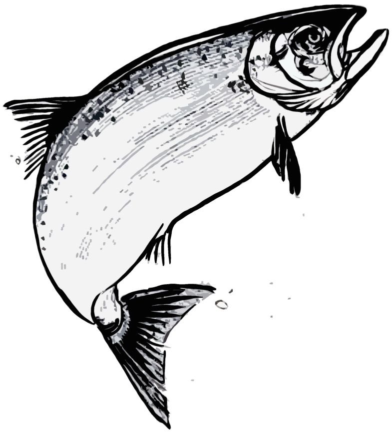
UNIVERSITY OF TROMSØ UIT

FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

# Staying Alive -

## The survival and importance of Atlantic salmon post-spawners



## Elina Halttunen

A dissertation for the degree of Philosophiae Doctor

Spring 2011

To Pauli and Olavi,

two truly curious naturalists

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## Summary

Atlantic salmon (*Salmo salar* L.) repeat-spawners might play an important role in population persistence by increasing both total recruitment and long-term stability of a population. This is because repeat spawners return at larger sizes and with greater fecundity than first time spawners, and the large majority of repeat-spawners are females. Nevertheless, little knowledge exists of this potentially significant population sub-unit.

We conducted a four-year field study in the River Alta, Northern Norway, using acoustic and radio telemetry combined with scale sample analysis and mark recapture, with the aim of 1) assessing the survival and migration patterns after spawning, 2) assessing the post and repeat-spawner mortality in the fisheries, and 3) quantifying the returning rate of post spawning females. These results were further used in combination with historical catch-records from both sea and in-river fisheries to 4) model the repeat spawning rate in the female population and the significance of repeat spawning for egg production during fluctuating maiden runs.

We found that 1) survival after spawning and early marine migration was high (63-80% and 96%, respectively), and that the post-spawners (kelts) in best condition waited longest in the river before migrating. 2) The fisheries mortality was low (4%) when exiting the river and fjord, and moderate (11 %) when re-entering the fjord and river upon return. 3) Female survival until spawning was on average 32 %, and 4) according to model simulations, on average 20% of the female population consisted of repeat-spawners, which might have an important stabilizing function reducing fluctuations in a population by contributing an average of 27% (2%-59%) of all the eggs spawned in the river.

We conclude that the post-spawners have high survival both in the river and the sea despite their weakened condition after spawning and overwintering in the river, and that repeat-spawners might contribute significantly to Atlantic salmon production. Their numeric and genetic contribution might be especially important during declining and fluctuating populations as a buffer against poor maiden recruitment years. Therefore post- and repeat-spawners are worthy of special conservational attention and management measures.

## List of original papers

The thesis is based on the following original papers, which are referred to in the text by their Roman numerals:

I. Halttunen, E., Rikardsen A.H., Davidsen, J.G., Thorstad, E.B. and Dempson, J.B. 2009. Survival, migration speed and swimming depth of Atlantic salmon kelts during sea entry and fjord migration. *In* Tagging and tracking of Marine Animals with Electronic Devices. *Edited by* J.L. Nielsen, H. Arrizabalaga, N. Fragoso, A. Hobday, M. Lutcavage and J. Sibert. Tagging and tracking of Marine Animals with Electronic Devices, Reviews: Methods and Technologies in Fish Biology and Fisheries 9. Dordrecht: Springer. pp 35-49.

II. Halttunen, E., Rikardsen, A.H., Thorstad, E.B., Næsje, T.F., Jensen, J.L.A., and Aas, Ø. (2010). Impact of catch-and-release practices on behaviour and mortality of Atlantic salmon (*Salmo salar* L.) kelts. Fish. Res. **105**: 141–147.

III. Halttunen, E., Jensen, J.L.A., Davidsen, J.G., Næsje, T.F., Thorstad, E.B., Chittenden, C.M., Primicerio, R., and Rikardsen, A.H**.** State-dependent migratory behaviour of post-spawned Atlantic salmon (*Salmo salar*) (manuscript).

IV. Halttunen, E., Rikardsen, A.H., Ugedal, O., Jensen, J.L.A., Thorstad, E.B., and Næsje, T.F. The significance of repeat spawning for the production of Atlantic salmon (*Salmo salar*) (manuscript).

# 1. Introduction

### *What is this study about?*

The Atlantic salmon (*Salmo salar* L.) is a fish species native to watersheds in the temperate and subarctic regions of the North Atlantic Ocean (Thorstad et al. 2011). It is an iconographic species with vast historic, economic and socio-cultural significance, and therefore also one of the most researched fish species in the world. One of the many fascinating characteristics of the Atlantic salmon is that it displays considerable phenotypic plasticity[1] and variability in life history characteristics (Thorstad et al. 2011, Fig 1). This PhD thesis is dedicated to studying a certain, relatively little researched life stage of Atlantic salmon – the post spawning stage (Fig 1, boxes and arrows marked in red). The overall aim of the study has been to *study the migration patterns* and *identify hotspots of mortality of post-spawners* and to *quantify the significance of repeat spawning* to the salmon population of River Alta, Northern Norway, in order to assess management and conservation issues.

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[1] The ability of an organism to change its **phenotype**[2] in response to changes in the environment.

[2] A **phenotype** is any *observable characteristic* or trait of an organism: such as its morphology, development, biochemical or physiological properties, behaviour, and products of behaviour (such as a salmon's nest). Phenotypes result from the expression of an organism's genes as well as the influence of environmental factors and the interactions between the two.

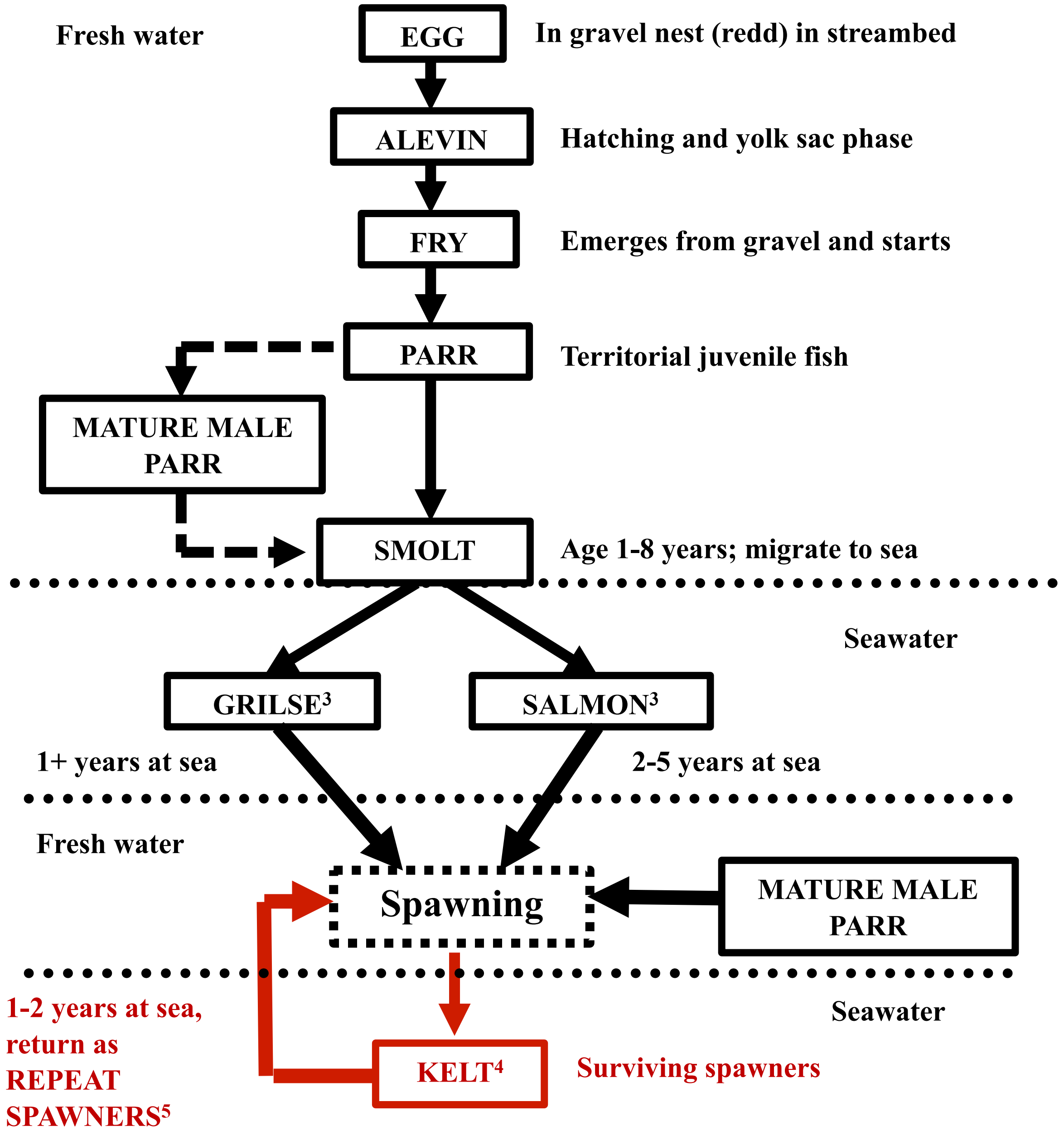


Fig. 1. Altantic salmon anadromous life cycle, the post spawning stage is marked with red (modified from Jobling et al. (2010), Fig. 12.8).

