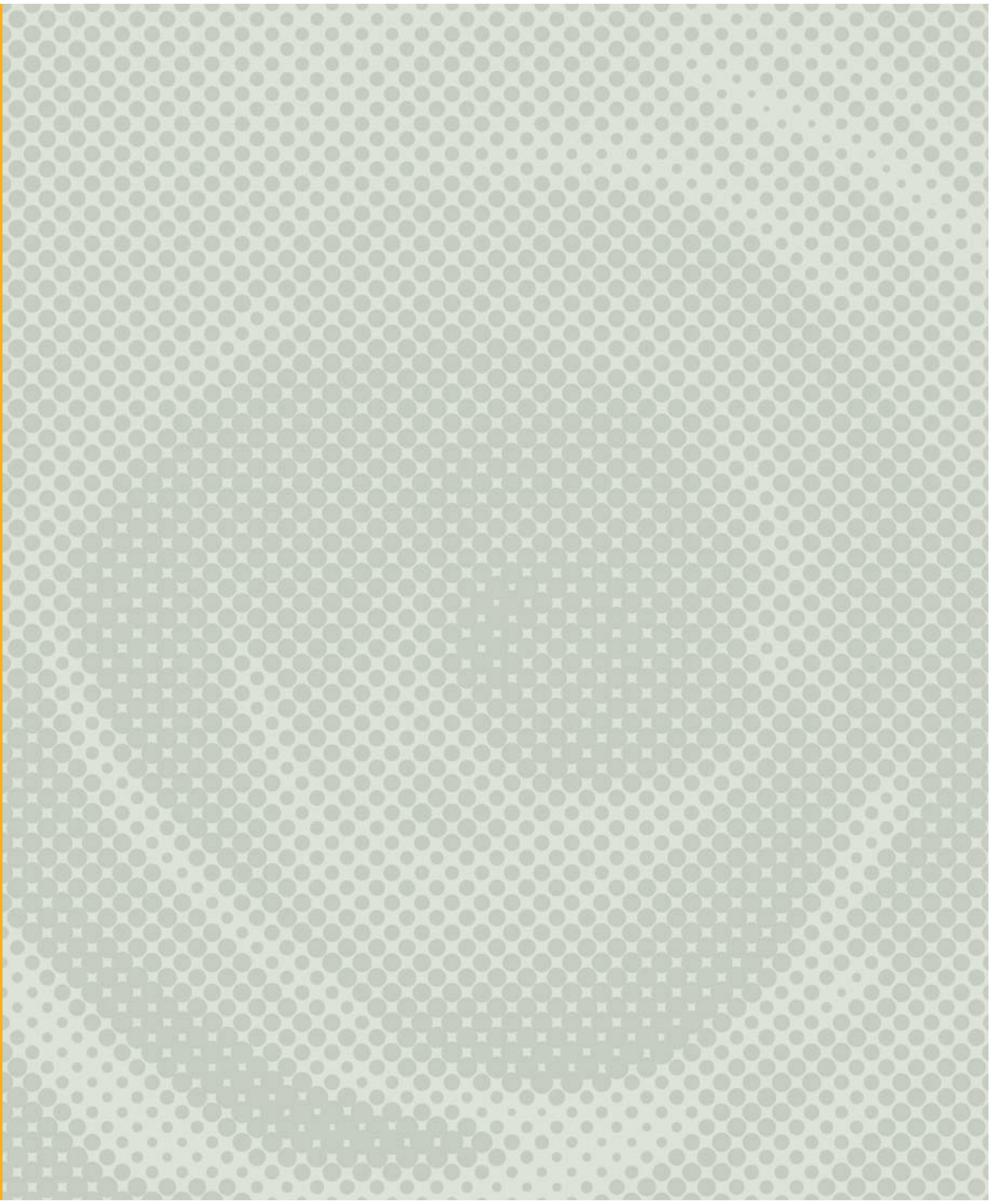
Salinity tolerance of rudd (*Scardinius erythropthalmus*) and risk for range expansion via brackish water

Birgit Solberg

Norwegian University of Life Sciences
Department of Ecology and Natural Resource Management
Master Thesis 30 credits 2012



Acknowledgements

This master thesis was given by the Norwegian Institute for Water Research (NIVA)

I warmly thank my main supervisor professor Thrond O. Haugen (dr. scient) for his engaging enthusiasm for fish, for ingenious help with my statistics, and for his patience in repeatedly explaining the statistical methods to me.

I also thank my second supervisor Frode Kroglund (cand. real) at NIVA for giving me this assignment, as well as providing helpful insight on rudd, the Storelva-Sandnefjorden system, basic knots, mermaids, and the realities of field work.

During my field work, I received invaluable help from my fellow field workers Bernhard and Sara. Their help and company were highly appreciated. Jim Güttrup from Tvedestrand municipality deserves special thanks for his contribution to my field work, and for always coming up with a solution to any practical problem.

My fellow master students at INA deserve huge thanks for many enjoyable lunches and coffee breaks, for advices on how to solve several master-related (and not master-related) issues, and for making the reading hall a place well worth spending a good proportion of my waking hours. I also thank Jørgen for letting me use his computer when my own broke down at a critical stage in the process.

For constructive comments on this thesis, I thank Elisabeth, Marte and my mother Eli.

Special thanks go to my close friends Lise, Tale, Anna, Ingeborg and Eirin, for always believing I could finish this thesis.

Ås, May 2012

Birgit Solberg

Abstract

Rudd (*Scardinius erythropthalmus*) is a naturally occurring species in Norway which over the last four decades has expanded its distribution far beyond its natural range. This invasion represents a threat to local ecosystems and biodiversity. In order to find the most efficient measures to prevent further spreading, it is crucial to find the spreading mechanism for this species. It is assumed that anglers are responsible for introducing rudd to new water bodies, but in this study I explore whether along-coast migration via brackish water may serve as an additional route. Rudd from Storelva water system in southern Norway regularly performs seawards migrations entering brackish water. In periods of high input of freshwater to the fjord system, the brackish surface layer expands outwards, and salinities along the coast decrease. To test whether brackish water represents a possible route for range expansion, the salinity tolerance of rudd was tested in a laboratory experiment, and was found to be between 12 and 15 ppt. These results were applied in a risk model to determine the potential distribution of rudd in relation to observed and simulated salinities in the Storelva-Sandnesfjorden system. According to this model, there is high chance (given salinity tolerance at 24 hrs) that rudd may spread all the way through the Storelva-Sandnesfjorden system at medium (8 m^3/sec) to high (100 m^3/sec) Storelva discharges. Similar assessments can be made for other water systems to predict the risk of range expansion along the Skagerak coast of Norway.

Contents

Appendices

1. Introduction

Invasive species represent one of the biggest threats to biological diversity (e.g Ricciardi & Rasmussen 1998; García-Berthou et al. 2005; Gederaas et al. 2007). Species entering a new system may alter the physical habitat, disrupt food webs and lead to the extinction of endemic species (Ricciardi & MacIsaac 2000; Paavola et al. 2005; Nilssen 2009). In general, biological invasions can lead to homogenisation of ecosystems, and decrease biological, economical and recreational value (García-Berthou et al. 2005; Paavola et al. 2005; Nilssen 2009). Lakes and estuaries are especially susceptible to invasions (e.g Mills et al. 1994; Cohen & Carlton 1998; Sala et al. 2000), and introduced aquatic species generally have a high colonization rate in freshwater (García-Berthou et al. 2005). In Norwegian lakes, non-native species constitute 26 % of the freshwater fish (Hesthagen & Sandlund 2007). When a new species has been established in a water system it is virtually impossible to remove it, and efforts in doing so will involve high costs (Ricciardi & Rasmussen 1998; Mikkelsen 1999; Johnsen et al. 2010). The most effective way to limit invasive species is therefore to focus on how the species is spreading and how to prevent further expansion of distribution (e.g Ricciardi & Rasmussen 1998; Johnsen et al. 2010; Winfield et al. 2011).

Freshwater fish can enter new water bodies in a number of ways, including intentional or unintentional release (e.g. as bait fish), or by natural range expansion (e.g Lodge 1993; Mills et al. 1993; Bringolf et al. 2005). The environmental tolerance is one of the most important predictors for the potential distribution of a species (Kilambi & Zdinak 1980; Moyle & Light 1996; Ricciardi & Rasmussen 1998). Salinity tolerance is an important factor that determines the distribution of most aquatic species (Paavola et al. 2005), and is mainly determined by the ability to withstand, avoid or compensate for osmotic stress (Williams & Williams 1991; James et al. 2003; Luz et al. 2008). According to Williams and Williams (1991) freshwater fish will not be negatively affected by external salinities below the ionic concentration in the blood. In most freshwater fish, the blood salt concentration lies between 10 and 12 ppt (Williams & Williams 1991). Tolerance of external salt concentrations above this level is dependent on the organisms' ability to maintain its internal ionic concentration and to compensate for loss of water (James et al. 2003; Luz et al. 2008). Species may be divided into groups based on their salinity tolerance, and may be either euryhaline, tolerating a wide range of salinities, or stenohaline, tolerating only small fluctuations in salinity. Salinity refers to the amount of ions in the water, and may be expressed in a number of ways (Dunlop et al. 2006). In this study salinity is expressed as parts per thousand (ppt).

Rudd (*Scardinius erythrophthalmus*) is an example of a fresh water fish species, which has become invasive in USA, New Zealand and parts of Europe, including Norway (e.g Ricciardi & MacIsaac 2000; Hicks 2003; Sandodden & Johnsen 2008). There is limited knowledge about the biology of rudd when it enters new water bodies. Yet, rudd is a generalist with a broad diet and high fecundity (Kennedy & Fitzmaurice 1974; Pethon 2005; Nilssen 2009), and these are traits generally possessed by invasive species (Moyle & Light 1996; Ricciardi & Rasmussen 1998). In absence of natural enemies, rudd will rapidly dominate the entire water column, and the large amount of fry may deprive the water for most food resources (Nilssen 2009). In some water systems introduction of rudd has not had much impact (Blackwell et al. 2009; Winfield et al. 2011), whereas in other waters it has caused severe negative effects (e.g Hicks 2003; Sandodden & Johnsen 2008; Nilssen 2009). The negative impact of invasive species on the local system is often greater when the species richness of the receiving community is low (Moyle & Light 1996). Most Norwegian waters are naturally low in number of fish species, and the impact of rudd is especially negative when they enter waters previously empty of fish (Nilssen 2009). Negative effects of rudd include loss of biodiversity and homogenisation of ecosystems, eutrophication and degradation of water quality and introduction of new parasites. Additionally, rudd may compete with more economically and recreationally valuable fish species like trout (*Salmo trutta*) and perch (*Perca fluviatilis*) (e.g Kennedy & Fitzmaurice 1974; Nilssen 2009; Berger 2010).

Rudd occurs naturally in Norwegian waters (Huitfeldt-Kaas 1918), but its original distribution in Norway is restricted to the area around the Oslo fjord and west to eastern parts of Telemark County (Pethon 2005). However, during the last century rudd has colonized new locations in southern Norway, and over the last four decades its distribution has expanded dramatically beyond its natural range (e.g Mikkelsen 1999; Nilssen 2009; Artsdatabanken 2012). It now occurs in ten counties in southern Norway, as far west as Rogaland County (Artsdatabanken 2012). In Aust-Agder County where this study was performed, rudd was in 2002 found at almost 50 localities (Hesthagen & Østborg 2002). Based on the rapid range expansion of rudd, and the adverse effects it may have on local ecosystems, the species is now classified as a high risk species on the Norwegian list of unwanted species (Gederaas et al. 2007; Nilssen 2009). This entails that efforts should be made to prevent rudd from further expansion.

The prevailing theory of rudd expansion mechanism in Norwegian waters is that anglers serve as vectors by using rudd as live bait (e.g Mikkelsen 1999; Simonsen & Matzow 2000; Nilssen 2009). In this study, an additional pathway of spreading is considered, namely via brackish water along the coast. Rudd has been observed to enter brackish water in several water systems (Kennedy & Fitzmaurice 1974; Pethon 2005; Vetemaa et al. 2006). In the Storelva-Sandnesfjorden water system, where this study was performed, rudd regularly performs seawards migrations to brackish water (Kroglund et al. 2011b; Kroglund et al. 2011c). At times of high input of freshwater from the river system, the surface water of the fjord may decline to relatively low salinities (Tjomsland & Kroglund 2010; Kroglund et al. 2011a; Kroglund et al. 2011b). If the salinity of the surface water at times can go below the upper salinity tolerance of rudd, this may represent a possible route for range expansion.

In order to predict the rudds potential for future range expansion via brackish water, the salinity tolerance of the species must be explored (e.g Kilambi & Zdinak 1980; Matern 2001; Paavola et al. 2005). Hardly any information exists regarding the salinity tolerance of rudd. This study contributes with new and important knowledge by undertaking a salinity tolerance experiment on rudd. The results from the experiment are applied in a model that predicts the risk of survival through a fjord system under influence of different freshwater inputs (river dicharges). I further discuss the relevance of using the model as a general tool for risk assessment for spreading of rudd via brackish water within and between watercourses along the Skagerrak coast of Norway.

2. Materials and method

2.1 Study area

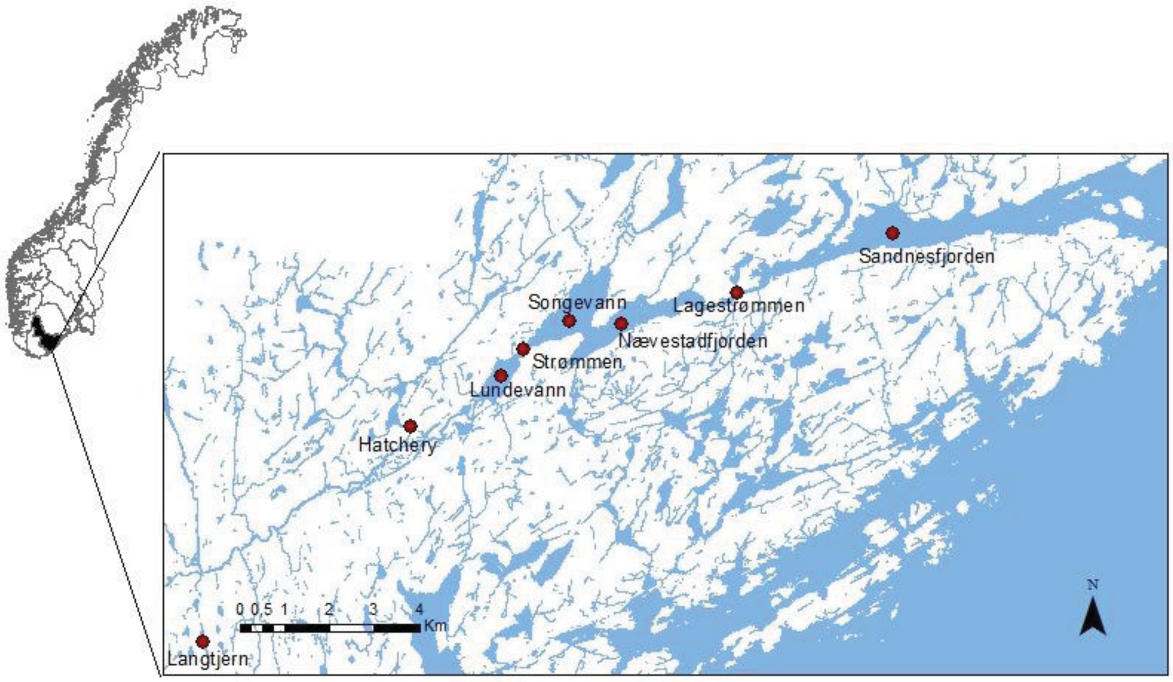


Figure 1: Map over study area, Storelva with fjord system, Aust-Agder County in southern Norway.