[3] Salmon spawning the first time: Maiden salmon. Synonyms: virgin salmon.

[4] Kelt: an anadromous salmon that has completed spawning but has not yet returned to the sea. Synonyms: post-spawner, black salmon, mended salmon.

[5] Repeat-spawner: a kelt becomes a repeat-spawner upon return. Synonyms: previous spawner, multiple spawner.

### *Background for the study*

One of the most fascinating features of Atlantic salmon life history is its migrations between the fresh water and marine environment. This type of migration pattern is called diadromy (Lucas and Baras 2001) and is found in only 1% of all the 27 977 known fish species (Helfman et al. 2009). Diadromy can be divided into anadromy, in which adult fish migrate from the sea to spawn in fresh water, catadromy, in which adult fish migrate from fresh water to spawn in the sea, and amphidromy, where fish migrate between fresh water and the sea (in both directions), but not for the purpose of breeding (McDowall 1987, 1997). Most Atlantic salmon populations are anadromous (Fig 1), although some populations complete their life cycle in fresh water (Thorstad et al. 2011). A diadromous life history will evolve through natural selection only when the migrations provide a gain to individual fitness (lifetime reproductive success) that exceeds the costs (Gross, 1987, 1988). In the case of Atlantic salmon the gains are better feeding conditions at sea compared to fresh water, resulting in better growth and a larger size (Rikardsen and Dempson 2011), and therefore higher fecundity upon return to the river. The costs include the energy invested in swimming considerable distances and an increased mortality risk owing to predation and diseases during migration (Gross et al. 1988; Jonsson and Jonsson 1993). From a management and conservation point of view these migrations present a significant challenge; the salmon moves across large areas without any respect for different jurisdictions and experiences a multitude of environments along its path.

Another captivating feature of salmon is their ability to home (i.e. to return to their natal river to spawn, see Quinn 1993), a behaviour responsible for the development of river-specific populations that differ both ecologically and genetically (Ståhl 1981, 1983; Hindar et al. 1991; Klemetsen et al. 2003; Verspoor et al. 2005). Not only do the salmon home with high precision to their natal *river* but also to the *part* of the river where they hatched, as ecological and genetic differences among subpopulations within rivers are also documented (Verspoor et al. 2007). The ability to home forms and maintains local adaptations and allows for variation in life history strategies to develop in different rivers (Schaffer and Elson 1975, Taylor 1991, Verspoor et al. 2005), and may be crucial for the buffering capacity of the population in changing environmental conditions (Schindler et al. 2010).

One of the most important life-history choices for Atlantic salmon individuals is deciding when to spawn and how many times to spawn (see Box 1). Atlantic salmon have been documented to spawn up to six (Ducharme, 1969) or even seven times (ICES, 2004) during a life time. However, post spawning mortality is generally considered high and most individuals spawn only once or twice (Jonsson et al. 1991a, Heggberget 1989; Shearer 1992, Klemetsen et al. 2003). Atlantic salmon typically enter coastal home waters and rivers from the sea several months prior to spawning, and the timing of the run (return spawning migration into the river) is highly variable both within and among populations (Klemetsen et al. 2003). During the homing and upstream migration periods, Atlantic salmon do not usually feed (Johansen et al. 2011), and energy reserves are used to fuel body maintenance, gonad growth, and migration. The total energy loss due to migration and spawning may amount to more than 60% of the body reserves present prior to upstream migration (Jonsson et al. 1997). The energy loss explains why many salmon die shortly after spawning. However, a part of the population might survive the spawning event, and these survivors, commonly called ‘kelts’, migrate to sea either shortly after spawning, or during the following spring or early summer (Jonsson et al. 1990). This sea feeding migration of kelts to replenish energy levels necessary for additional spawning migrations is a key component to the repeat spawning strategy of Atlantic salmon.

Even though Atlantic salmon can survive spawning and spawn several times, little is known about survival after spawning and the repeat spawning rate (Anon. 2009, Thorstad et al. 2011). It almost seems like the Atlantic salmon management and research community has treated return spawners as an oddity, not worth serious attention. Kelts are often ignored in management plans, for instance when constructing bypasses to hydropower plants or implementing fishing regulations (Wertheimer and Evans 2005). Perhaps of equal concern is that repeat-spawners are usually not accounted for when estimating recruitment to spawning stocks (Hindar et al. 2011). This neglect of the post spawning stage of salmon is surprising, as repeat-spawners usually have a much larger body size than first time spawners, and large salmon are also considered valuable both for commercial and recreational fisheries. From the manager's point of view, repeat-spawners contribute with increased recruitment and might add stability to the population. This is because repeat-spawners can contribute proportionately more to the production of a new generation than their numbers would indicate due to their larger size that leads to higher fecundity (Niemelä et al. 2006). In addition, the large majority of repeat-spawners are females (Mills 1989; Erkinaro et al. 1997; Niemelä et al. 2000, Shearer 1992), which are usually the limiting factor for production. Therefore, repeat-spawners can be especially important to Atlantic salmon populations at times when survival to first spawning (recruitment) is low (Niemelä et al. 2006).

In consequence, even though typically less than 10% of Atlantic salmon are believed to return to breed again (Fleming and Reynolds 2004), the role of repeat-spawners might be increasingly important as Atlantic salmon populations are in decline through most of their native distribution range (Hansen et al. 2008, ICES 2008, Anon 2010 ). The reasons for the declines are believed to include many anthropogenic factors working in concert, in addition to reduced survival and growth at sea (ICES 2008, Anon 2010, Jensen et al. 2011). Anthropogenic factors include a range of impacts, such as freshwater habitat degradation in the form of hydropower development, physical impacts from land use and pollution, overexploitation (both at sea and in rivers), transfer of parasites and diseases both in the river and the sea, and genetic and ecological impacts from escaped farmed salmon. To mitigate the observed decline, a wide range of mitigating and compensating measures have been applied, such as stocking, liming, eradicating parasites, reducing salmon fisheries, and restoring river habitats. Nevertheless, the populations have not recovered, and many are in a dire state (Anon 2009, Hindar et al. 2011). The complex and highly worrying situation for Atlantic salmon brings us back to repeat-spawners, as they might not be as susceptible as first time migrants to variability in the marine environment, for instance due to different dietary requirements (Rikardsen and Dempson 2011). Therefore, repeat-spawners might be important in mitigating the effects of variation in post-smolt marine survival. Indeed, there are indications that repeat-spawners might be increasing in numbers and in importance (Chaput et al. 2001, Dempson and O'Connell 2004, Anon 2010).

Box 1. Theoretical background for the study; life history theory

Life history theory posits that the schedule and duration of key events in an organism's lifetime are shaped by natural selection to produce the largest possible number of surviving offspring. Life history characteristics are traits and can be imagined as various investments in growth, reproduction, and survival. A fundamental assumption of life-history theory is that there is a continuous trade-off between these traits (Roff 1992, Stearns 1992).

An example of a trade-off is the choice between reproducing once (semelparity) or several times (iteroparity). For iteroparous reproduction to prevail, the current investment in relation to the predicted future investments ought to be low. Such a reproductive scheme is found under conditions of high P/Y (where P is parental survival rate and Y is juvenile survival rate). In other words, iteroparous species have low adult mortality relative to juvenile mortality and therefore spread the risk of reproduction both temporally and spatially, whereas semelparous species have high expected adult mortality, making it more economical to put all reproductive effort into the first and final reproductive episode. Fishes in the subfamily Salmoninae exhibit both iteroparity (*Salmo, Salvelinus*) and semelparity (most species of Pacific salmon *Oncorhynchus;* the two exceptions are the more ancestral species, Steelhead *Oncorhynchus mykiss* and Cutthroat trout *Oncorhynchus clarki*). Semelparity is believed to have evolved from iteroparity, and once a semelparous strategy has evolved there seems to be no going back to iteroparity (see Crespi and Teo 2002).

In summary, repeat spawning might be important in maintaining the Atlantic salmon populations, but little knowledge exists of this particular life-stage. There are considerable knowledge gaps regarding the post spawning survival, migration patterns in and out of the river, and mortality hot spots. In addition, there is little information available on the variation in life-history strategies of repeat-spawners, their weight gain during sea-migration, their life-time reproductive success, and most importantly, there are few quantified estimates on the contribution of repeat-spawners to stock recruitment and stability. More knowledge on all the issues mentioned above could be important in order to mitigate the negative trend observed in the recruitment and production of Atlantic salmon. Consequently, this thesis aims to answer the following questions given below and in Fig. 2:

1) How many salmon survive spawning and overwintering in the river? (**paper III**)
2) Who survives the spawning and overwintering in the river? (**paper III**)
3) What steers the kelt out-migration? (**paper III**)
4) What is the mortality of kelts during the out-migration? (**paper I and II** )
5) What are the maturation schedules of repeat-spawners?(**paper IV**)
6) How large is the repeat-spawner weight gain at sea? (**paper IV**)
7) How many repeat-spawners return from the sea? (**paper IV**)
8) What is the repeat-spawner fisheries mortality during in-migration? (**paper IV**)
9) How much do repeat-spawners contribute to the production of eggs in the river? (**paper IV**)

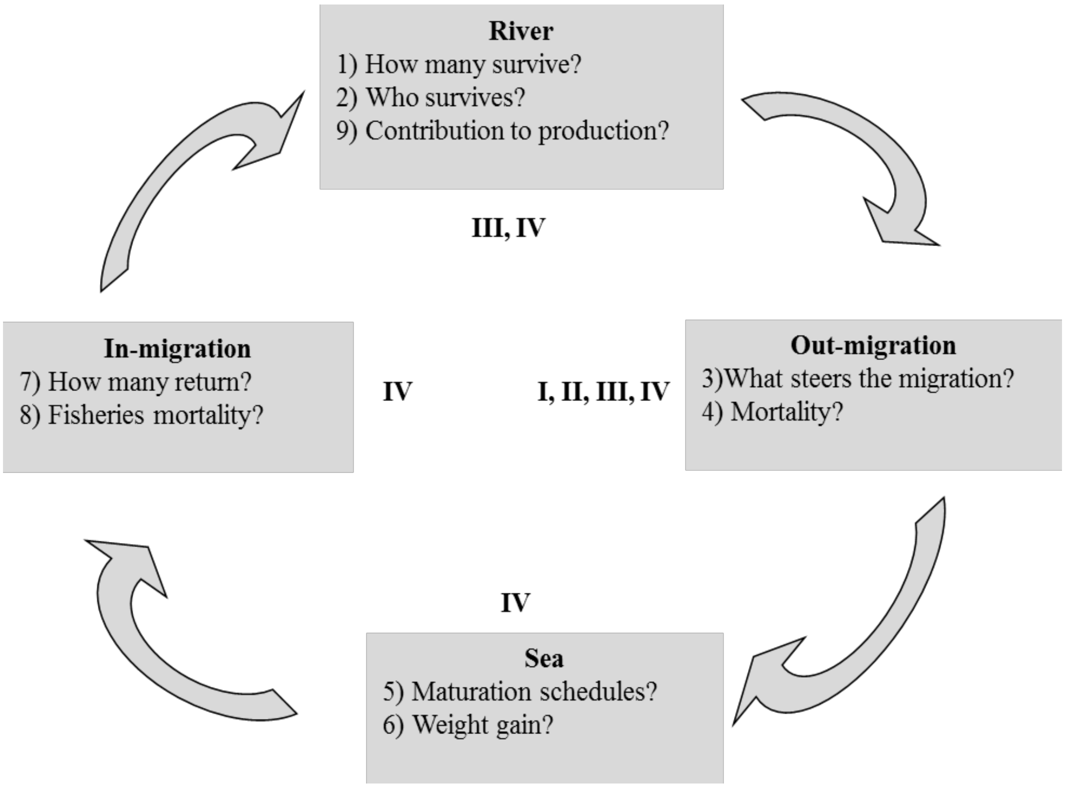


Fig. 2. Research objectives of the thesis. The Roman numerals refer to the original papers included in the thesis.

# 2. Material and methods

## 2.1. Study area

All the studies included in this thesis were conducted in the years 2007-2010 in the sub-Arctic River Alta (70°N 23°E) , which is one of the most productive Atlantic salmon rivers in the world, relative to its size (Eikeset et al. 2001, Anon 2010, Hindar et al. 2011). The River Alta is especially renowned for the size of its salmon, and is therefore one of the top sports fishing destinations in the world. The River Alta has registered in-river catches between 6 and 32 tonnes (records from 1974 to 2008, Halttunen et al. 2009), and additional 4-45 tonnes are caught in the commercial fisheries in the fjord before the salmon reach the river (Halttunen et al. unpublished data). Despite the heavy harvest, the population is considered sustainable (Anon 2009). The healthiness of the population is often attributed to the strong management regime in the river, driven by the local river-owners (Alta laksefiskeri interessentskap; ALI). There is a good reason for strong management, as the bustling angling based business is economically important for the community. The locals love their river vehemently and the European aristocracy and the international plutocracy are known to frequent the river. A disputed hydro-power dam was built in the upper reaches in 1986 above the stretch accessible for anadromous fish. For maps, details on geography, hydrography and demographics see papers (**I-IV**).

The River Alta is an ideal study site, as it is a simple and a relatively short system (46 km up to the dam) with only one tributary (River Eiby). The river is well studied (long time series of diverse data due to hydro-power funded research), the local managers have a good system for collecting catch statistics from the anglers since 1974, and both the managers and the locals are in general well-disposed to co-operation with researchers.

## 2.2. Methodological approach

All the studies included in the thesis are empirical, observational and conducted entirely in the field over a 4-year period. All the studies are based on telemetry methods that allow following the movements of tagged individual fish without the need of recapture. Movements of tagged individuals can be recorded by following signals from the attached transmitters using a portable receiver, or by installing fixed automatic listening stations that record tagged fish within the range of the station. The two telemetry methods used to study survival and behaviour in this thesis were: 1) acoustic telemetry (**papers I- IV**) and 2) radio telemetry (**paper III**). In addition we used mark-recapture methods to assess exploitation rates in the fisheries (**papers I and II**) and scale analysis to assess wild origin and life history parameters (e.g. age, repeat spawning) (**papers II – IV,** see Fig. 3).

### 2.2.1. Telemetry methods

The main benefits of telemetry are that it is a reliable method for quantitative estimates on behaviour, and that it enables observing fish *in situ*. Telemetry eliminates the issues associated with holding fish in captivity (crowding, water quality, abrasion, lack of predators, stress due to an unfamiliar environment, limited movement behaviour, reviewed by Donaldson et al. 2008), which often confound the results of behavioural and mortality studies. Therefore, the field-based approach makes the observational results more realistic and representative.

Using telemetry in a river on an economically-important fish species with a predictable migration pattern entailed several advantages; for example, there was no uncontrolled emigration from the study area (all fish had to pass the arrays when exiting the river), there was a reliable way to determine the viability of a fish (registrations at the arrays in the fjord when exiting or entering and registrations of movement within river), the harvesting was controlled and well-documented by local managers, and finally, reference groups could be established by tagging fish at different life-stages (**paper II**).

A major drawback in telemetry studies is the cost of the tags and the infrastructure. In addition, it may be difficult and expensive to catch a large number of fish for tagging, and the tracking effort may be challenging and time-consuming when following a large number of individuals. This often results in small sample sizes, which further results in poor power of analysis and therefore insecurity in drawing inferences.

Furthermore, it is important to use transmitters and catching, handling and tagging methods with minimal impacts on the fish. This is important not only to conform to international ethical requirements, but also to minimize the impact on fish behaviour and survival, and therefore ultimately the conclusions of the study (reviewed by Jepsen et al. 2002, 2005, Bridger and Booth 2003).

In accordance to the 3R's (Reduce, Replace and Refine) of the ethical guidelines for conducting experiments on animals (Russell and Burch 1959) that have the aim of minimizing the number of animals used in experiments and the effect on experimental animals, we have used the state-of- the-art tagging techniques and the same tagged fish to answer several different research questions (**papers I-IV**).

#### 2.2.1.1. Acoustic telemetry

Acoustic telemetry relies on the propagation of sound waves through water. Acoustic tags are electronic devices that send out a unique acoustic code, as well as environmental data if required, for example the depth or temperature the fish experiences. As the tagged fish passes near a submerged hydrophone receiver, the transmitted code is detected and recorded by the receiver along with the date and time of the detection. Acoustic telemetry works well both in fresh and sea water, but the range varies a lot with wind and wave action and debris in the water, i.e. everything that can create obstacles for the movement of the pressure waves sound consists of (Thorstad et al. 2000b).

We have used acoustic telemetry to study small and large scale migration patterns in the river and the fjord (e.g. migration timing, migratory speed, swimming depth, horizontal distribution in the fjord, marine survival and the inter-spawning interval). See papers (**I-IV**) for details on tags, tagging and tracking procedures.

#### 2.2.1.2. Radio telemetry

Radio telemetry relies on the propagation of radio waves through water. Radio tags are electronic devices that transmit on a given frequency, which may transmit along with the identity, for example the depth or temperature the fish experiences. When the tagged fish is within the detection range of a receiver, the transmitted frequency is detected along with the date and time of the detection. Radio telemetry works only in fresh water, as the conductivity of sea water reduces the range to the effect that it becomes unusable at sea. In fresh water the range is very good - up to several kilometres - depending on the depth of the tag and the surrounding topography. In addition, radio telemetry works through ice and snow, which is a considerable asset when working throughout the winter in the sub-arctic. Radio transmitters are advantageous for use in rivers, because acoustic transmitters often have a reduced range in turbulent and flowing water (Thorstad et al. 2000b).

We used radio telemetry to assess in-river survival and migratory patterns. See paper **III** for details on tags and tagging and tracking procedure.

### 2.2.2. Mark and recapture

*Mark and recapture* is commonly used in ecology to evaluate hypotheses about behaviour (Block et al. 1998), fishing mortality (Hearn et al. 1998, Latour et al. 2003), natural mortality (Hoenig et al. 1998, Gaertner and Hallier 2003) and the temporal and spatial distribution of the target species (Dupuis 1995; Block et al. 2002). However, in most cases it has proven difficult to use these data in stock assessment due to the multiplicative effects of exploitation rate, natural mortality, tag-induced mortality, tag expulsion, tag failure and tag reporting rate, and therefore the data remain highly uncertain.