This experiment is based on rudd from the Storelva water system located in Aust-Agder County in southern Norway (Figure 1), where part of the population regularly migrates to brackish water. The rudd has been present in Storelva since 1940 (Simonsen & Matzow 2000). The entire Storelva water system is 551 km^2, and contributes with approximately 74 % of the drainage area to Sandnesfjorden (Tjomsland & Kroglund 2010). Storelva contains two lakes, but rudd is only found in the lowermost one, Lundevann. Water runs from Lundevann into the Storelva-Sandnesfjorden system through Strømmen, a 250 m long stream. The inner part of the fjord system consists of Songevann and Nævestadfjorden, which are connected by a 230 m wide strait. Nævestadfjorden is in turn connected to the outer fjord Sandnesfjorden through the 1.5 km long canal, Lagestrømmen. From Songevann and outwards, the water system is affected by coastal water.

The salinity of the Storelva-Sandnesfjorden system is highly dynamic, and is affected by input of both fresh (river water)- and saltwater (tidal water), and by direction and strength of wind (Kroglund et al. 2011a). In periods of low discharge from Storelva, coastal water enters into the system in accordance with tides and wind, and the water can reach relatively high salinities (Kroglund et al. 2011b). On the other hand, in periods of high discharge in Storelva, the salt concentration of the coastal water is diluted and the salinity in the fjord system decreases. The freshwater has a lower specific weight and will therefore float on top of the more saline coastal water (Økland & Økland 2006). Due to this, the surface water will have a low salinity, while the salinity may be considerably higher towards the bottom (Tjomsland & Kroglund 2010; Kroglund et al. 2011c). The water has lowest salinity closest to Strømmen. The salinity in the water system from Strømmen through the fjord system does not change gradually, rather there are abrupt changes, and salinities may vary considerably within a day (Kroglund et al. 2011c).

Both water temperature and the input of freshwater vary greatly between years and seasons. A simulation of salinities and water current in the fjord system done by Tjomsland and Kroglund (2010) showed that the salinity in the outer part of the fjord can become quite low, well below 16 ppt. According to this model, after a period of 2 months with high levels of precipitation, the top five meters of the water column in the outer part of the fjord was estimated to consist of 40 % water from Storelva (Tjomsland & Kroglund 2010).

2.2 Study species

Rudd (Figure 2) is primarily a freshwater species belonging to the Cyprinidae family. It occurs over large parts of Eurasia, and it has as mentioned also been introduced to America and New Zealand (e.g Ricciardi & MacIsaac 2000; Hicks 2003; Blackwell et al. 2009). It may become relatively large, reaching 45 cm and 2 kg, but in Norway it rarely becomes more than 35 cm and 600 g. A rudd can grow at least 20 years old. Rudd matures at ages of 2-3 years (Pethon 2005). The fecundity is high, and each female may produce approximately 100 000 – 230 000 eggs (Kennedy & Fitzmaurice 1974; Pethon 2005). The species prefer lowland, shallow, still waters with vegetation, and within its natural range it is generally observed in the littoral zone (e.g Kennedy & Fitzmaurice 1974; Hicks 2003; Pethon 2005). It is known to have a broad environmental tolerance (Kennedy & Fitzmaurice 1974; Nilssen 2009).

The temperature tolerance of rudd is quite wide (Hicks 2003), but it requires relatively high summer temperatures to complete its lifecycle (Borgstrøm 2000). In Kennedy and Fitzmaurice (1974) examples are given for rudd in Scandinavia spawning in temperatures ranging from 14-20 °C. In temperate waters, the lower temperature threshold for growth in cyprinids lies between 12-15 °C, but at high latitudes, cyprinids can acclimate to lower temperatures (Mann 1991). Rudd in Irish waters are inactive during the winter, and do not start feeding activity until temperatures become favourable (Kennedy & Fitzmaurice 1974).

Although the salinity tolerance of rudd until now has been largely unknown, the species has in several water systems been observed in salinities ranging from 0-12 ppt (Simonsen & Matzow 2000; Vetemaa et al. 2006; Johnsen unpublished), and it may be termed as euryhaline. In an experiment performed by Schmitz (1956, cited in Hynes 1970), the salinity tolerance of rudd was found to be between 15.5 and 17 ppt, but it is not mentioned how this experiment was performed, or how long the fish were exposed.

Figure 2: Rudd from Storelva.

2.3 Experiment

Salinity tolerance of rudd was tested in an experiment where the main object was to record mortality over time after direct transfer to different salinities. However, during the sampling period some of the experimental fish were exposed to saline water (see below). The experiment was performed in a former hatchery over two periods between 23rd May and 7th June 2011. Each experiment lasted seven days. The experiment was approved by the Norwegian ethical committee for experimental animals (Permit No: 2011/87798).

2.3.1 Fish used in the experiment

The fish used in the first round of experiment was collected between 5th May to 23rd May, and fish for the second round was collected between 23rd May to 31st May. Most of the fish were trapped in a rotary screw fish trap (Figure 3). This mode of trapping fish is regarded as fairly gentle, and the fish had no visible damage. The trap was placed in Strømmen (Figure 1), and was checked and emptied twice a day. The rudd collected in this trap belonged to the migrating part of the population in Lundevann.

Figure 3: Rotary screw fish trap used for trapping rudd.

The fish was moved from the trap to a 200 litre tank which was kept 10 meters below the outflow of Strømmen, and they were kept here until the experiment started. The tank was perforated to allow water exchange. Salinity and temperature during the storage period was recorded every 15 min by a WTW Cond 3310. During this storage period, the salinity of the surrounding water fluctuated, while the temperature remained more constant. The temperature averaged 13 ± 0.6°C (SD) for the first period and 12.6 ± 0.5°C (SD) for the second period. The salinity averaged 4.5 ± 3.1 ppt (SD) in the first period. In the second period, the salinity averaged 6.1 ± 3.2 ppt (SD). During storage, fish have at times been temporarily exposed to relatively high salinities (Figure 4).

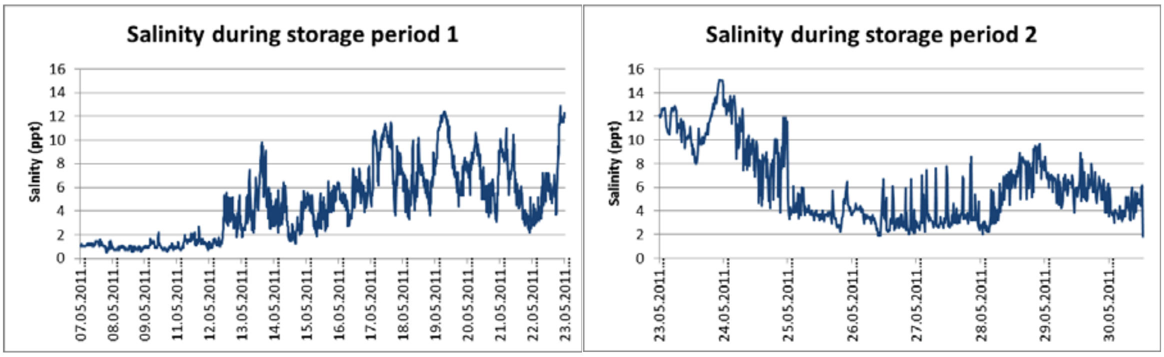


Figure 4: Salinity during storage periods prior to experimental rounds.

Due to shortage of fish from Strømmen for the first round of experiment, additionally 49 fish were collected by gillnets from Langtjern, a small local lake that drains into the Storelva watersystem (Figure 1). The nets were checked every 2-3 hours, and the fish were removed carefully and kept in a keep net in the lake. This lake is not affected by coastal water, and is therefore very low in salinity. Fish from Langtjern where marked by cutting the left pectoral fin, so that any bias from using fish from different populations could be accounted for. Some of these fish were slightly wounded from being caught in the net, and some were infected by intestinal worms. Individuals that presumably died from reasons other than the laboratory exposure treatments were not included in the data analysis. Fish from Langtjern were only used in the first round of the experiment (Table 1). The fish from Langtjern were significantly larger ($p = 0.0002$) and older ($p = 2.976e-05$) than the fish from Strømmen (Appendix I and II).

The total length of the fish used in the experiment averaged 12.2 ± 4.1 cm (SD) and total wet weight averaged 24.6 ± 28.8 g (SD). These sizes represent the size distribution that was caught in the stream in this period, and varied from 5.7 – 24 cm in length, and 1.2 – 220 g in weight. The different sizes were distributed evenly among all the test treatments to get a similar size range in all treatments. There was no difference in the size distribution between salinity treatments ($p = 0.99$) or the two experimental rounds ($p = 0.99$) (Appendix III and IV). The average size in the treatments varied between 10.5 - 13.2 cm and 12.6 - 31.5 g (Table 1).

The fish were transported from Strømmen by car to the experimental location at the hatchery (Figure 1). Fish were kept in four white plastic buckets filled with 20 l of lake water. The buckets had no circulation pump during the transportation. Time spent from taking the fish from Strømmen until they were distributed in the test tanks was less than one hour for both rounds. At this point the fish seemed to be in good condition, and any individual that seemed reduced or damaged was not used in the experiment.

2.3.2 Tank set-up

The experiment consisted of two tanks (170 cm x 170 cm x 50 cm), each containing seven individual buckets that was filled with water of different salinities (Figure 5, Table 1). The buckets were made from black plastic, each containing 65 litres of water. Each bucket had one circulation pump and one oxygen pump with an air stone. The fish were distributed among buckets by first picking the larger individuals and putting one in each bucket, and then doing the same with the largest of the remaining fish until all individuals were distributed. When the fish was distributed, the buckets were covered with a net to keep fish from jumping out. In order to avoid visual stress from moving staff, black plastic covers were placed on top to maintain dark surroundings.

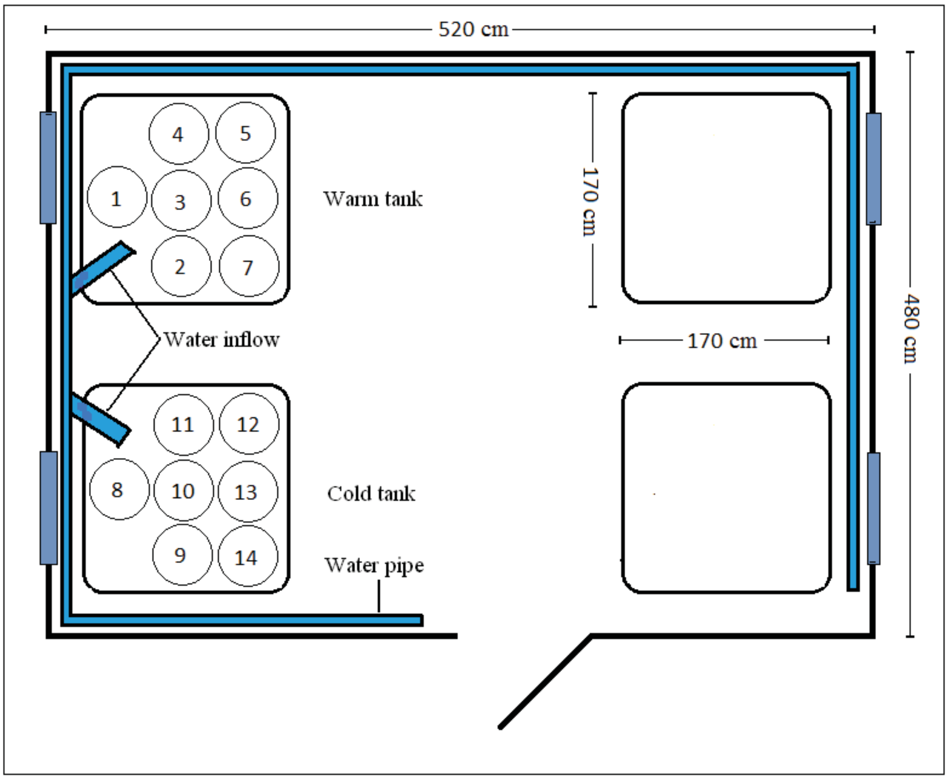


Figure 5: The tank set-up in the experiment. Numbers represents ID of experimental buckets. See **Table 1** for further details on the experimental buckets.

Table 1: Overview of the experimental conditions, treatment levels and characteristics of the experimental fish.

Round 1

Bucket	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Salinity	0	3	6	9	12	15	18	0	3	6	9	12	15	18
Mean temperature	15	15	15	15	15	15	15	13.5	13.5	13.5	13.5	13.5	13.5	13.5
Nr. of fish	11	11	11	11	12	11	11	11	11	10	11	13	11	11
Nr. of fish from Langetjern	5	4	4	4	4	4	3	3	3	3	3	3	3	3
Mean lenght (cm)	12.3	12.9	12.1	12.2	12.8	12.3	11.7	10.5	11.9	12.1	12.3	11.9	13.3	12.8
Mean weight (g)	31.5	31.3	24.2	24.1	30.8	23.7	21.9	12.6	23.6	26.5	27.2	23.9	26.8	26.7

Round 2

Bucket	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Salinity	0	3	6	9	12	15	18	0	3	6	9	12	15	18
Mean temperature	17.3	17.3	17.3	17.3	17.3	17.3	17.3	16.1	16.1	16.1	16.1	16.1	16.1	16.1
Nr. of fish	11	11	12	9	13	10	11	11	11	11	11	12	11	11
Mean lenght (cm)	12.7	12.7	12.3	12.5	11.8	12.2	11.9	12.4	12	12.2	11.81	11.7	12.5	12.2
Mean weight (g)	27.3	25.1	24.1	26.3	20.8	24.3	21.4	23.3	27.8	25.4	33.2	22	25.7	25.9

2.3.3 Treatments for exposure

In order to determine the upper salinity level for the main experiment, and hence the salinity level resolution, a 68 h pilot study was performed. This was done by exposing fish to salinities of 0, 10, 20 and 30 ppt at 11 °C. Each tank received 12 individuals, except the control, that received 28 fish. Mortality was checked after 11 hours. All fish died in the 20 and 30 ppt treatments within 16 hours, while all fish in 10 ppt and the control treatment were alive at the end of the 68 h experiment. The surviving fish seemed to be in good condition and showed no evident signs of stress.