In this thesis, mark recapture was used in papers **I** and **II** to assess the capture rate of kelts in the fisheries, as a complementing material for the acoustically tagged kelts. This was done to increase the sample size that would otherwise have been too low to provide reliable estimates. In addition, all the acoustically tagged kelts were also tagged externally with modified Carlin tags with contact and reward information for reporting recaptures, and can therefore be considered as a part of a mark-recapture study as well. As the fishermen in both the river and the fjord were informed about the project by personal letters and the reward for reporting recaptures was high, we deem the reporting rate relatively reliable. Due to the reported recaptures we were also able to estimate tag failure and tag expulsion rates.

### 2.2.3. Scale analysis

Scale analysis is a method commonly used in the study of fish, as it can give a lot of information on the age and growth of the fish (Bagenal 1974). This is based on different growth patterns in the summer (fast growth period) and winter (slow growth period). The slow growth in winter results in closely spaced growth marks on the scale that can be seen as a darker area, and used to assess the age of the fish (Van Oosten 1957). Spawning leaves also a noticeable mark on the scale, and therefore scale analysis is a valuable method in assessing the life-history of a given individual (White and Medcof 1968, Ducharme 1969). It is also a non-invasive method especially suitable to be combined with behavioural studies with telemetry. However, scale analysis is a subjective method, and requires a certain degree of expertise. Therefore, scales read by different analysts might not be directly comparable. The scales used in all the studies included in this thesis were analysed by the same experienced person (**papers II-IV**).

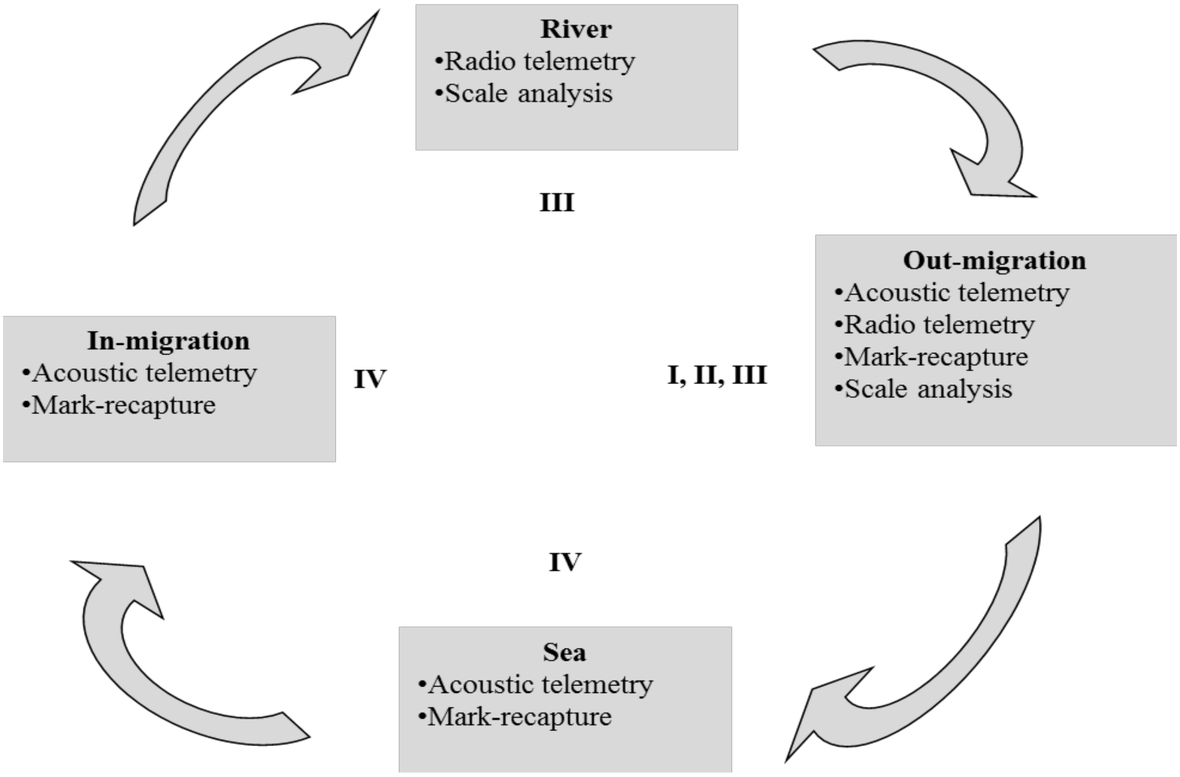


Fig. 3. Main methods used in the four different studies included in this thesis.

### 2.3. The assumptions behind the study design

The study design relies on three assumptions:

1) We have tagged a representative group of fish.

The sampling methods used in this study (bagnets and angling) were chosen for their gentleness, in order to avoid abrasion, scale loss and other wounds from gillnets (Mäkinen et al. 2000, Jokikokko 2002, Rivinoja 2005). Nevertheless, both sampling methods have their limitations regarding random sampling – which is a crucial element in drawing statistical inferences of the study population. The assumption of random sampling is relatively robust regarding the bagnet-based sampling in the fjord, but due to the size-selectivity of the nets, one sea winter (1SW) fish were under-represented in the study material. Therefore additional sampling by angling was arranged in the river for the smallest size-class (**paper III**). The fish tagged from the bag nets spread out in the river in a random manner (Jensen et al. 2010), and therefore all the data-points from individual returning salmon can be considered independent from each other.

Randomly sampling the whole river by angling was impossible, as we were logistically restrained to sampling at accessible fishing locations. Therefore the sampling design was haphazard rather than random. As fish were caught only in seven different locations, care was taken to assess the independence of the data points in analysis. However, sampling by angling might introduce an unknown element in the study material; when angling we only sampled fish that took the bait, and since we do not know what affects this behaviour we cannot claim for sure to have tagged a representative group of the kelts in the river. However, our sample sizes were quite large and most of the biological characteristics were normally distributed. Therefore, we have confidence that our sampling design was relatively robust. In addition, we have compared the behaviour of the two groups sampled with different methods against each other and found no significant differences (**paper III**).

2) We do not affect the survival, behaviour or growth with our method.

   It is a well-known fact that handling and tagging of the fish may influence its behaviour and swimming performance (Brown et al. 2006), growth, and survival (Rikardsen 2000). In addition, external tagging might increase the risk of being captured in fisheries (Rikardsen and Thorstad 2006). However, most of these effects can be mitigated by handling the fish as gently as possible, and by choice of tagging timing, method and tag. Consequently, we have caught the fish as early as possible to reduce tagging effects in behaviour during the time of interest, we have tagged with gentle methods as mentioned above and minimized their time in captivity, we have tagged while the fish were under anaesthesia and have used small tags (~0.001% of bodyweight). We feel confident that we have done all in our power to minimize the handling and tagging effect.

   The returning salmon were tagged externally since exertions during migrations may open up surgical incision during upstream migrations through rough river sections (Thorstad et al. unpublished data). In addition, external attachment of tags is a quick tagging method, which reduces handling stress. Usual problems related to external tags are effects on swimming performance, fouling and tag loss due to mechanical stress (e.g. due to entanglement in vegetation, shedding of tags in waterfalls and fish ladders) (Johnsen et al. 1998, Rivinoja et al. 2001). The same type of tag used in this study (**paper III**) did not affect the swimming performance of smaller salmon in a previous study by Thorstad et al. (2000a), no fouling of tags was observed on recaptured fish, and only few tag-losses were reported (there are no fish ladders in the study river and only one small waterfall in the upper reach of the river).

   The kelts were tagged internally with acoustic tags in order to achieve long term retention of the tags. Nevertheless, we observed 20% tag expulsion upon return after one or two years at sea throughout the study (**paper IV**). Immediate recovery of tagged kelts was rapid, as the kelts were operated in cold water and the post spawning life-stage tolerates handling quite well (Brobbel et al. 1996 **papers I and II**). The long term effect on survival is difficult to assess, but we have assessed it indirectly by comparing the growth rate of tagged fish against untagged individuals in the same age-classes from the in-river catch statistics, and found no significant differences, indicating that carrying the tag does not affect the feeding capacity.

3) The tagged fish home back to the same river.

   Salmon in general show high fidelity to their natal rivers (Quinn 1993, Jonsson et al. 2003), and Hansen and Jonsson (1994) verified experimentally that replaced post spawning Atlantic salmon returned to their natal river which they left as smolts. As no tags were reported recovered in neighbouring rivers, we have confidence that our straying rates are minimal.

## 3. Results and discussion

This thesis succeeded in answering the questions posed in the beginning of the study;

1) How many salmon survive spawning and overwintering in the river? (**paper III**)

The minimum post spawning survival rate in River Alta was high (63-80%) and consistent with the estimate by Thorstad et al. (2003) for the same river (80%). The other few estimates that are available report kelt survival in the wild in the large range of 30-80 % (Jonsson et al. 1990, 1991a) indicating a great spatial and temporal variability in survival rates.

The post spawning survival is obviously the key component in an iteroparous reproductive strategy, but the factors affecting the survival are most likely numerous and complex. For example, the morphology, hydrography and latitude of the river might play important parts in explaining post spawning survival patterns. Physical constraints, like the lack of suitable pools, lack of adequate water levels through winter, and sub-optimal ice-conditions might decrease overwintering survival. On the other hand, increasing latitudes often equal lower temperatures, and lower temperatures render migratory and spawning energetics less costly. Therefore, more energy is left for survival. In addition, in higher latitudes freshwater environments become more unpredictable (for example large variation in the timing and duration of the spring flood from year to year), and this can lead to strong inter-annual variations in the survival of eggs and larvae (Leggett and Carscadden 1978, Glebe and Leggett 1981). This, according to life-history theory, should select for a temporal spread of reproductive risk and therefore favor iteroparity (Stearns 1992, Roff 1992). However, this still remains to be proven for Atlantic salmon, and the relationship between the post-spawning survival of kelts and environmental factors needs to be assessed with long-term data from heterogeneous rivers at varying latitudes.

Abiotic factors aside, the biotic factors play an important role too, and they are often dependent on abiotic factors (see Fig. 4). For example, the general condition of the fish when entering the river might directly affect post spawning fate (**paper III**), and the condition of salmon when entering the river is dependent on feeding conditions it has experienced at sea, which in turn are dependent on variations in climate, for example temperature (Rikardsen and

Dempson 2011). Climate might also affect the temperatures in the spawning river and increase energy expenditure during up-stream migration and spawning, susceptibility to diseases and fresh water parasites (for example fungi *Saprolegnia* and gill-maggots *Salmincola salmonea* L.), and in consequence elevate mortality. High densities of conspecifics may also increase energy expenditures via higher competition among individuals during spawning, and therefore reduce post-spawning survival. Finally, predation and harvest in the river obviously affect survival rates directly, and may in addition target specific size-classes. Taken into consideration all the known and unknown possible factors, one would expect high inter-annual variation in the post spawning survival. Unfortunately, no long-term studies exist and are sorely needed to assess the driving forces behind the survival patterns.

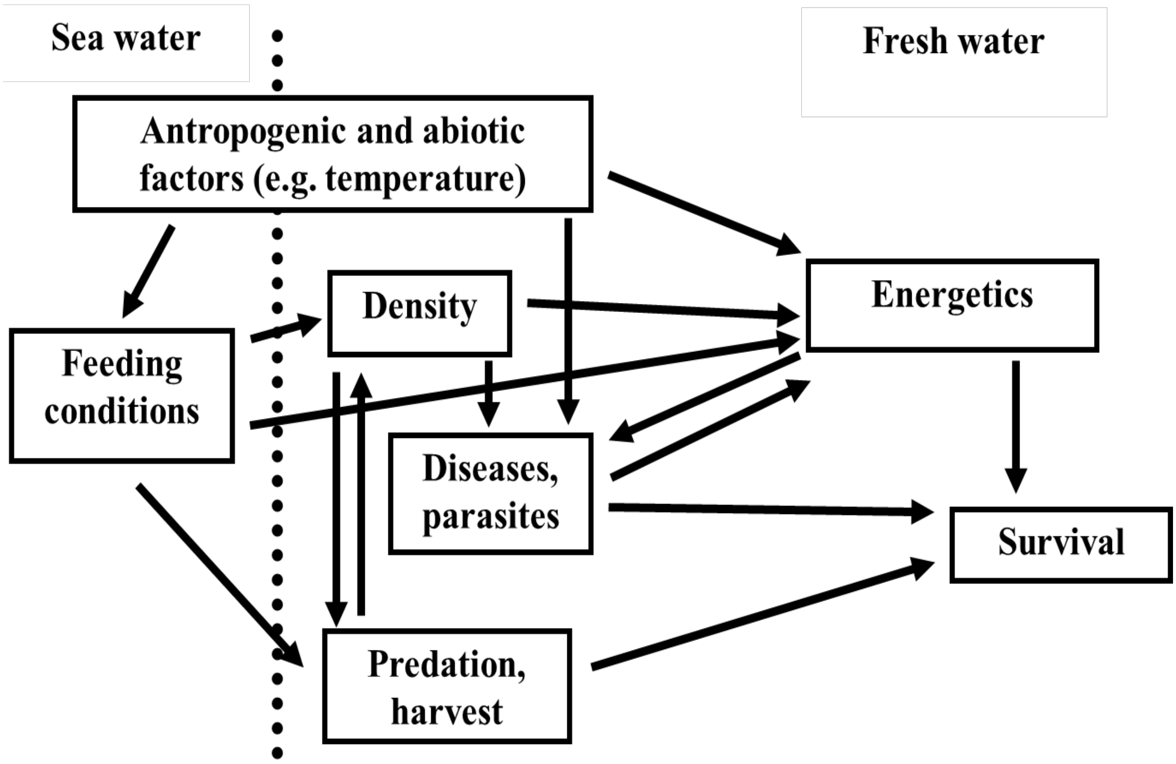


Fig. 4. A schematic presentation of some of the main factors and their potential interactions affecting the post-spawning survival of Atlantic salmon.

2) Who survives the spawning and overwintering in the river? (**paper III**)

Based on two years of data, the multi sea winter (MSW) females had a higher post spawning survival than (MSW) males (74% vs. 43% survival, respectively), but there was no difference in survival between MSW females and 1SW males (62% survival).

The difference in post spawning mortality is most likely due to different energy allocation in the spawning event (Jonsson et al. 1991b). Male Atlantic salmon are known to invest a lot of energy in spawning (35% of somatic energy, 59% of total energy reserves) (Jonsson et al. 1991b), as a result of active and aggressive behaviour and investments in secondary sexual traits. This energy loss, when added to injuries acquired during intense male-male competition, may lead to high post-spawning mortality among males (Bagiliniere et al. 1990, 1991, Jonsson et al. 1990, Fleming et al. 1997, Fleming 1998). On the other hand, 1SW males might spend less energy during spawning than MSW males, as the secondary sexual characteristics and mating success are positively related to body size (Fleming and Gross 1994, Jonsson et al. 1997, Jonsson and Jonsson 2003). In contrast to males, females invest less of their somatic energy in spawning (25%), even though total investments in spawning are on par with males (59%, Jonsson et al. 1991b). This is because females invest most of their reserves in egg production (~30%, Jonsson and Jonsson 2003), little in aggression, and therefore they suffer lower post-spawning mortality (Bagiliniere et al. 1990, 1991, Jonsson et al. 1990, Fleming et al. 1997, Fleming 1998). Consequently, repeat spawning is more common in females than males (**paper IV**, Mills 1989, Erkinaro et al. 1997, Niemelä et al. 2000).

3) What steers the kelt out-migration? (**paper III**)

Prior to their ocean feeding migration, Atlantic salmon kelts often remain in fresh water for extended periods, despite low food availability. We hypothesized that this extended freshwater stay is the outcome of adaptive, state-dependent habitat use. We expected that due to different sex and size-dependent energy allocation in the spawning event (Jonsson et al. 1990, 1997, Fleming et al. 1997, Niemelä et al. 2000) (*i*) fish in poor body condition would leave the river early, (*ii*) males would leave the river earlier than females, and (*iii*) large fish would leave earlier than small fish. We found that the body condition and sex were strong predictors for the migration behaviour as expected, but found no or contrary evidence for the effect of size.

The seaward migration occurred in two periods – in autumn and early winter (October-January) and spring (April-July). The autumn migrants were mostly MSW males with low repeat spawning probability, whereas MSW females and 1SW males with higher repeat spawning probability waited until the spring. The body condition of Atlantic salmon, both when entering the river and after overwintering, was a strong predictor for the migration behaviour; the fish in lower body condition left the river earlier. Among the spring migrants, the kelts in best condition waited the longest to migrate to the sea, coinciding with the out-migrating smolts, which suggests that kelts might benefit from staying in the river until an optimal energetic trade-off regarding the river and sea habitats.

We conclude that the seaward migration of kelts unfolded according to the asset protection principle (Clark 1994), that predicts that individuals with low energy reserves and a low probability to reproduce again should accept risky, productive habitats (in this case, the sea), whereas individuals with large reserves and a high probability to reproduce again should choose safe, less productive habitats (the river). Further, as females had high post-spawning survival and overwintering probability, the management and conservation implications of the findings of **paper III** are to ensure over-wintering and out-migration success of females, in order to increase their chances of returning as repeat spawners.

4) What is the mortality of kelts during the out-migration? (**paper I,II** and **IV**)

Based on three years of data, the mortality of kelts during the out-migration was low, as on average 91% survive the fishing season start, sea entry and fjord migration. Only 0.5% were caught and killed in the in-river fisheries and 4% in the fjord fisheries (**paper IV**).

The low mortality in the in-river fisheries was surprising, as in years of long overlap between kelt migration start and fishing season many kelts get caught and released (C&R) in the river (**paper II**). Evidently, kelts have a high tolerance for being caught and released, as C&R did not significantly affect immediate or delayed post release mortality when compared to an uncaught control group. C&R affected the post release behaviour of kelts only by delaying the river descent, but did not affect timing of sea entry or migration speeds. Hence, releasing angled kelts can be recommended as a viable management strategy to enhance the return rate of repeat-spawners.

The low mortality in the fjord fisheries might be due to the swimming patterns of kelts. Judging from the swimming speeds observed (mean minimum velocity 1.6 km/h, **paper I**), the kelts swim quite directly through the fjord and into the open sea, and in consequence do not get easily caught in the fishing gear placed along the shore-lines.

Generally, the results indicate that sea-entry and early sea migration is not a bottleneck of survival for Atlantic salmon kelts, despite their weakened condition after spawning and overwintering in the river and the overlap in migration timing with the fishing season both in the river and the fjord (**paper I, II and IV**). This conclusion is supported by the observations of Hubley et al. (2008) and Hedger et al. (2009) who also concluded with high out-migration survival (70-90%) of Atlantic salmon kelts in Canada by the use of similar study methods and design.