Based on findings from this pilot study, the fish were exposed to salinities of 0, 3, 6, 9, 12, 15 and 18 ppt at two different temperature regimes for 7 days. The experiment was repeated twice, but the water temperatures differed between the two rounds of experiment. Other factors differing between the two rounds include duration of the storage period and salinity conditions during the storage. The fish did not receive any food prior to or during the experiment.

The targeted salinities were obtained by mixing synthetic seawater (made from Red Sea Coral Pro Salt: salinity 33.5 ppt: Ca 450 ppm, Mg 1340 ppm, Alk /KH 4.3 meq/L/12.2 °dKH) with fresh water from a stream by the hatchery (pH 6.3, conductivity 2.6 mS/m, and Ca 1.27 mg/l). The chemical values in the stream water are not expected to have any negative effect on fish. The instant sea salt was dissolved in freshwater until saturation and left for 24 hours. The saturated salt solution was then mixed with stream water to achieve the targeted salinities. The temperatures in the exposure treatments were achieved by letting water circulate around the individual buckets in the tanks. This water was taken directly from a nearby stream, and therefore the temperature in the two tanks followed the natural fluctuations in the stream. These temperatures represent more or less the ambient temperatures for rudd in the Storelva watersystem during the study period. In one of the two tanks in each round the temperature was increased additionally by 1-2 °C by putting heating elements in the tank. The temperature gradually increased during the two rounds of experiments (Figure 6). Mean temperatures during the experimental rounds are given in Table 1. The temperature in the first round of the experiment was more or less constant, with only slight peaks. In the second round, the temperature increased throughout the experiment, and there was more variation between night and day.

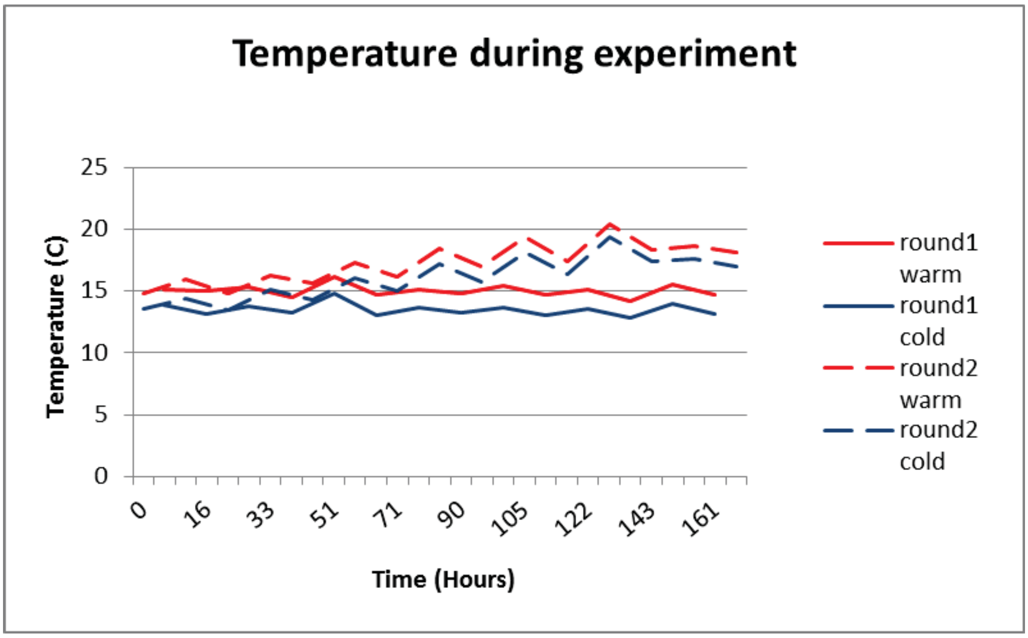


Figure 6: Development of temperatures during the two rounds of experiment.

2.3.4 Experimental protocol

Each of the two rounds of experiments lasted 7 days, or 161 and 167 hours respectively. Mortality, temperature and salinity were registered twice a day, in the morning and in the evening. Dead fish were continuously removed from the experiment. General condition of the remaining fish was also observed. At the end of the experiment all fish were killed by a sharp blow to the head. All fish used in the experiment were measured for length and weight. In addition, scales were sampled from all individuals for subsequent age determination.

2.4 Salinity in the fjord system

Another part of this study was to explore the salt concentration in the fjords outside of Strømmen, where rudd has been migrating. To get a picture of the spatial distribution of salinities in the fjord system, data were obtained in two ways. Simulations of daily salinities in the period 1st January 2007 – 1st September 2009 were derived from a numeric model used by Tjomsland and Kroglund (2010). This model uses lake topography, water temperature, meteorology, wind, discharge, tides, and salinity in the outer end of the fjord system as input-data, and simulates salinity according to these factors. The model was calibrated with manual measurements, and an excellent correlation was detected between the observed and simulated data, differing with no more than one ppt (Tjomsland & Kroglund 2010).

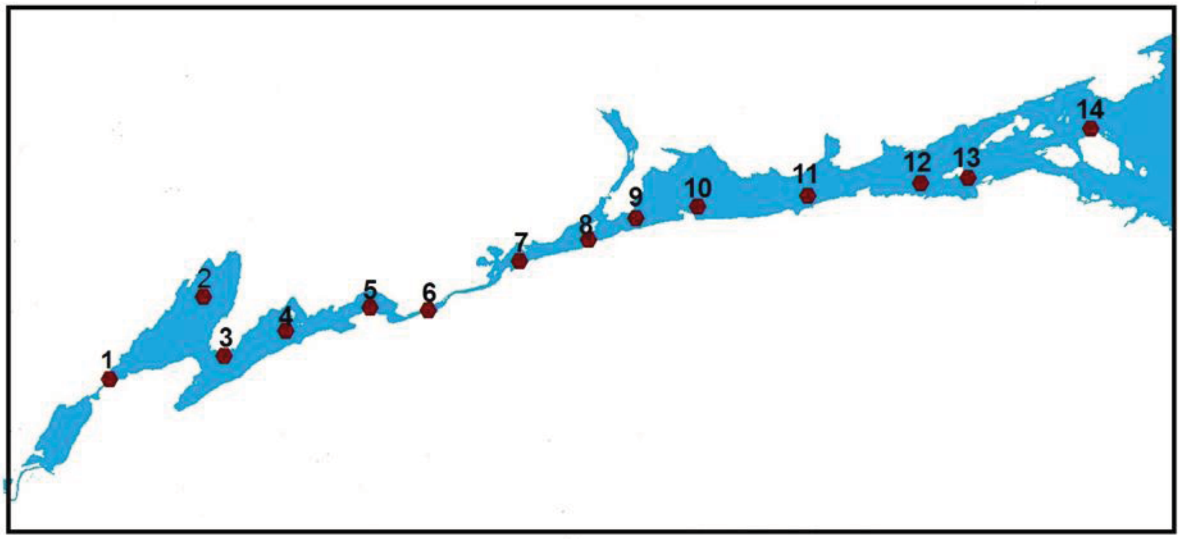


Figure 7: Points for measurements of salinity in the fjord system.

In addition to these estimated salinities, field measurements of salinity were collected during the study period. This was done by continual logging and manual measuring of salinity in the fjord system. The manual measuring was done at regular points (Figure 7), although not all points were measured each time. The points closest to the coast were skipped when high salinities were found at shallow depths further into the fjord. At each point salinity and temperature were measured at 0.5 m intervals, from 0.5 – 6 m depth. Manual measurements were performed five times: at 30th April, 5th May, 27th May, 1st June and 4th June. Measurements of salinities at 1 m depth were also done in connection with gill-net fishing for sea trout, at 2nd June and 6th July 2011.

The continuous logging was done at three stations, at point 1, 3 and 5. At the two latter stations, salinity was measured at two depths. Two individual loggers were attached to a buoy, and the censors were placed at 0.5 m and 2 m. This logging lasted from 5th May to 4th June. At point 1, the logging was done by the shoreline at 0.5 m depth, and lasted from 7th May to 23rd May. All loggers were set to register salinity and temperature at 15 minute intervals.

Manual measurements of salinity in the fjord system during the study period 2011 show that the measured salinities are relatively high compared to the simulated salinities. A salinity of 25.4 ppt was measured at 0.5 m depth at station 8 on 4th June. Salinity at 0.5 m depth at the outermost station was never measured to be lower than 18.6 ppt. The continual logging shows that salinities during the study period were highly variable, and fluctuations occurred within short periods of time (Figure 8).

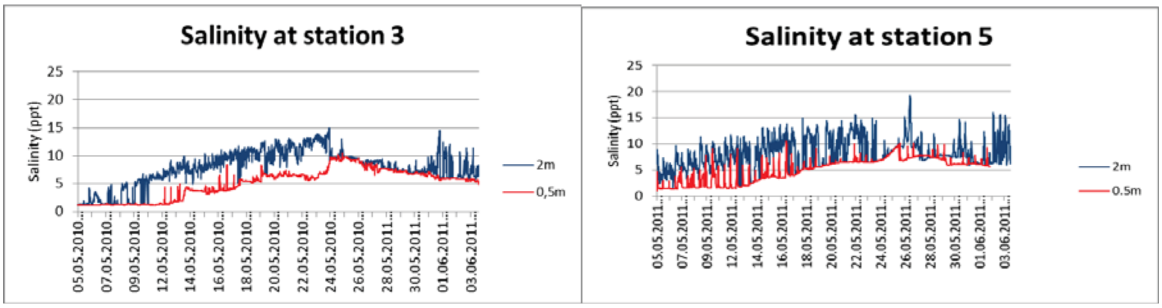


Figure 8: Continual logging of salinities at station 3 and 5.

2.5 Discharge from Storelva

Observations of daily discharge from Storelva in the 22nd November 2007 – 31st December 2011 period were obtained from the Norwegian Water Resources and Energy Directorate. The observed discharges from Storelva in this period varied between 140 m^3/sec and 0.78 m^3/sec, with an average of 11.75 m^3/sec, and median of 6.32 m^3/sec (Figure. 9). Highest discharges seem to occur in fall and winter, while summer months seem to be drier.

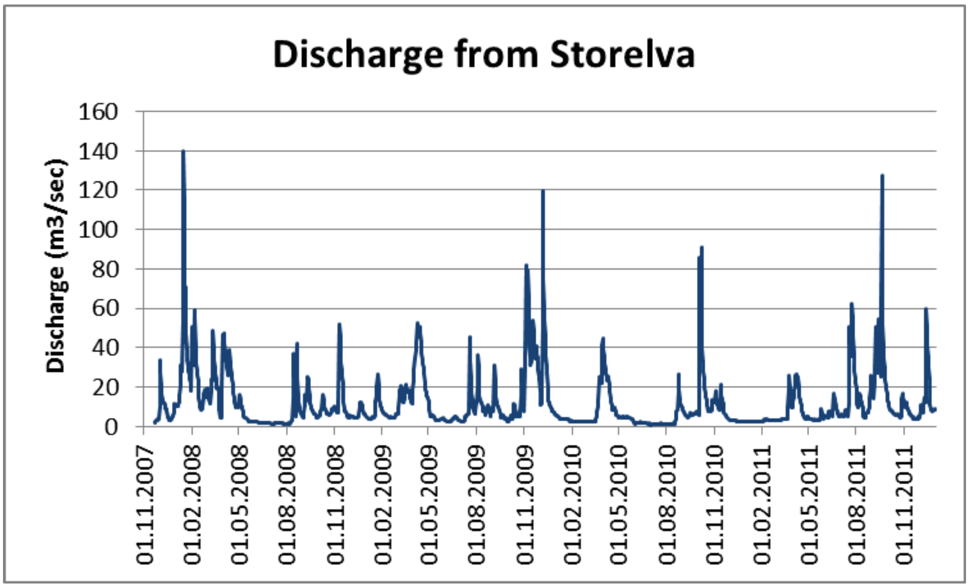


Figure 9: Discharge from Storelva from November 2007 – Desember 2011

Data of discharge was not available for the whole simulated period, but the available data show that this period included the largest observed discharge in Storelva since November

2007. The median discharge of the available data during the simulation period was 7.5 m^3/sec. The discharges during the 2011 field measurements were comparatively low, with a range of 4 – 10.9 m^3/sec and median of 4.8 m^3/sec.

2.6 Statistical analysis

For all statistics involved in this thesis, model selection was performed based on AIC (Burnham & Anderson 2002; Anderson 2008). The candidate models were in general based on ecologically-founded reasoning. Hence, all theoretical possible combinations of predictor variables have not been fitted for the respective models. All statistics were performed using program R version 2.14.2. (R Development Core Team 2010).

Whenever checking for differences among groups, e.g. size differences among observation units in the experiment, this was performed by fitting linear models, with subsequent analysis of variance (ANOVA, using the lm and anova procedures in R). If there was evidence of heteroscedasticity among groups, Welch anova was used (Welch 1951), using the oneway.test procedure.

Cumulated mortality trajectories were modeled as Cox proportional hazards regression models using the method described in (Andersen & Gill 1982). This approach allows for inclusion of both categorical (e.g., treatment and population) as well as continuous (covariates like individual length or temperature) predictor variables. The assumptions behind proportional hazards were tested using the method described in (Grambsch & Therneau 1994). The models were fitted using routines implemented in the survival library.

In order to determine the 50% lethal concentration (LC50*, i.e.* the concentration at which probability of death is 50% after a given time period of exposure) for survival periods of 24 hrs, 48 hrs and 96 hrs, logistic regression models were fitted for survival data subsets covering these respective time spans. In these models, the salinity levels from the experiment were treated as a continuous variable. The logistics regressions were fitted as generalized linear models (GLM) using the glm procedure. LC50 with corresponding confidence limits were accessed by applying the logistic model in the dose.p procedure (mass library).

In order to fit a model that could be used for making predictions of surface water salinity along the Storelva-Sandnesfjorden gradient as function of Storelva water discharge, I fitted generalized additive models (GAM, gam procedure in R, MGCV package) to daily mean of simulated salinity data retrieved from Tjomsland & Kroglund (2010). Technically, I used thin-plate regressions as this technique allows for interaction effects between multiple covariates (Wood 2003). Thin-plate regression produces response surfaces as function of n-dimensional predictor variables where the surface complexity is selected by means of generalized cross-validation (GCV) procedures (Gu & Wahba 1991). Hence, the parameter under estimation constitutes estimated degrees of freedom (edf, i.e., number of surface knots). I explored various delay-responses of salinity to the water discharge and allowed the water discharge delays to interact with distance to river mouth. The most supported delay level was selected using AIC.