5) What are the maturation schedules of repeat-spawners? (**paper IV**)

Based on the returns of the acoustically tagged kelts, the most common time for kelts to mend between successive spawnings is two years (94%, called alternate spawners). In practice this usually means only one whole year at sea, as the large majority of kelts overwinter in the river (**paper III**). The remaining 6% of the returning kelts spent three years mending (i.e. two years at sea).

To complement the data amassed from the acoustically tagged kelts, a 29-year long time-series of scale material from the in-river fisheries was used to estimate parameters used in the simulation model in **paper IV** (referred to in the paper as unpublished data, presented below in Tab. 1)**.** Scales from the in-river fisheries were obtained from anglers 1981-2010 (n=12 213). For each individual, catch location and date, sex, length and weight were recorded. An eroded zone in the scale was used as the criterion to identify repeat-spawners (White and Medcof 1968; Ducharme 1969).

| **Maidens** | | | | | **Repeat-spawners** | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Female** | | **Male** | | | **Female** | | **Male** | |
| **SW** | **n** | **%** | **n** | **%** | **SW** | **n** | **%** | **n** | **%** |
| **1** | 334 | 7 | 4829 | 77 | **1S1C** | 0 | 0 | 2 | 4 |
| | | | | | **1S1** | 23 | 14 | 13 | 23 |
| | | | | | **1S2** | 5 | 3 | 5 | 9 |
| | | | | | **1S3** | 1 | 1 | 1 | 2 |
| | | | | | **1S1S1C** | 3 | 2 | 0 | 0 |
| | | | | | **1S1S1** | 4 | 3 | 0 | 0 |
| | | | | | **1S1S1S1C** | 1 | 1 | 0 | 0 |
| **2** | 493 | 11 | 398 | 6 | **2S1C** | 3 | 2 | 5 | 9 |
| | | | | | **2S1** | 65 | 41 | 21 | 38 |
| | | | | | **2S2** | 2 | 1 | 2 | 4 |
| | | | | | **2S1S1** | 3 | 2 | 0 | 0 |
| **3** | 3654 | 78 | 861 | 14 | **3S1C** | 6 | 4 | 0 | 0 |
| | | | | | **3S1** | 35 | 22 | 7 | 13 |
| | | | | | **3S1S1C** | 1 | 1 | 0 | 0 |
| | | | | | **3S1S1** | 4 | 3 | 0 | 0 |
| **4** | 171 | 4 | 206 | 3 | **4S1C** | 2 | 1 | 0 | 0 |
| | | | | | **4S1** | 1 | 1 | 0 | 0 |
| **5** | 9 | 0 | 3 | 0 | **-** | - | - | - | - |
| **7** | 1 | 0 | 0 | 0 | **-** | - | - | - | - |
| **Sum** | **4662** | **100** | **6297** | **100** | **Sum** | **159** | **100** | **56** | **100** |

Tab. 1. Life-history characteristics of maiden and repeat-spawners caught in the river 1981-2010. Scales were analyzed to differentiate between maiden (1SW, 2SW, etc. where 1SW denote one sea winter, and so on) and repeat-spawners (1S1, 2S1, etc. where 1S1 denote one year at sea followed by first spawning (S) and reconditioning period of 1 year (1) at sea and second spawning run). Consecutive spawners (repeat-spawners spawning the consecutive year after less than a full year at sea), are marked with an additional C to differentiate from alternate spawners spending a full year at sea.

Corresponding roughly to the findings from the acoustically tagged kelts (**paper IV**), 90% of the female repeat-spawners from the in-river fisheries were caught during their second spawning trip to the river (Table 1), 9 % were caught during their third trip, and only 1% during their fourth trip. All the caught repeat spawning males were second time spawners. The most common strategies for both females and males were 1S1, 2S1 and 3S1, and these three life history strategies combined accounted for 78 and 74% of all strategies, respectively (Table 1). The most common time period needed to mend between successive spawnings was 2 years (82 %, alternate spawners), but, 7% of the repeat-spawners spent two whole years and 1% three whole years at sea before return. In addition, 7% of the second time spawners returned the consecutive year (consecutive spawners) and, 4% of the multiple spawners changed their strategy from alternate to consecutive (Table 1). Consecutive spawners must have left the river right after spawning (autumn migrants) or returned the same year as their kelt outward migration after only a summer at sea.

The females had a greater diversity in life-history strategies than males, and young maidens (1 and 2SW) had the highest probability to spawn again in both sexes ($\chi^2$, $P < 0.01$). For example, females spawning for the first time after 1SW and 2SW constituted only 7 and 11% of the maiden spawners, but 25 and 46% of repeat-spawners (Table 1). Based on the scale material from the in-river catches, the  proportions of repeat-spawners were on average 4% for females (range 0-10%) and 1% for males (range 0-5%).

Maturation schedules represent an intriguing energetic bet-hedging. For example, fecundity increases with body size, which is achieved by prolonging the growth period; on the other hand, the probability of surviving to reproduce decreases with prolonged sea-migration (Jonsson et al. 1991a, 2003). The complex array of life-history variation observed also in this study is possibly a compensating or bet-hedging tactic for life in stochastic environments (Fleming and Reynolds, 2004). Different age at maturation and overlapping generations provides a recovery potential in the event of catastrophic failure of any single brood year, and an important source of genetic variation to populations over multiple generations (Schindler et al. 2010).

### 6) How large is the repeat-spawner weight gain at sea? **(paper IV)**

The acoustically tagged kelts increased their weight at sea by 47% on average (range 10-74%) and had an average weight of 13 kg upon return. Based on the scale material from the in-river catches (presented above), the average weight of the four most common second time spawners were 9, 12, 15 and 16 kg for 1S1, 2S1, 3S1 and 4S1 salmon, respectively, used as such in the model built in the **paper IV**.

7) How many repeat-spawners return from the sea? (**paper IV**)

Based on two years of data, the returning rate of post-spawned Atlantic salmon was high; an average of 39% for females and 19% for males. The estimate given is an absolute minimum estimate due to documented tag loss and failure. Based on the tag expulsion and failure rates (20%-45%, **paper IV**), the assumed return rate of females could be in the range of 47%-57%. The high return rate indicates that the post spawning Atlantic salmon might face relatively low predation pressure and other mortality at sea. Nevertheless, one has to bear in mind that there is generally high variability in return rate both among rivers as well as among years within rivers, depending on a variety of factors both in the river and the sea (Dempson et al. 2004), and one would need several more years to assess the variability in returning rate.

It is important to emphasise that there are uncertainties in earlier repeat spawning estimates. Repeat spawning has commonly been determined from scale sample reading (e.g. Heggberget 1989) or mark-recapture studies (e.g. Berg et al. 1988). Both methods, albeit widely used, have their limitations: mark-recapture is often dependent on the reporting rate of fishermen (Berg et al. 1988), while scale sample reading is a subjective method and might be especially vulnerable for recognizing repeat-spawners due to the frayed edges of scales resulting from spawning and overwintering in the river (Gunnel Østborg, personal communication). Telemetry methods circumvent these particular limitations, and as seen from the model output from **paper IV**, the repeat spawning rate in the Alta female population was considerably higher (average of 20%) when estimated by the use of telemetry than when estimated from scale samples from in-river catches (3%; Heggberget 1989, 4%; Halttunen et al. unpublished data).

8) What is the repeat-spawner fisheries mortality during in-migration? (**paper IV**)

Based on three years of data, the mortality both in the coastal and in-river fisheries were moderate (average of 11 %). Most of the mortality (8%) occurred in the fjord-fisheries that use bag-nets and bend-nets. This might be due to the large size of repeat-spawners that exposes them to size selective gear in the fjord. Increased susceptibility of repeat-spawners to being caught in the sea fisheries was also reported by Jonsson et al. (2003), Niemelä et al. (2006) and Anon. (2010).

In contrast, our estimates of the mortalities in the in-river fisheries (4% for females) were surprisingly small compared to the estimated capture rate for maiden female fish (17%, Jensen et al. 2010). Low capture rates of repeat-spawners in the river might be due to reduced catchability. One can speculate that the catchable maidens may get caught during their first spawning migrations, and the uncatchable maidens become uncatchable repeat-spawners. Individual fish within a population show individualistic behavioral traits (Greenberg and Giller 2001), and studies indicate that the catchability between individuals vary in a number of fish species (Askey et al. 2006; Lewin et al. 2006). A lower catchability of repeat spawners in the fisheries could also imply that their proportion in the spawning population could be seriously underestimated in scale samples collected from the fisheries.

9) How much do repeat-spawners contribute to the production of eggs in the river? (**paper IV**)

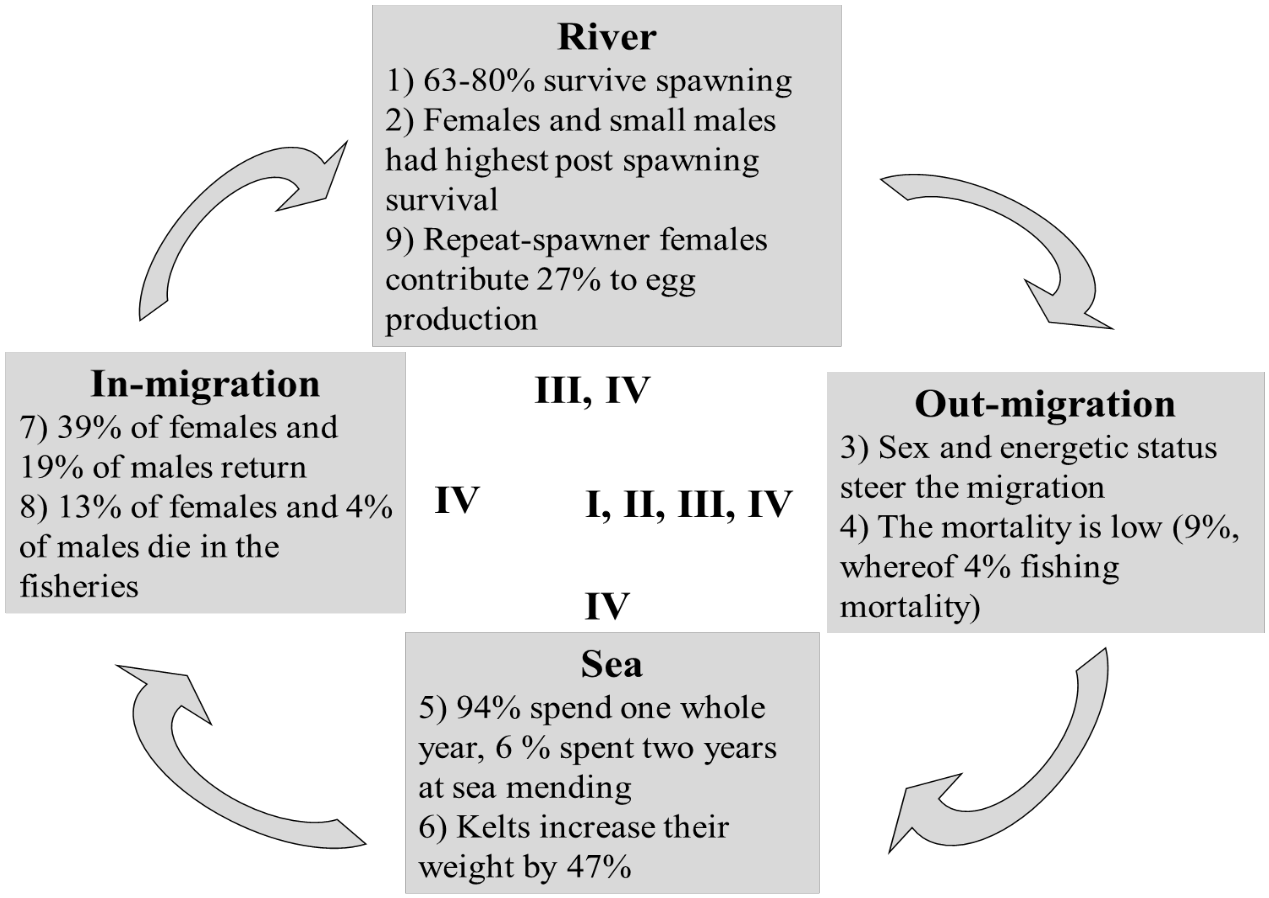
Based on an age-structured simulation model built in **paper IV,** in average 20% (range 2%-46%) of the female population in the River Alta consisted of repeat-spawners and contributed on average with 27% (range 2-59%) of all the eggs spawned in the river. The variation coefficient was significantly smaller in the presence of repeat-spawners than in the absence of them (0.34 (range 0.28-0.40; and 0.41 (range 0.34-0.48), respectively (t-test, $P < 0.001$), which translates in to a more stable population. In consequence, the repeat-spawners might be significant in stabilizing short term fluctuations in a population, and may act as an important buffer for demographic risk and be crucial in population persistence, especially as the maiden survival at sea can be highly variable (Friedland et al. 2005).

The estimates from the model conform to other findings from Canada and Northern Europe. For example, Moore et al. (1995) reported that repeat-spawners contributed more than 40% of the total egg depositions to the Miramichi River, and Niemelä et al. (2006) calculated that repeat-spawners could amount up to 20% in mass (and therefore, in eggs) in their time-series from River Tana. Previous spawners have also been reported to form a considerable portion of spawning stock in many other Atlantic salmon rivers (Chadwick 1988, Mills 1989, ICES 2004).

## 4. Concluding remarks

As the title of this thesis conveys, post spawning Atlantic salmon stay alive in a much larger extent than we anticipated and what is generally documented in the scientific literature available (see introduction and the references therein). The survival was high over winter (**paper III**), during sea-migration (**paper I, II and IV**) and in the fisheries (**paper I, II and IV**), and consequently, the repeat-spawners might contribute significantly to the production of Atlantic salmon (**paper IV**). Repeat-spawners could be especially important during declining and fluctuating populations as a buffer against poor maiden recruitment years (**paper IV**).

This is one of the first detailed studies on Atlantic salmon kelt migrations, and one of the first attempts made in quantifying the contribution of repeat-spawners (See Figure 5 for a summary of the main findings of the thesis). We also provide one of the first estimations of the return rate based on following individuals without the need of recapture (telemetry), and the use of this method has possibly circumvented some potential biases of traditional methods used to assess repeat spawning (mark-recapture and scale sample analysis). The findings from this thesis might be used to modify the management of the Atlantic salmon populations by strengthening the focus on protecting this potentially important population sub-unit.



**River**
1) 63-80% survive spawning
2) Females and small males had highest post spawning survival
9) Repeat-spawner females contribute 27% to egg production

**Out-migration**
3) Sex and energetic status steer the migration
4) The mortality is low (9%, whereof 4% fishing mortality)

**Sea**
5) 94% spend one whole year, 6 % spent two years at sea mending
6) Kelts increase their weight by 47%

**In-migration**
7) 39% of females and 19% of males return
8) 13% of females and 4% of males die in the fisheries

Fig. 5. The main findings from the research objectives of the thesis.

### *Management implications*

In this thesis we have focused on studying post spawning Atlantic salmon in the river and the fjord where management measures are easiest to implement. Potential management actions of our findings are:

- Ensuring over-wintering and down-stream migration success of kelts. In regulated rivers it is crucial to maintain high enough base-discharge throughout the winter to facilitate the overwintering of kelts. In addition, constructing by-passes for down-stream migrating kelts is crucial as mortality of kelts migrating past hydro-power plants without by-passes has been shown to be high (see Kraabøl et al. 2009).

- Protecting out-migrating kelts from mortalities in the fisheries by implementing compulsory release of kelts both in the rivers and fjords. Alternatively, in areas where the overlap between kelt-migration and the fishing season is considerable, delaying the fishing season start both in the rivers and adjoining coastal areas.

- Protecting returning repeat-spawners from mortalities in the fisheries by delaying the fishing season start, both in the rivers and fjords. Alternatively, closing the fisheries.

### *Future research needs*

As **paper IV** demonstrates, the main mortality of post-spawners occurs during their sea feeding migration. The reasons for this are still unknown as the sea phase of salmon has been little studied due to logistical constraints. Mapping the migration routes and feeding areas at sea would be crucial in assessing the reasons and locations for mortality at sea. This remaining knowledge gap will soon be bridged by novel technologies (e.g. pop-up data-logging satellite tags and genetics) already in use in on-going studies. The location of feeding areas for salmon originating from different areas around the Northern Atlantic is of special interest from a management point of view, as it would enable estimating the potential of by-catch mortalities of salmon in the fisheries, and the effect of fisheries and climate change on the prey of repeat-spawners. Knowledge on the feeding areas could also help to understand why the survival and growth of salmon from different areas often oscillate out of step (Jensen et al. 2011), and to better predict the salmon runs.

More information is also needed on the contributions of repeat-spawners in order to adjust stock-recruitment models of Atlantic salmon, as the survival of post-spawners (and therefore ultimately the production of repeat-spawners) is not affected by the density dependent mortality of juveniles in the river that the traditional models base upon. Of special interest would be to assess the life-time reproductive success of repeat spawning Atlantic salmon and the survival costs versus reproductive gains of different repeat-spawner maturation schedules.

The natural step further from merely quantifying the contribution of repeat spawning would be to explain what regulates the rate of return spawning in a population. Are the main factors permanent or temporal, in the river or at the sea? Potential permanent factors are latitude, size and morphology of the river, and the migration distance to sea feeding areas. Potential temporal factors are for example climactic variations affecting hydrology and productivity both in the river and sea, variations in density of conspecifics, parasites and diseases, and variation in predation and harvest rate. The key component in assessing the potential of repeat spawning is estimating the adult mortality rate in relation to the juvenile mortality rate, and how human activities affect the mortality rates of both adults and juveniles. For example, fisheries and habitat degradation have probably been increasing the adult mortality rates of many populations while stocking of hatchery reared juveniles may have reduced juvenile mortality rates, and therefore, human activities may have been selecting for semelparity. On the other hand, recent expansions in aquaculture might have contributed to increased juvenile marine mortality due to sea lice infestations (Finstad et al. 2011), and kelts are possibly less susceptible to sea lice due to their larger size and thicker skin. In addition, the commercial fisheries might increase the juvenile marine mortality through cascading top-down effects in fish communities. Therefore, human activities may as well select for iteroparity. In sum, the jury is still out on this one, and despite our extensive knowledge base, we have barely scratched the surface in trying to understand the role of repeat spawning in the life history strategies of Atlantic salmon.

## Acknowledgements

Science is a learning process and I am grateful to many people who have helped me to climb the steep learning curve of my graduate project.