Finally,by applying the logistic 24h survival models on estimated surface salinities (the most supported GAM model), I produced spatial gridded risk maps for the Storelva-Sandnesfjorden system under different river discharge settings. The gridded maps were constructed by kriging under a spherical autocorrelation structure (Cressie 1993). The smoothing parameter t, was set to 300 for these plots. The kriging was performed using the Krig procedure in the fields library. For comparison, I also estimated risk predictions for salinities that were measured in 2011.

3. Results

3.1 Salinity tolerance

3.1.1 Survival at different salinities

The model selection procedure for fitted survival models pointed towards that survival was most parsimoniously predicted from additive effects of nominal salinities and individual length (Table 2), and this model could explain 77.5 % of the variation. However, temperature should also be taken into account since two out of four models that had ΔAIC lower than 4 had temperature included as a predictor.

Table 2: Ordered model selection table based on AIC for fitted candidate Cox Proportional Hazards survival models. Predictor variables that are provided with a capital first letter are categorical predictors, whereas the others are continuous.

Model structure	df	AIC	ΔAIC
Nominal Salinity + length	2	659.8515	
Nominal Salinity	1	659.8878	0.0363
Nominal Salinity + temperature	2	661.869	2.0175
Nominal Salinity * temperature	3	662.1677	2.3162
Nominal Salinity + Round	3	665.6311	5.7796
Nominal Salinity + Round + length	4	665.9481	6.0966
salinity * temperature	3	673.4864	13.6349
Nominal Salinity * length	3	675.3204	15.4689
salinity	1	679.4224	19.5709
salinity + temperature	2	681.2899	21.4384

The survival curves fitted a Cox proportional hazard model show clear trends in the salinity tolerance of rudd (Figure 10). All fish in 18 ppt died within the first 16 h of the experiment, while practically all fish in treatments 9, 6, 3 and 0 ppt survived throughout the experiment. The only salinity treatments with a gradual mortality were 12 and 15 ppt. All fish in 15 ppt were dead within 51 h. There was a lower mortality rate in 12 ppt, and by the end of the experiment, 73% of the fish in the two rounds were still alive in this concentration. This indicates that the salinity tolerance of rudd found in this experiment lies between 12 and 15 ppt.

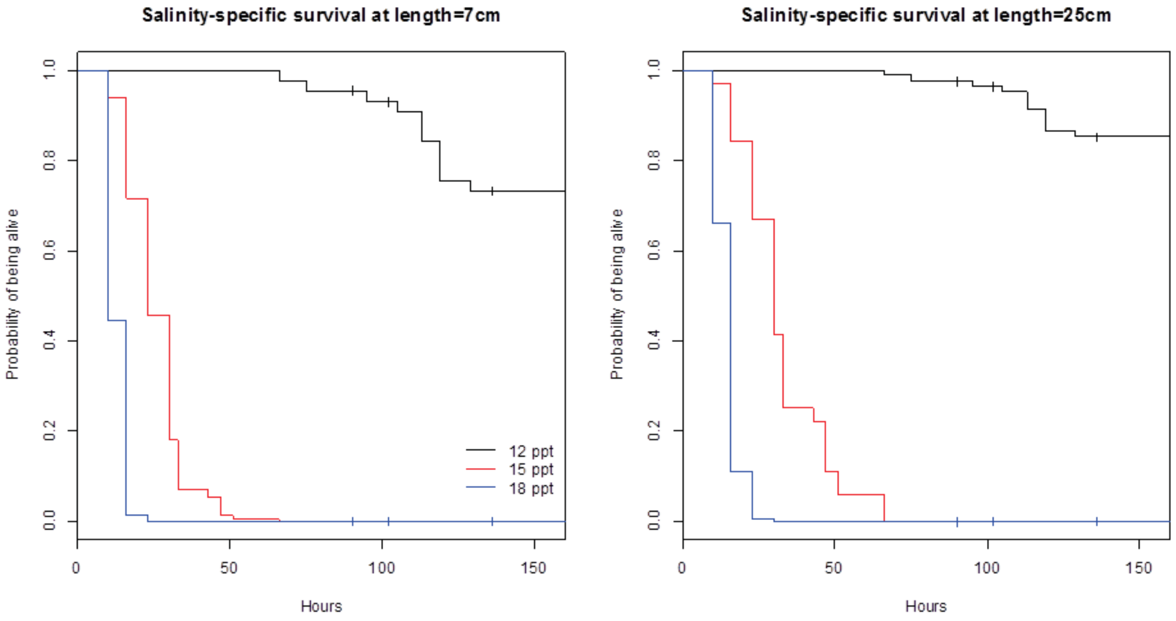


Figure 10: Estimated accumulated probability of being alive over time in different salinities for length 7 cm and 25 cm. The estimates have been retrieved from the most supported Cox proportional hazard

model (**Table 2**). Vertical markers on the survival curves represent individuals that have been censored from the experiment.

3.1.2 Lethal Consentration (LC):

The estimated LC10 and LC50 values were established at 24, 48 and 96 hours (Table 3). The LC-estimates show a gradual decrease in salinity tolerance over time, and fish can survive at higher salinities after 24 hours compared to 48 and 96 hours. The LC-values were very similar for the estimated 10 % and 50 % survival. The lack of data on survival in salinities between 12 and 15 ppt makes it impossible to calculate reliable confidence intervals for survival in this range.

Table 3: LC10 and LC50 values at 24, 48 and 96 hours. Standard errors are given in brackets.

	24 h	48 h	96 h
LC10	14.7 (114)	13.4 (691.3)	12 (17.5)
LC50	15 (7.8)	13.5 (698)	12.3 (174.5)

3.2 Survival trends in salinities 12 and 15

Most factors had no significant effect on survival in this experiment. As salinity 12 and 15 were the only salinity treatments with a gradual mortality, these were examined more closely to see if any of the factors had an effect in these salinities.

3.2.1 Population-specific survival

No significant difference was found in the mortality of fish from Storelva and Langtjern in salinity 12 and 15 (Figure 11), although there is a weak trend that fish from Langtjern die at an earlier stage ($p = 0.10$)

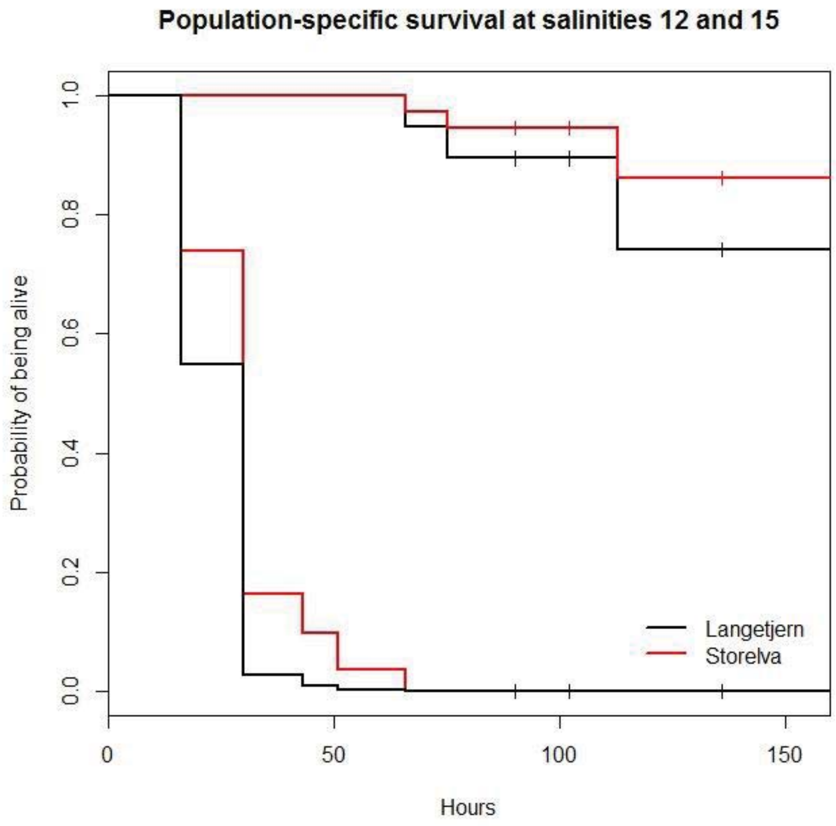


Figure 11: Estimated survival curves for the Langtjern and Storelva populations at salinities 12 an 15. Curves are derived from the Cox proportional hazard model.

3.2.2 Round-specific survival

The survival in the two rounds of experiment was very similar, and although some difference was found at salinities 12 and 15 ppt, the difference was far from significant (p = 0.3). In these salinities the fish died slightly earlier in the second round of experiment compared to the first (Figure 12).

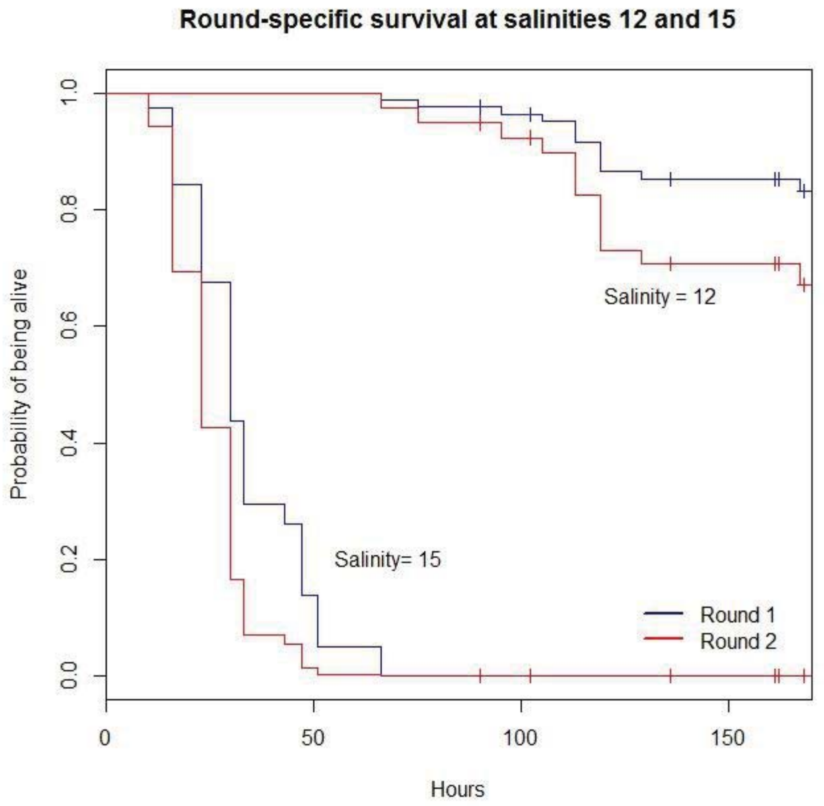


Figure 12: Estimated survival curves in salinities 12 and 15 ppt in the two rounds of experiment. The curves have been derived from the Cox proportional hazard model.

3.2.3 Length-specific survival

Salinity 15 was the only treatment were size-dependent mortality was found (Figure 13). In this treatment smaller fish die at an earlier stage than larger fish ($p = 0.034$).

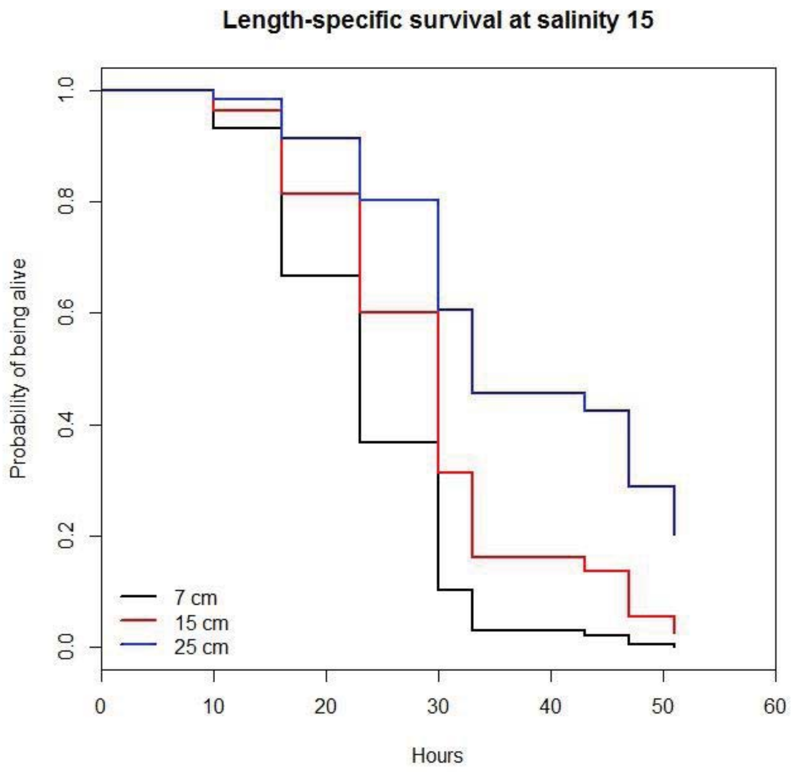


Figure 13: Estimated length-specific survival curves in salinity 15 ppt. Curves are derived from the Cox proportional hazard model.

3.2.4 Temperature-specific survival

Temperature was not found to have significant additive effect on mortality in any of the treatments, although there seemed to be a weak trend in salinity 15 ppt ($p = 0.065$). In this salinity fish died slightly faster at low temperatures compared to high temperatures (Figure 14). Although temperature did not have a significant additive effect on mortality, the interactive effect of salinity and temperature was found to have a weak trend when all salinity treatments were considered ($p = 0.069$).

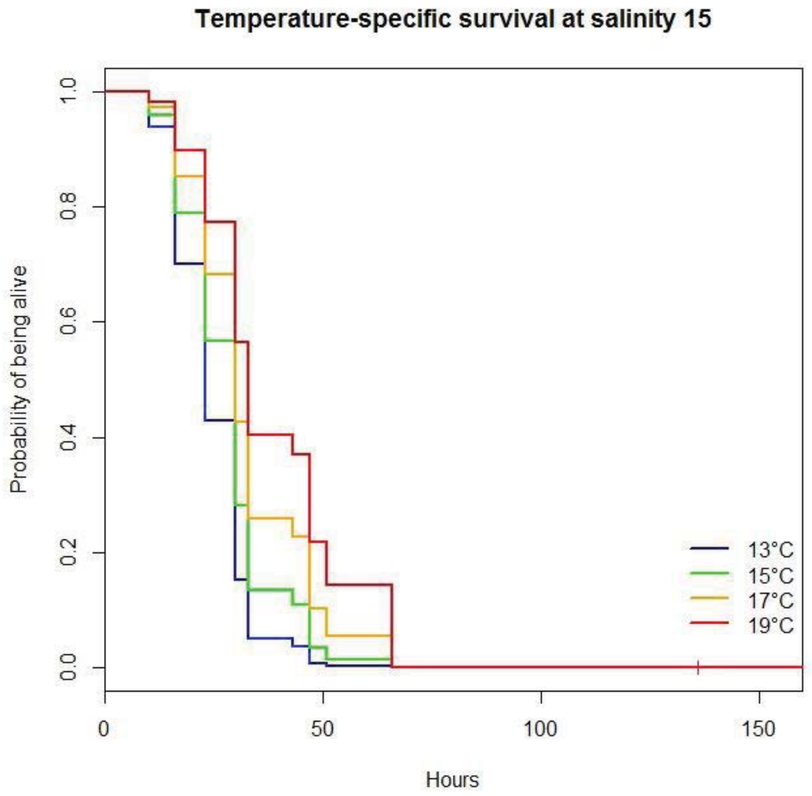


Figure 14: Estimated temperature-specific survival curves at salinity 15 ppt. Curves are derived from the cox proportional hazard model.

3.3 Mapping and assessment of risk

Discharge could explain 92 % of the variation in the data of simulated salinities in the fjord system, and discharge is therefore considered as a good predictor for salinity. Salinity decreases with increases in discharge (Figure 15). The model that explained most of the variation was the one applying discharge with two days delay (moving average 3) (Table 4), which implies that there is a delay in the system from the water leaves Strømmen to salinities in the fjord are affected. The salinity increases with distance from Strømmen.

Table 4: Ordered model selection table based on AIC for GAM, predicting surface salinities as function of distance to Storelva delta and water discharge in Storelva.

Model structure	edf	AIC	*ΔAIC*
moving average 3: 2 days delay	10.69109	20354.82	
moving average 2: 1 day delay	10.67588	20713.37	358.55
moving average 1: no delay	10.65765	21131.43	418.06

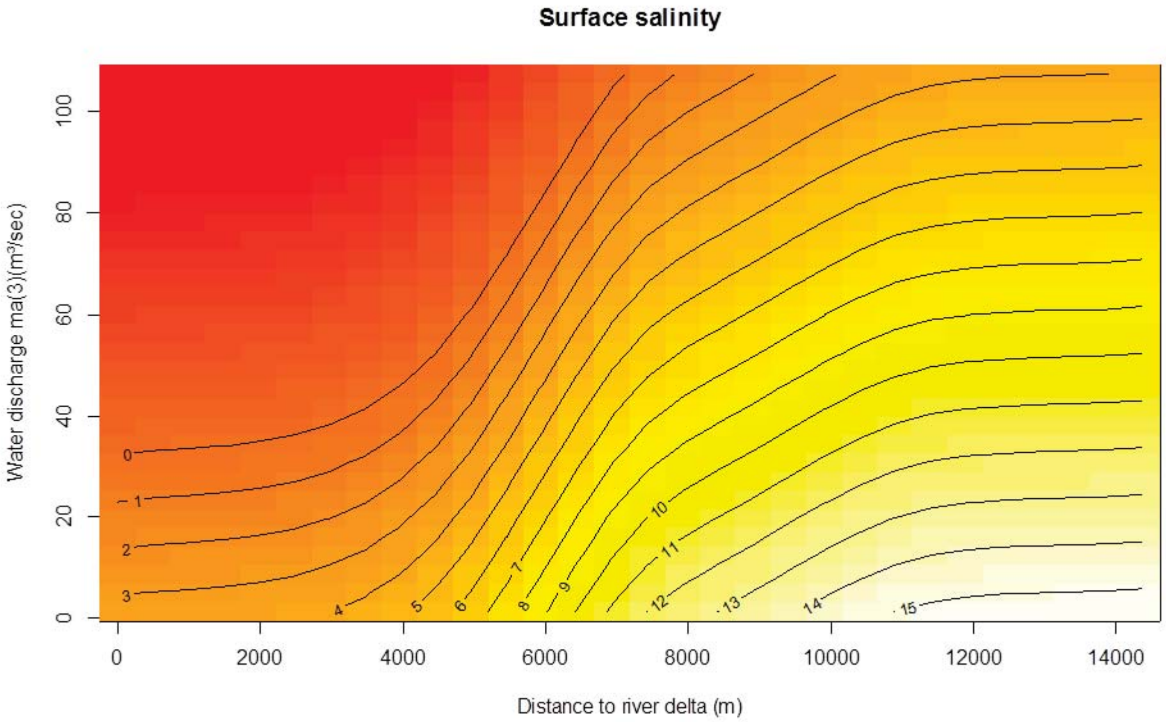


Figure 15: Estimated surface salinities based on GAM that predicts surface salinities as function of distance to Storelva delta and two-day moving average of water discharge in Storelva. Isoclines represent halinoclines (ppt).

The combined model of simulated salinities in the fjord system, and the 50 % probability of survival at 24 h were plotted at high (100 m^3/sec), medium (8 m^3/sec) and low (2 m^3/sec) discharges, based on observed discharges during the simulated period. This model shows that there is a high probability of survival in the outer part of the fjord at high discharge (Figure 16). The risk for survival in the outer fjord at medium discharge is slightly lower, but there is still a good potential for survival. The probability of survival in the outer fjord is low at low discharges. The predictions from this model were compared to probability of survival in relation to observed data of salinities in 2011. The probability of survival based on observed salinities decreases rapidly at a distance of 8-12 km from Strømmen.

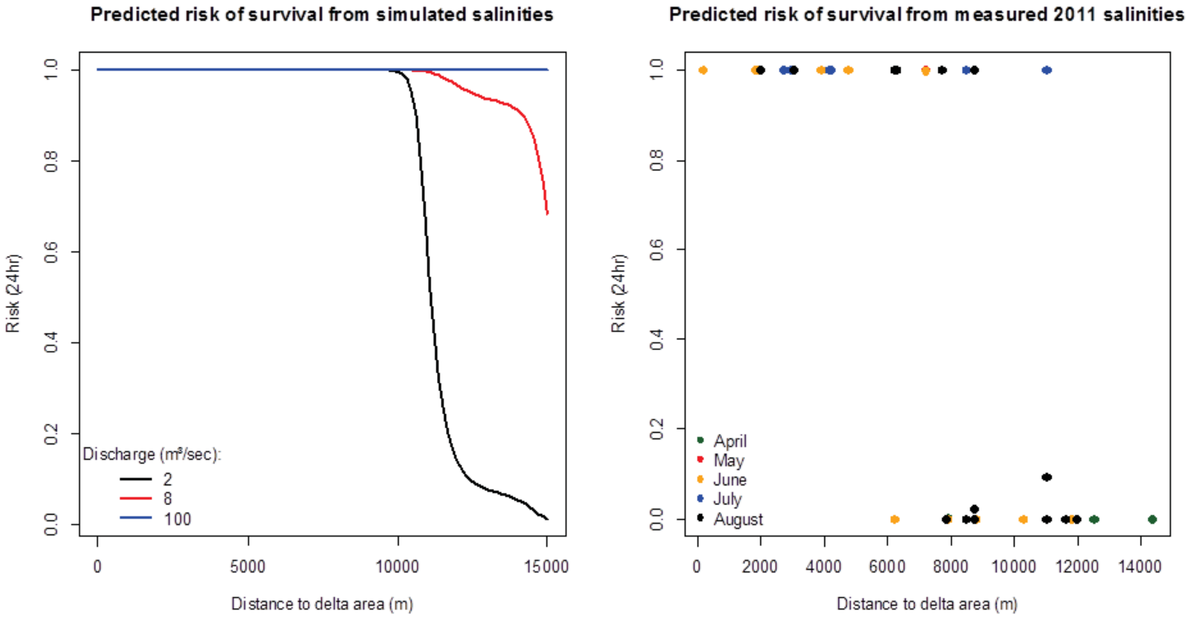


Figure 16: Estimated 24h probability of survival for rudd as function of distance to the Storelva river delta. Estimates have been derived from logistic survival model applied on estimated salinities (GAM model) in the left panel. In the right panel estimates have been retrived from measured salinities in 2011.

To give an example of possible application of the model, it was used to map the potential distribution of rudd in the fjord system at the three different discharge regimes (Figures 17, 18 and 19). The maps show the probability of survival at 24 hours in relation to distance from Strømmen.

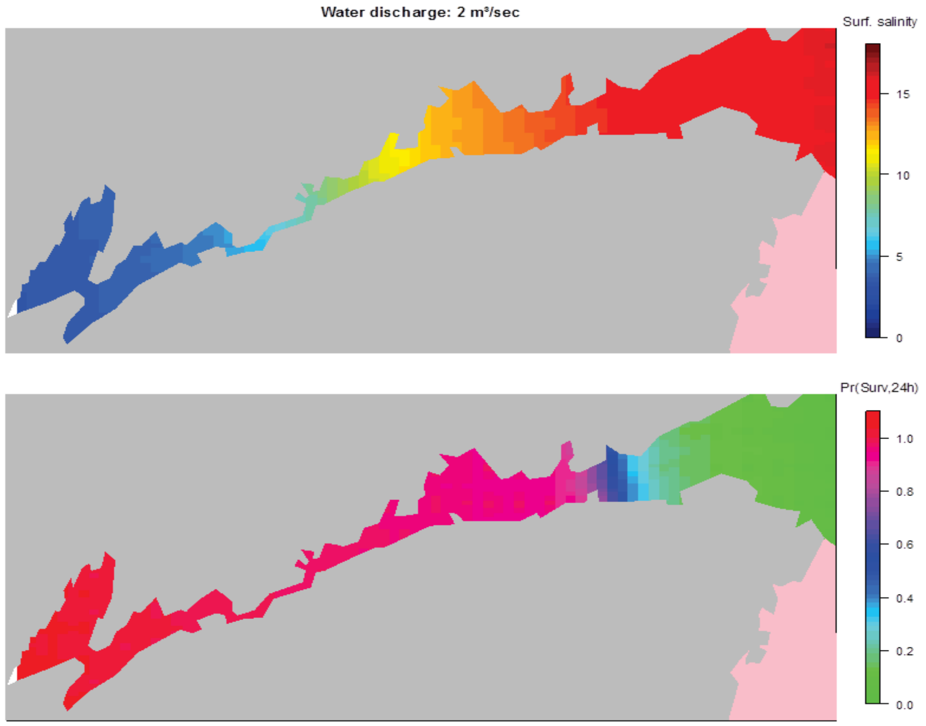


Figure 17: Map presentation of estimated probability of 24h survival when applied to simulated salinities under low discharge (2 m^3/sec). Pink areas constitute areas for which I have no salinity data.

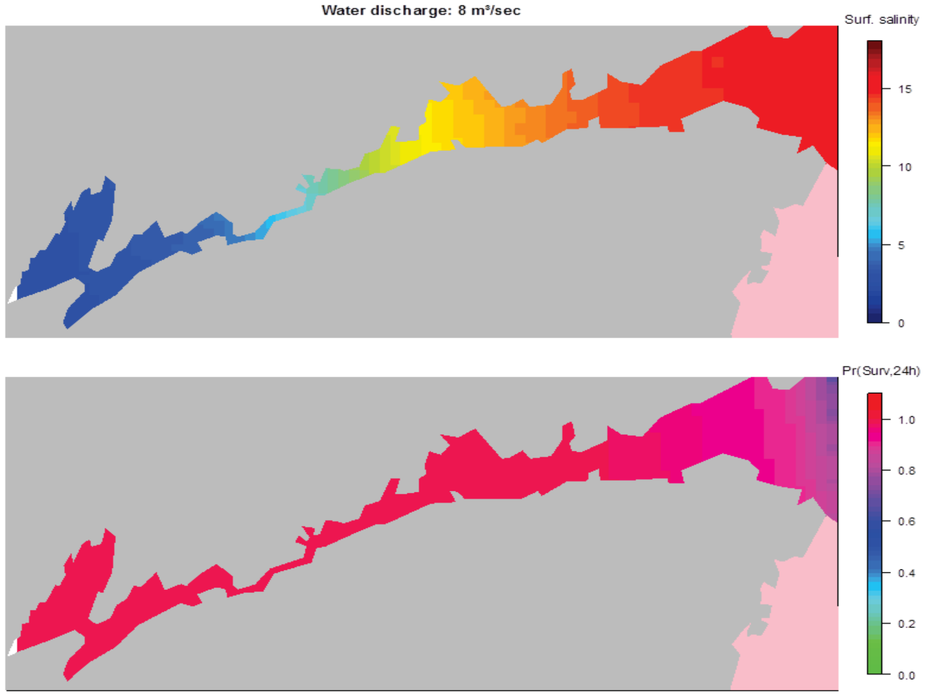
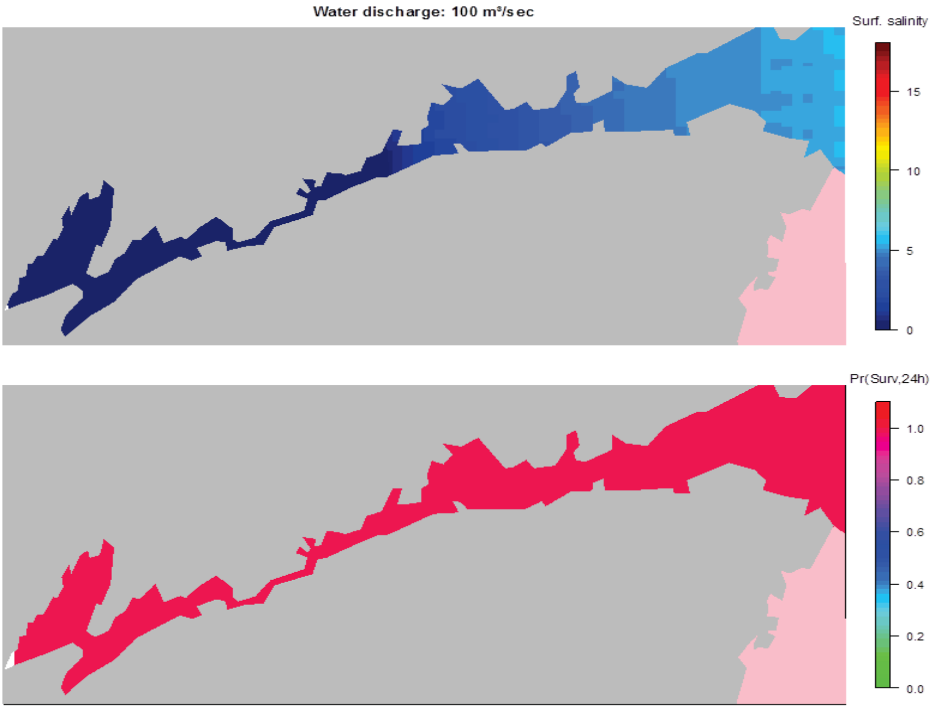


Figure 18: Map presentation of estimated probability of 24h survival when applied to simulated salinities under medium discharge (2 m^3/sec). Pink areas constitute areas for which I have no salinity data.



Figur 19: Map presentation of estimated probability of 24h survival when applied to simulated salinities under high discharge (100 m³/sec). Pink areas constitute areas for which I have no salinity data.

4. Discussion

This study shows that rudd are able to tolerate weeklong exposure to mesohaline (i.e., water with salinity of 5-18 ppt) water, and the tolerance threshold found under experimental conditions lies between 12 and 15 ppt. This salinity tolerance may be high enough to allow range expansion of rudd via brackish water. The combined model of salinity tolerance of rudd and simulated salinities in the Storelva-Sandnesfjorden system predicts that the salinities in the outer part of the fjord may become low enough to allow potential spreading of rudd at intermediate to high discharges. If this is the case, it needs to be considered in future management of rudd. However, this model makes several assumptions, and the results should be interpreted with some caution. These assumptions include that 1) the salinity tolerance found in the laboratory experiment reflects the actual salinity tolerance and distribution of rudd under natural conditions, 2) that simulated salinities are representative for the real field situation, and 3) that rudd possess a behavior that enables them to reach the coast within a relatively short time.

4.1 Salinity tolerance

Several biotic and abiotic factors can affect the salinity of rudd. Among these factors are size, life history stage, age and physical condition of individuals, temperature, water chemistry, former exposure to salinity, treatment prior to exposure, and length of exposure (James et al. 2003; Dunlop et al. 2006). There may also be regional differences in salinity tolerance between populations (Kefford et al. 2004; Dunlop et al. 2006). In addition, most studies have shown that former exposure or gradual increases in salinity lead to acclimation, which reduce osmotic stress and increases the salinity tolerance (e.g Kilambi & Zdinak 1980; James et al. 2003; Kefford et al. 2004). Such factors may explain the higher salinity tolerance found by Scmitz (1956, cited in Hynes 1970), compared to this study.

The survival curves at different salinities in this study were very clear, despite of several differing factors that could potentially influence the salinity tolerance. Apart from salinity, no factors had any considerable effect on the survival, which may be due to the coarse resolution of salinity treatments in the experiment. The LC10 and LC50 values were very similar at both 24, 48 and 96 hours, which is due to the fact that in most salinities all fish either lived throughout the experiment, or died within a relatively short time. This implies that mortality curves are very steep in salinities between 12 and 15 ppt. Perhaps would effects of temperature, population, size and experimental rounds have been more apparent if the most sensitive area for salinity tolerance was tested at a finer resolution. There was more effect of these factors when only salinity 12 and 15 were considered. In order to weed out random effects, the experiment should have contained more replicates, and for instance using a randomized block design to take into account eventual gradients in the experimental set-up (Barnard et al. 2007). Unfortunately, such a design was not applicable under the prevailing experimental facilities due to space limitations.

The lack of significant difference in mortality between the population from Langtjern and the population from Strømmen, despite differences in size, age, growing conditions, mode of trapping and handling, storage period and former exposure to salinity implies that the effect of salinity is so strong that it overrules the effect of these other factors. The weak trend that fish from Langtjern die quicker than fish from Strømmen in salinities 12 and 15 may be due to both the less gentle way of trapping fish from Langtjern, the lack of former exposure to salinity, or other population-related factors. Since the factors are not independent of each other and cannot be tested separately, it is not possible to say which factor that was most important. It may be that the effect of one factor differing between the two populations is neutralized by the effect of another. For example, the possible increased salinity tolerance in the Stømmen population due to former exposure might be compensated by the larger size of fish from Langtjern.

There was a weak tendency that fish in the second round of experiment died earlier than fish in the first round in salinities 12 and 15, although the difference was far from significant. These differences may be explained by temperature, use of fish from Langtjern in the first round, duration of storage period, and exposure to higher mean salinity prior to the second round compared to the first. In addition, other unknown factors may contribute. As with population-dependent mortality, the individual contribution of these factors cannot be estimated. Nevertheless, fish had a possible better survival in round one in spite of use of fish from Langtjern, which seem to die quicker, and despite lower mean temperatures, which seem to decrease survival. This might suggest that other factors than population and temperature was responsible for the possible difference in round one and two.

The only treatment with a weak additive effect of temperature was salinity 15, where fish seem to die quicker at lower temperatures. The slightly higher survival at higher temperatures is in accordance with rudds' preference for warmer habitats (Borgstrøm 2000). Although it was not significant, a weak interactive effect of temperature and salinity was also found, and temperature may therefore have some influence on the mortality at different salinities. The mean temperatures in the experiment differed with 3.8°C, and the effect of temperature might have been greater if a wider range of temperatures was tested. In any case, the experimental temperatures should be kept within the range that is most biologically relevant for migrating rudd.

There was a relatively large proportion of small fish used in this experiment compared to average size of the migrating part of the population from earlier years (Frode Kroglund, personal communication, April 2011). Size is known to influence the salinity tolerance of fish (Kilambi & Zdinak 1980; Williams & Williams 1991). Larger fish generally have a higher salinity tolerance, which seems to be related to the gill surface to body volume ratios (Williams & Williams 1991). As there was a large proportion of small fish in this experiment, the salinity tolerance of some individuals may potentially be higher than what was found in this study. In a study on migration in rudd in the Storelva-Sandnesfjorden system by Johnsen (unpublished), rudd longer than 15 cm (TL) had a profoundly higher survival in brackish water than rudd shorter than 12 cm. However, size-dependent mortality was only found in the 15 ppt treatment in this experiment, where smaller fish die at an earlier time than larger fish. Size may therefore only be important for survival in the most sensitive area of salinity tolerance. The effect of size might also be more important in the field, because larger fish have a higher swimming speed Blaxter (1969, cited in Hammer 1995), and may move more quickly out of unfavorable salinities. Under experimental conditions, fish are not able to escape high salt concentrations.

4.2 Model predictions and risk assessment:

It is assumed in this study that the salinity tolerance found in the experiment corresponds to the actual field distribution of rudd. According to Kefford et al. (2004), salt tolerances found in lab experiments correspond well to maximum salinity at which species of freshwater fish are found, especially when fish are acclimated prior to the experiment. As mentioned, there are several field observations of rudd in waters with salinities between 0-12 ppt (e.g Simonsen & Matzow 2000; Vetemaa et al. 2006; Johnsen unpublished). In the study by Johnsen (unpublished), rudd was caught in gill-nets at a salinity of 19.5 ppt, and as far out as 6 km from Strømmen. In connection with gill-net fishing for sea trout at 6th July 2011, one rudd was caught almost 13 km from Strømmen. In the study by Johnsen, the amount of rudd in gill-net caches decreased rapidly when salinities exeeded 12 ppt. This seems to be in accordance with the findings in the laboratory experiment, where mortality started to occur at salinity 12. On the other hand, observations of field distribution of rudd may not necessarily reflect its upper salinity tolerance. Other limiting factors may change in accordance with salinity, such as pH, dissolved oxygen, temperature, and availability of habitats and food resources (Kefford et al. 2004; Bringolf et al. 2005).

In addition to having a sufficiently high salinity tolerance, migratory behavior outwards in the fjord system is a necessity in order to be able to spread via brackish water (Bringolf et al. 2005). Rudd from Storelva is observed to enter brackish water, although it is not certain how far out they migrate, or what causes this behavior. Neither is it known how fast rudd migrate through the fjord system, or how long it takes for them to reach the coast. Blaxter (1969, cited in Hammer 1995) made the general assumption that fish can maintain a swimming speed of 2 body lengths/s for up to 200 minutes. If we follow this rule of thumbs, the largest individual used in this experiment would be able to swim 1.73 km/h, and would theoretically be able to reach the coastline within 8.5 hours. Based on this, the 24 hr LC50-values seemed most relevant for this risk assessment. Then again, this is a very theoretical approach, and the migration speed may be considerably slower. More research should be done on the migratory behavior of rudd in this system, including speed of migration and which conditions that trigger the behavior. According to Johnson (unpublished), increasing discharges seem to trigger outwards migration, while increased salinities in the fjord system seem to trigger the return to freshwater. It would be of interest to know whether discharge and salinity also affect the speed of migration. For example, osmotic stress at high salinities may lower the swimming speed of fish (Brauner et al. 1994; McKenzie et al. 2001), while the stronger outwards current at higher discharges might increase the swimming speed. Furthermore it would be interesting to see whether this migratory behavior is dependent on temperature, as the highest discharges, and hence the lowest salinities, seem to occur during fall and winter.

We do not know whether fish from Storelva experience a gradual increase in salinity as they migrate outwards in the fjord system, and if so whether this increases their salinity tolerance. As mentioned, acclimation is generally proved to increase the salinity tolerance in fish (Kilambi & Zdinak 1980; James et al. 2003; Kefford et al. 2004). According to Kroglund et al (2011c), and the continuous salinity measurements during the 2011 field season (Figure 8), the salinity in the fjord system is highly variable with abrupt changes. On the other hand, fish are mobile, and should therefore be able to move away when they encounter salinities above their tolerance threshold. Perhaps rudd can choose to stay in waters with moderate salinities until they are acclimated, and thereby increase their salinity tolerance? In a risk assessment one must consider the possibility that fish may in fact become acclimated on their way out, and hence have a higher salinity tolerance and higher potential for migration. It would be interesting to know more about how rudd move in relation to depths and salinities once they enter brackish water.

The predicted high risk of range expansion of rudd at medium to high discharges was based on simulated salinities derived from the model applied by Tjomsland & Kroglund (2010). These simulations show that even at discharges down to 1.2 m^3/sec, salinities never exceed 17 ppt in the surface of the outer part of the fjord. However, the observed data from the field measurements in 2011 show salinities above 25 ppt at 0,5 m depth 6 km off Strømmen. Discharges during the 2011 field measurements were quite low, and it is likely that the measured salinities would have been lower if there had been more input of freshwater during this period. Still, the simulated period included periods of lower discharge than the 2011 field season. Some of this disparity may be explained by the influence of wind on water currents that partly determines the salinity distribution (Frode Kroglund personal communication, May 2012). In addition, the model simulation does not account for short-term and small-scale changes in salinity, and hence show less temporal and spatial salinity variation (Tjomsland & Kroglund 2010). It is possible that the model based on simulated salinities overrates the risk in this study, and the salinities in the outer part of the fjord should be monitored more closely to get a clearer and more unambiguous picture of the actual field situation. The same goes for salinities along the coast, as this study do not consider the salinities outside the fjord system.

This study suggests that rudd survive best at lower salinities and maybe at higher temperatures. To my knowledge, no studies have been done on the survival of rudd in relation to temperature, but cyprinids in general are favored by increased temperatures (Graham & Harrod 2009). Climate change may therefore create new scenarios regarding the risk of range expansion by brackish water. Most models predict that there will be an increase in temperatures and precipitation in Norway. Moreover, extreme flood events are likely to happen more frequently over the next 30 years (Haugen et al. 2008). In the case of Storelva, this might entail that there at times can be considerable inputs of freshwater to the fjord system which will decrease the salinity in surface water, and expand the brackish surface layer outwards. Bringolf et al (2005) describes a situation in the Neuse River Estuary (North Carolina, USA) where the salinity of the water was 20 ppt in the fall, but declined to 0 ppt in an event of extreme flood. Risk of range expansion via brackish water is not determined by the normal state, but by extreme events such as this (Bringolf et al. 2005). According to Hesthagen & Sandlund (2007), Norwegian waters are likely to become more susceptible to invasions of existing non-native species with climate change. Warmer and wetter winters are likely to increase the invasion potential and establishment success in new waters (Hesthagen & Sandlund 2007).

Rudd has existed in Norway for several thousand years (Huitfeldt-Kaas 1918), yet the recent dramatic range expansion has happened within the last four decades (Mikkelsen 1999; Nilssen 2009; Artsdatabanken 2012). It is hard to prove whether this spreading is due to live bait fishing alone, or if part of the range expansion has happened by migration through brackish water. Genetic studies could show whether or not rudd found in different water systems in Aust-Agder County are from the same source population (Knutsen et al. 2001). If the local populations are genetically different, this suggests that rudd has been repeatedly introduced by anglers, and migration through brackish water is an unlikely explanation. Study of distribution patterns may also be a meaningful approach to assess possible mechanisms for spreading. In any case, the main objective of this study was not to explain the current distribution of rudd, but to assess the probability of further range expansion through brackish water. Even though there is no current evidence that rudd has reached new water systems by this route, this study shows that we cannot rule it out as a possible mechanism for range expansion.

Rudd is an invasive species along the coast of large parts of southern Norway. In this study I have shown that brackish water may be a route for range expansion in the Storelva-Sandnesfjorden system, and similar spreading may be possible in other fjord systems and estuaries as well. The clear results regarding the salinity tolerance of rudd is therefore highly relevant, and can be applied in similar risk models in other systems connected to coastal water. Although many biotic and abiotic factors can differ between localities, and thereby affect the salinity tolerance, the differences in population, exposure to salinity, size of fish and temperature had negligible effect in this study. It is therefore likely that the same tolerance is found in rudd from other Norwegian water systems as well, despite local differences. Consideration of range expansion by this mechanism should be given in future management strategies of rudd.

5. Conclusion

Salinity tolerance of rudd was found under experimental conditions, and this knowledge can be used to predict potential distribution and range expansion of rudd. In the Storelva-Sandesfjord system, rudd may be able to spread by brackish water at medium to high discharges, and this should be considered in future management of rudd. More effort should be made to assess the field salinities in the outer part of the fjord in relation to discharge. It would also be beneficial to get a better understanding of the migratory behavior of rudd in order to predict under which conditions other than salinity range expansion is likely.

The salinity tolerance found in this study can be used to predict distribution of rudd in other water system affected by brackish water, where distribution of salinities is known. However, it should be considered that there may be regional differences in salinity tolerance.

6. References

Andersen, P. K. & Gill, R. D. (1982). Cox's regression model for counting processes: a large sample study. *The Annals of Statistics*, 10 (4): 1100-1120.

Anderson, D. R. (2008). *Model based inference in the life sciences: a primer on evidence*. New York: Springer Science Business Media, LLC. 184 pp.

Artsdatabanken. (2012). *Statistikk for sørv (Scardinius erythropthalmus): antall objekt fordelt på tiår*. http://artskart.artsdatabanken.no/FaneStatistics.aspx (accessed: 30.04.2012).

Barnard, C., Gilbert, F. & McGregor, P. (2007). *Asking questions in biology. A guide to hypothesis-testing, experimental design and presentation in practical work and research projects*. 3 ed. Essex, England: Pearson. 243 pp.

Berger, H. M. (2010). Sørv og sjøørret i Kigevannet i Mandal kommune.Tilstandsvurdering og forslag til tiltak 2010: Landbruksforvaltningen Mandal - Lindesnes IS. 29 pp.

Blackwell, B. G., Kaufman, T. M. & Miller, W. H. (2009). Occurrence of rudd (*Scardinius erythrophthalmus*) and dynamics of three populations in South Dakota. *Journal of Freshwater Ecology*, 24 (2): 285-291.

Borgstrøm, R. (2000). Ferskvannsfisk - en viktig ressurs i fortid og nåtid. In Borgstrøm, R. & Hansen, L. P. (eds) *Fisk i ferskvann: et samspill mellom bestander, miljø og forvaltning*, pp. 11 - 20. [Oslo]: Landbruksforlaget.

Brauner, C. J., Iwama, G. K. & Randall, D. J. (1994). The effect of short-duration seawater exposure on the swimming performance of wild and hatchery-reared juvenile coho salmon (*Oncorhynchus kisutch*) during smoltification. *Canadian Journal of Fisheries and Aquatic Sciences*, 51 (10): 2188-2194.

Bringolf, R. B., Kwak, T. J., Cope, W. G. & Larimore, M. S. (2005). Salinity tolerance of flathead catfish: implications for dispersal of introduced populations. *Transactions of the American Fisheries Society*, 134 (4): 927-936.

Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. 2 ed. New York: Springer. 488 pp.

Cohen, A. N. & Carlton, J. T. (1998). Accelerating invasion rate in a highly invaded estuary. *Science*, 279 (5350): 555-558.

Cressie, N. A. C. (1993). *Statistics for spatial data*. 2 ed. New York: Wiley.

Dunlop, J., McGregor, G. & Horrigan, N. (2006). Potential impacts of salinity and turbidity in riverine ecosystems : characterisation of impacts and a discussion of regional target setting for riverine ecosystems in Queensland. Brisbane: Queensland Department of Natural Resources and Water. 64 pp.

García-Berthou, E., Alcaraz, C., Pou-Rovira, Q., Zamora, L., Coenders, G. & Feo, C. (2005). Introduction pathways and establishment rates of invasive aquatic species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, 62 (2): 453-463.

Gederaas, L., Salvesen, I. & Viken, Å. (eds). (2007). *Norsk svarteliste 2007: økologiske risikovurderinger av fremmede arter*. Trondheim: Artsdatabanken. 152 pp.

Graham, C. T. & Harrod, C. (2009). Implications of climate change for the fishes of the British Isles. *Journal of Fish Biology*, 74: 1143 - 1205.

Grambsch, P. M. & Therneau, T. M. (1994). Proportional hazards tests and diagnostics based on weighted residuals. *Biometrika*, 81 (3): 515 - 526.

Gu, C. & Wahba, G. (1991). Minimizing GCV/GML scores with multiple smoothing parameters via the Newton method. *SIAM Journal on Scientific Computing*, 12 (2): 383 - 398.

Hammer, C. (1995). Fatigue and exercise tests with fish. *Comparative Biochemistry and Physiology Part A: Physiology*, 112 (1): 1-20.

Haugen, J. E., Køltzow, M. & Iversen, T. (2008). Mer ekstrem nedbør og vind i Norge. *Klima - Norsk magasin for klimaforskning*, 2008 (2): 36 - 38.

Hesthagen, T. & Østborg, G. (2002). Kartlegging av innsjøer med naturlige fiskesamfunn og fisketomme lokaliteter på Sørlandet, Vestlandet og i Trøndelag. Trondheim: Norsk Institutt for Naturforskning, Opprdagsmelding 724. 48 pp.

Hesthagen, T. & Sandlund, O. T. (2007). Non-native freshwater fishes in Norway: history, consequences and perspectives. *Journal of Fish Biology*, 71: 173-183.

Hicks, B. J. (2003). Biology and potential impacts of rudd (Scardinius erythrophthalmus L.) in New Zealand. In Munro, R. (ed.) *Managing invasive freshwater fish in New Zealand. Proceedings of a workshop hosted by Department of Conservation. May 10-12, 2001*, pp. 49 - 58. Hamilton, New Zealand: Department of Conservation.

Huitfeldt-Kaas, H. (1918). *Ferskvandsfiskenes utbredelse og indvandring i Norge: med et tillæg om krebsen*. Kristiania: Centraltrykkeriet. 106 pp.

Hynes, H. B. N. (1970). *The ecology of running waters*. Liverpool: Liverpool University Press. 555 pp.

James, K. R., Cant, B. & Ryan, T. (2003). Responses of freshwater biota to rising salinity levels and implications for saline water management: a review. *Australian Journal of Botany*, 51 (6): 703-713.

Johnsen, S. E. (unpublished). *Estuarievandring hos sørv (Scardinius erythropthalmus) i Storelvavassdraget - effekter på vekst og overlevelse*: Department of Ecology and Natural Resource Management, University of Life Sciences, Norway. Unpublished manuscript.

Johnsen, T. M., Sandlund, O. T., Often, A., Jelmert, A. & Hobæk, A. (2010). Kartlegging og overvåkning av fremmede skadelige arter i Norge: Norsk Institutt for Vannforskning, LNR 5969. 57 pp.

Kefford, B. J., Papas, P. J., Metzeling, L. & Nugegoda, D. (2004). Do laboratory salinity tolerances of freshwater animals correspond with their field salinity? *Environmental Pollution*, 129 (3): 355-362.

Kennedy, M. & Fitzmaurice, P. (1974). Biology of the rudd (*Scardinius erythrophthalmus* L.) in Irish waters. *Proceedings of the Royal Irish Academy*, 74 (section B): 245-303.

Kilambi, R. V. & Zdinak, A. (1980). The effects of acclimation on the salinity tolerance of grass carp, *Ctenopharyngodon idella* (Cuv. and Val.). *Journal of Fish Biology*, 16 (2): 171-175.

Knutsen, H., Knutsen, J. A. & Jorde, P. E. (2001). Genetic evidence for mixed origin of recolonized sea trout populations. *Heredity*, 87 (2): 207-214.

Kroglund, F., Haraldstad, T., Teien, H. C., Guttrup, J. & Johansen, Å. (2011a). Mobilisering av aluminium i brakkvann og akkumulering på fiskegjeller; Storelva datarapport brakkvann.: Norsk Institutt for Vannforskning, LNR 6149. 29 pp.

Kroglund, F., Høgberget, R., Haraldstad, T., Teien, H. C., Rosseland, B. O., Salbu, B., Nilsen, T. O., Stefansson, S., Guttrup, J. & Johansen, Å. (2011b). Påvirkes smoltvandring av aluminium i brakkvann? Storelva 2008: Norsk Institutt for Vannforskning, LNR 6246. 69 pp.

Kroglund, F., Teien, H. C., Rosten, C., Hawley, K., Guttrup, J., Johansen, Å., Høgberget, R., Kristensen, T., Tjomsland, T. & Haugen, T. (2011c). Betydningen av kraftverk og predasjon fra gjedde for smoltproduksjon og aluminium i brakkvann for postsmoltoverlevelse: Norsk Institutt for Vannforskning, LNR 6084. 103 pp.

Lodge, D. M. (1993). Biological invasions: lessons for ecology. *Trends in Ecology & Evolution*, 8 (4): 133-137.

Luz, R. K., Martínez-Álvarez, R. M., De Pedro, N. & Delgado, M. J. (2008). Growth, food intake regulation and metabolic adaptations in goldfish (*Carassius auratus*) exposed to different salinities. *Aquaculture*, 276 (1–4): 171-178.

Mann, R. H. K. (1991). Growth and production. In Winfield, I. J. & Nelson, J. S. (eds) *Cyprinid Fishes. Systmeatics, biology and exploitation*, pp. 456 - 482. London: Chapman & Hall.

Matern, S. A. (2001). Using temperature and salinity tolerances to predict the success of the shimofuri goby, a recent invader into California. *Transactions of the American Fisheries Society*, 130 (4): 592-599.

McKenzie, D. J., Cataldi, E., Romano, P., Taylor, E. W., Cataudella, S. & Bronzi, P. (2001). Effects of acclimation to brackish water on tolerance of salinity challenge by young-of-the-year Adriatic sturgeon (Acipenser naccarii). *Canadian Journal of Fisheries and Aquatic Sciences*, 58 (6): 1113-1121.

Mikkelsen, K. O. (1999). Kartlegging av introduserte ferskvannsfisk i Ryfylke og Nord-Rogaland 1999: Rådgivende Biolog, Rapport nr 2-1999. 22 pp.

Mills, E. L., Leach, J. H., Carlton, J. T. & Secor, C. L. (1993). Exotic Species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research*, 19 (1): 1-54.

Mills, E. L., Leach, J. H., Carlton, J. T. & Secor, C. L. (1994). Exotic species and the integrity of the Great Lakes. *BioScience*, 44 (10): 666-676.

Moyle, P. B. & Light, T. (1996). Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation*, 78 (1–2): 149-161.

Nilssen, J. P. (2009). Vedvarende menneskeindusert spredning av bredspektret ferskvannsfisk til og internt i Norge: et holarktisk, økologisk perspektiv. Drøbak: Müller-Sars Selskapet, Rapport nr. 10-2009. 78 pp.

Paavola, M., Olenin, S. & Leppäkoski, E. (2005). Are invasive species most successful in habitats of low native species richness across European brackish water seas? *Estuarine, Coastal and Shelf Science*, 64 (4): 738-750.

Pethon, P. (2005). *Aschehougs store fiskebok*. 5. ed. Aurskog: Aschehoug. 468 pp.

R Development Core Team. (2010). R: a language and environment for statistical computing, eds 2.10.1. In *R Foundation for Statistical Computing*. Vienna, Austria.

Ricciardi, A. & Rasmussen, J. B. (1998). Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Canadian Journal of Fisheries and Aquatic Sciences*, 55 (7): 1759-1765.

Ricciardi, I. & MacIsaac, H. J. (2000). Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology & Evolution*, 15 (2): 62-65.

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., et al. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287 (5459): 1770 - 1774.

Sandodden, R. & Johnsen, S. I. (2008). Bekjempelse av signalkreps (*Pasifastacus leniusculus*) og sørv (*Scardinius erythrophthalmus*) i Dammane landskapsvernområde. *Veterinærinstituttets rapportserie 15-2008*. Oslo: Veterinærinstituttet. 34 pp.

Simonsen, J. H. & Matzow, D. (2000). Regnlaue *Leucaspius delineatus* - ny fiskeart i Norge. *Fauna*, 53 (3): 151 - 153.

Tjomsland, T. & Kroglund, F. (2010). Modellering av strøm og saltholdighet i Sandnesfjorden ved Risør: Norsk Institutt for Vannforskning, LNR 6049. 31 pp.

Vetemaa, M., Eschbaum, R., Verliin, A., Albert, A., Eero, M., Lillemägi, R., Pihlak, M. & Saat, T. (2006). Annual and seasonal dynamics of fish in the brackish-water Matsalu Bay, Estonia. *Ecology of freshwater fish* (15): 211 - 220.

Welch, B. L. (1951). On the comparison of several mean values: an alternative approach. *Biometrika*, 38: 330 - 336.

Williams, M. & Williams, W. (1991). Salinity tolerances of four species of fish from the Murray-Darling River system. *Hydrobiologia*, 210 (1): 145-150.

Winfield, I., Fletcher, J. & James, J. (2011). Invasive fish species in the largest lakes of Scotland, Northern Ireland, Wales and England: the collective UK experience. *Hydrobiologia*, 660 (1): 93-103.

Wood, S. N. (2003). Thin plate regression splines. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 65 (1): 95 -114.

Økland, J. & Økland, K. A. (2006). *Vann og vassdrag 3. Kjemi, fysikk og miljø*. 2d ed. Stabekk: Vett & viten. 201 pp.

Appendices

Appendix I: Box-plot of differences in size between the two populations

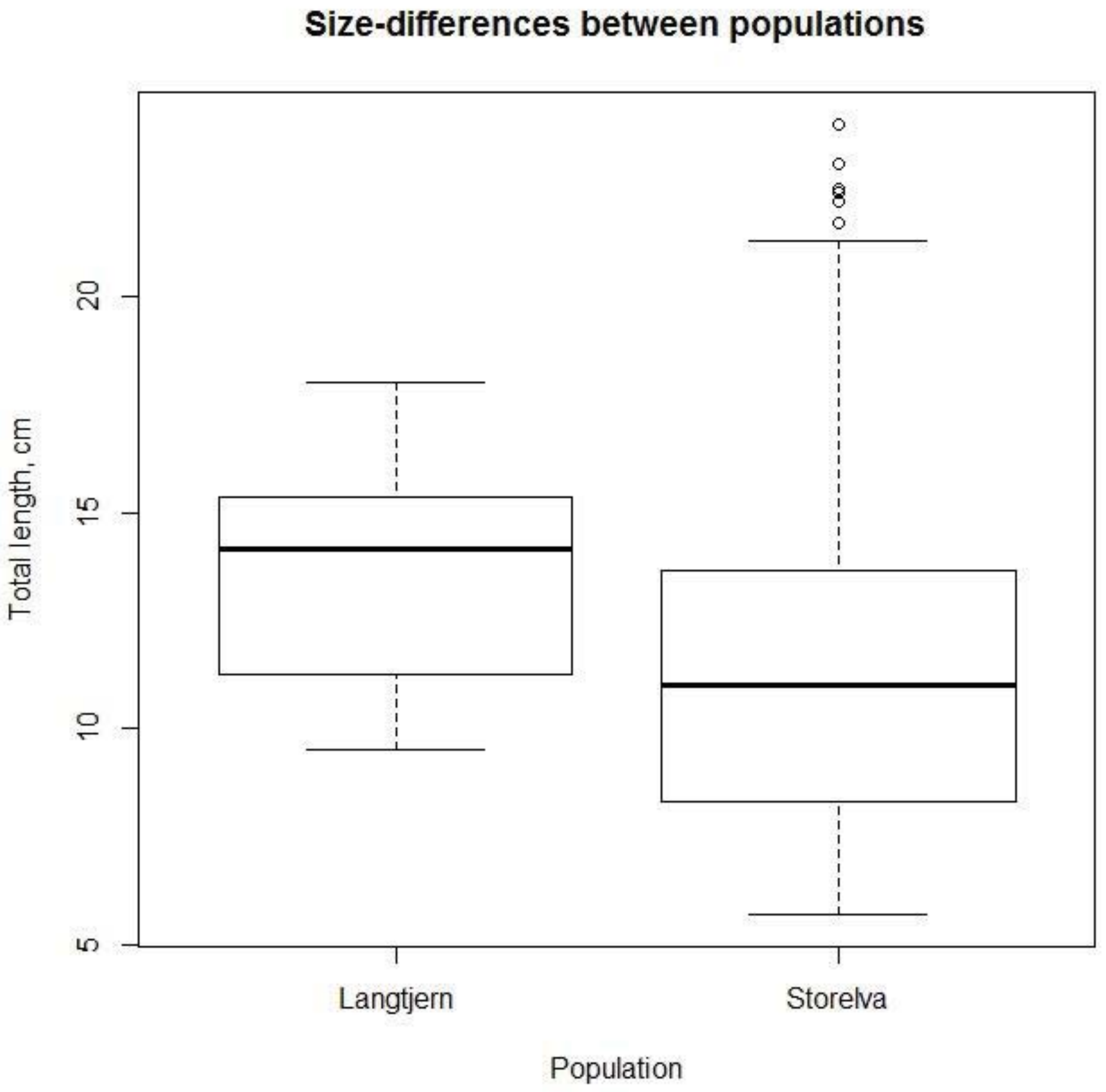


Figure 20: differences in size between the two populations. Significant difference found using Welch ANOVA (p = 0.0002)

Appendix II: Box-plot of differences in age between the two populations

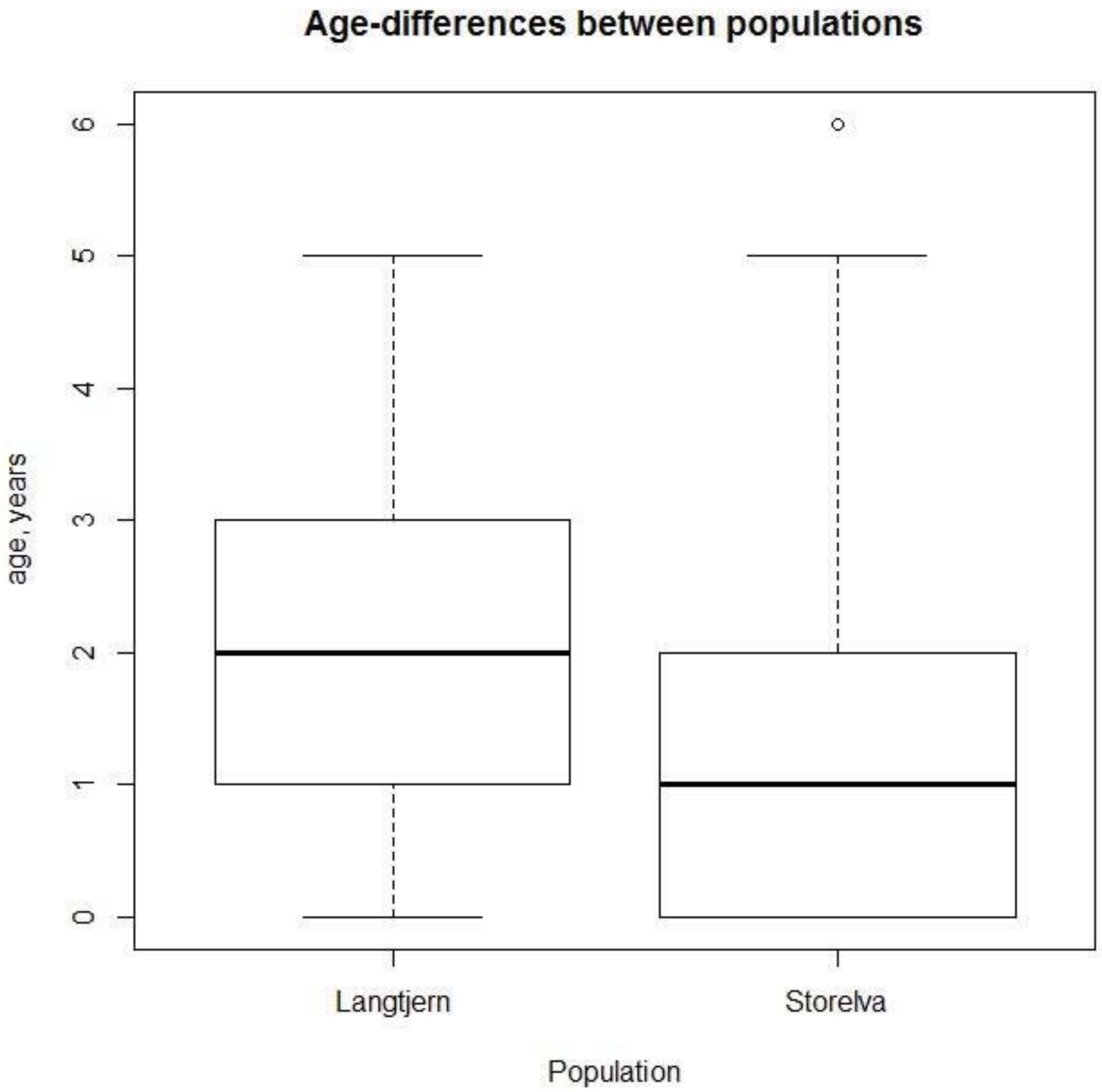


Figure 21: Differences in size between the two populations. Significant difference found using Welch ANOVA (p = 2.976e-05).

Appendix III: Box-plot of size-distribution between the two rounds of experiment

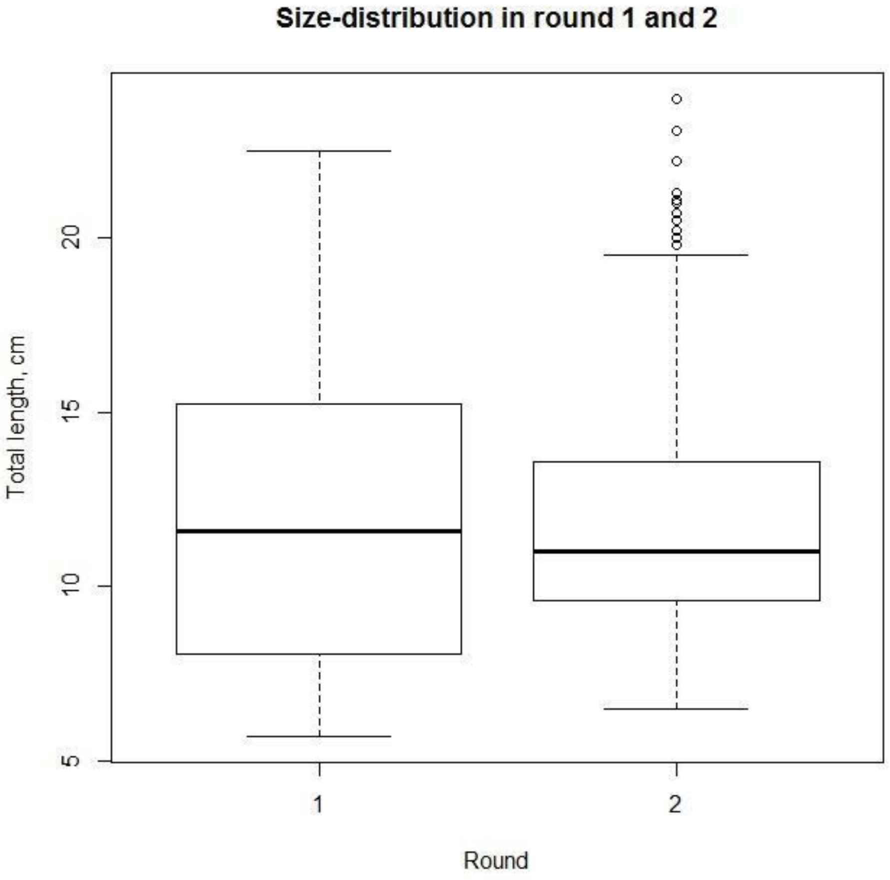


Figure 22: Size-distribution in round one and two. No difference found using ANOVA (p = 0.99)

Appendix IV: Box plot of size-distribution between salinity treatments

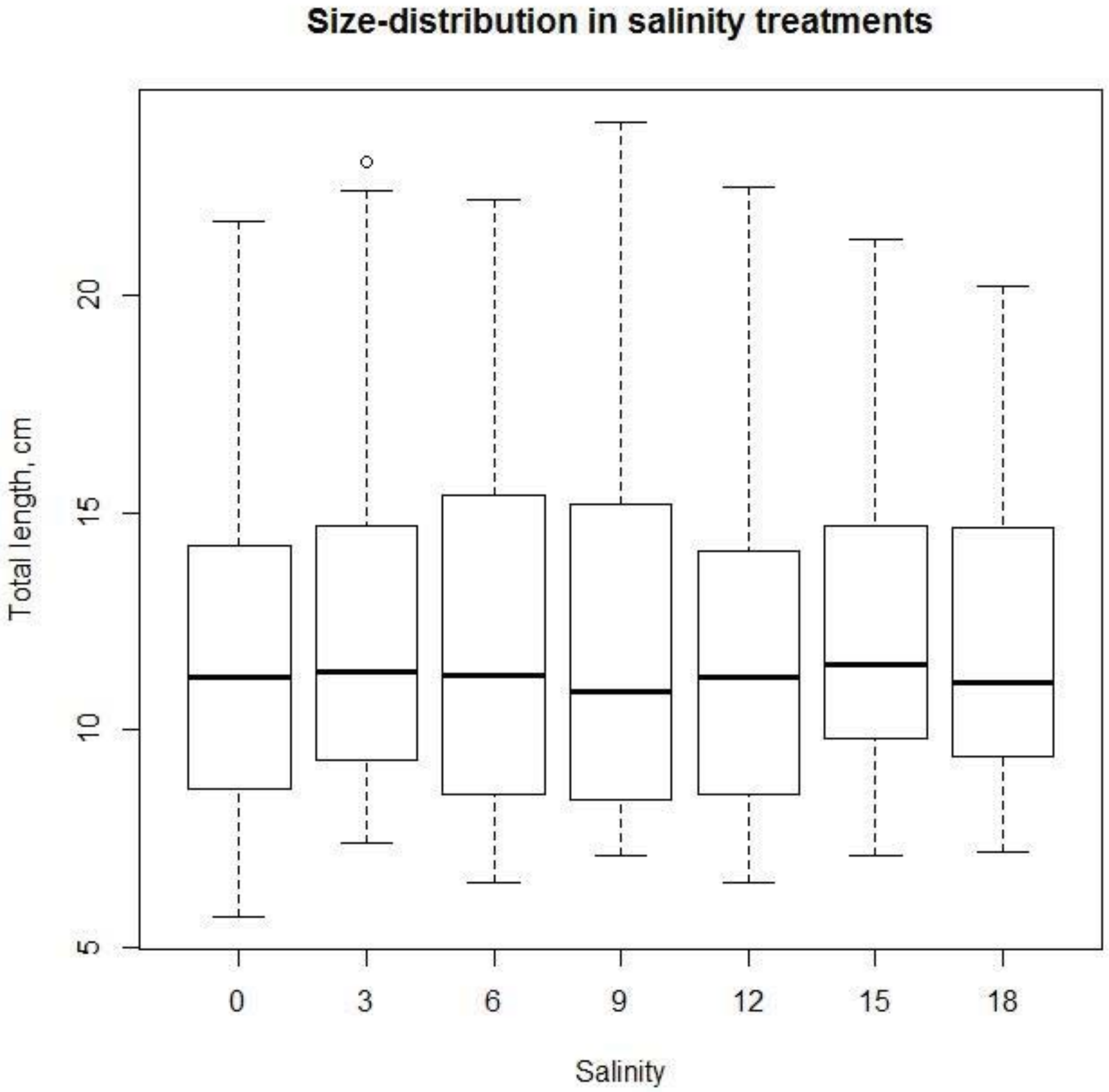


Figure 23: Size-distribution between salinity treatments. No difference found using ANOVA (p = 0.99).

Appendix V: Current distribution of rudd in southern Norway

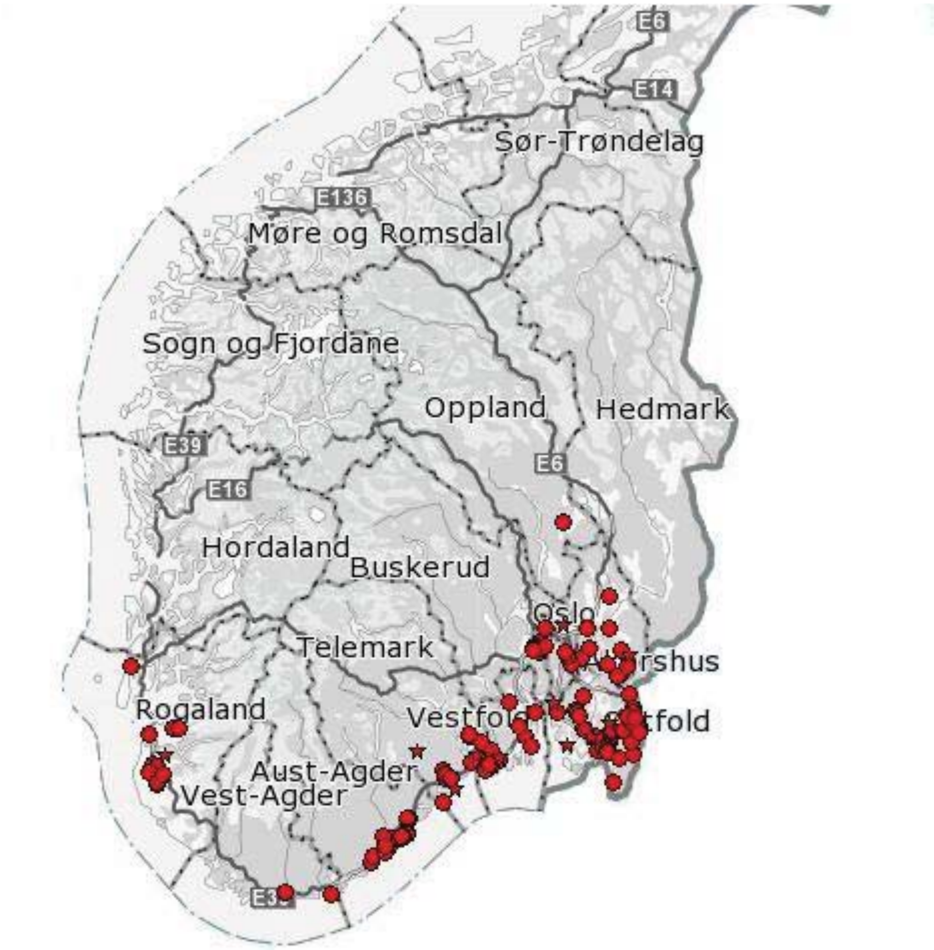


Figure 24: Current range distribution of rudd in southern Norway (Artsdatabanken 2012).