First of all, I'd like to thank my main supervisor Audun for his relentless energy, cheerfulness and optimism, his enthusiasm when working in the field, and for showing me that it is also possible to do science while running, driving and flying. I also greatly appreciate his ability to see possibilities where other people see problems, and his way of thinking big and aiming high. He truly is an inspiring character.

Then I'd like to thank the rest of our team; my closest colleagues Jan, Jenny and Cedar, with whom I have toiled endless hours in the field. I think that we have complemented each other beautifully, and have epitomized the very idea of that there are no perfect scientists - just perfect scientific teams. And our little team would never have been able to muscle through years of hard field-work without Jenny - she deserves special thanks as an irreplaceable and tireless field-worker and the main radio-tracker in our projects.

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And last, I'd like to thank my parents, both successful scientists in their own fields, who obviously have influenced my intellectual progress in countless ways, but I think I can convey the essence of their most important lessons by reciting their favourite mottos; my mother's "*Only you can do it, but you can't do it alone*", and my father's "*Only practice makes a master and a master practices always*".

Elina Halttunen,

Tromsø,

spring 2011

## My scientific oath

As a member of the international community of research scholars and I declare the following:

I acknowledge my fallibility, and shall never forget that whatever small contributions I may make to science are possible only because of the collective contributions of all those who have come before me.

I swear that I shall devote my professional life to act with skill and care in all scientific work and maintain up to date skills and assist their development in others.

I also swear to take steps to prevent corrupt practices and professional misconduct and will declare any conflicts of interest. I promise never to allow financial gain, competitiveness, or ambition cloud my judgment in the conduct of my work. I will ensure that my work is lawful and justified, and minimize and justify any adverse effect my work may have on people, animals and the natural environment.

I swear to be alert to the ways in which my research derives from and affects the work of other people, and respect the rights and reputations of others. I will seek to discuss the issues that science raises for society and listen to the aspirations and concerns of others. I will not knowingly mislead, or allow others to be misled, about scientific matters, and I swear that I will present and review scientific evidence, theory or interpretation honestly and accurately.

The oath is modified from the universal code of ethics for researchers by Sir David King (2007), written by Elina Halttunen and Sigurd Tønnessen.

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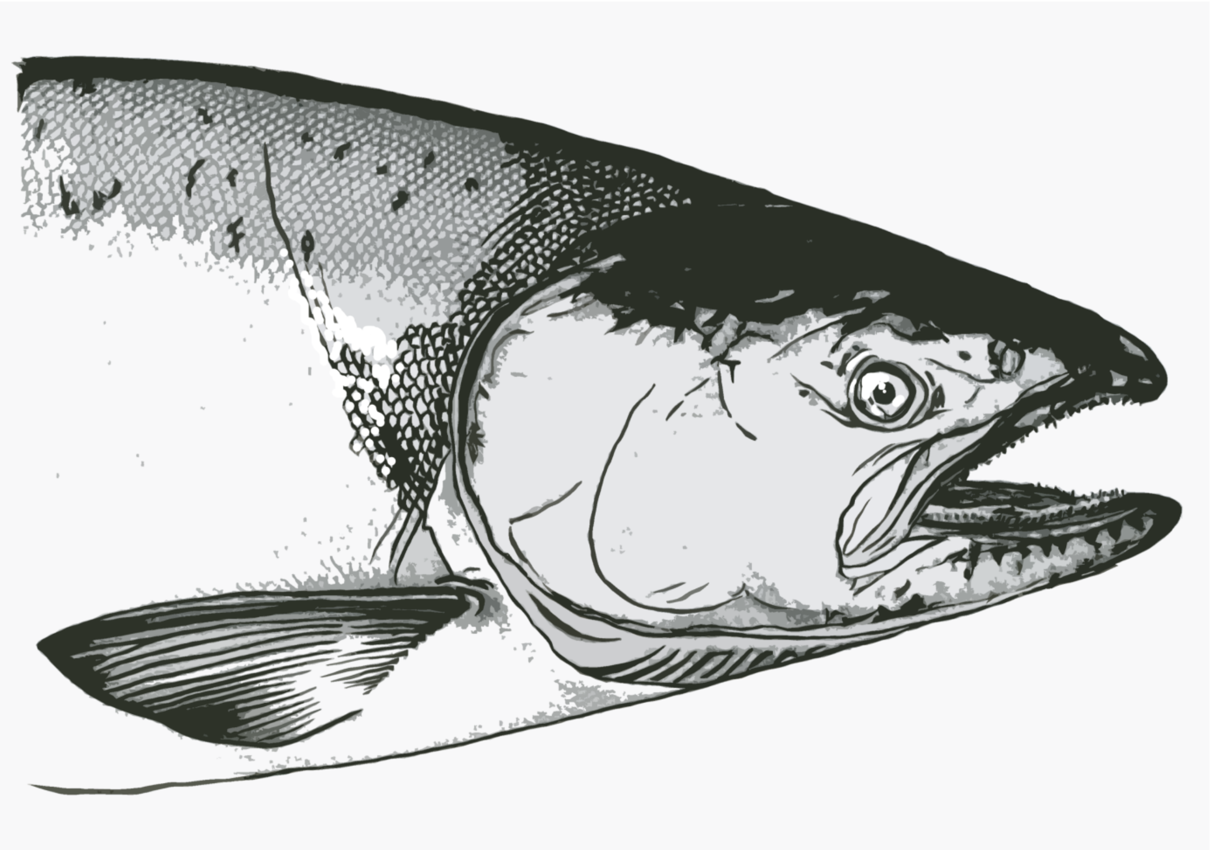
# Paper I



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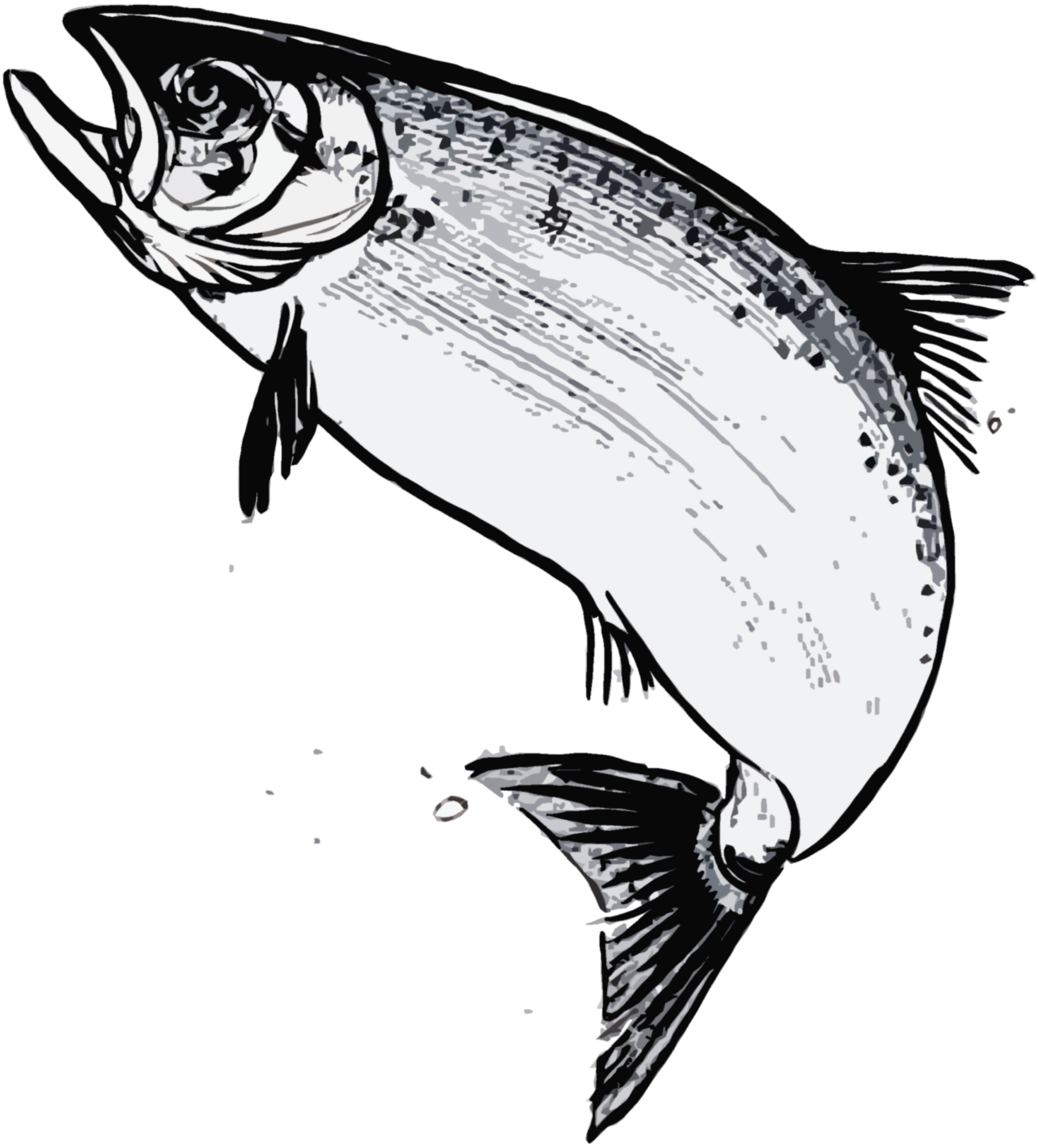
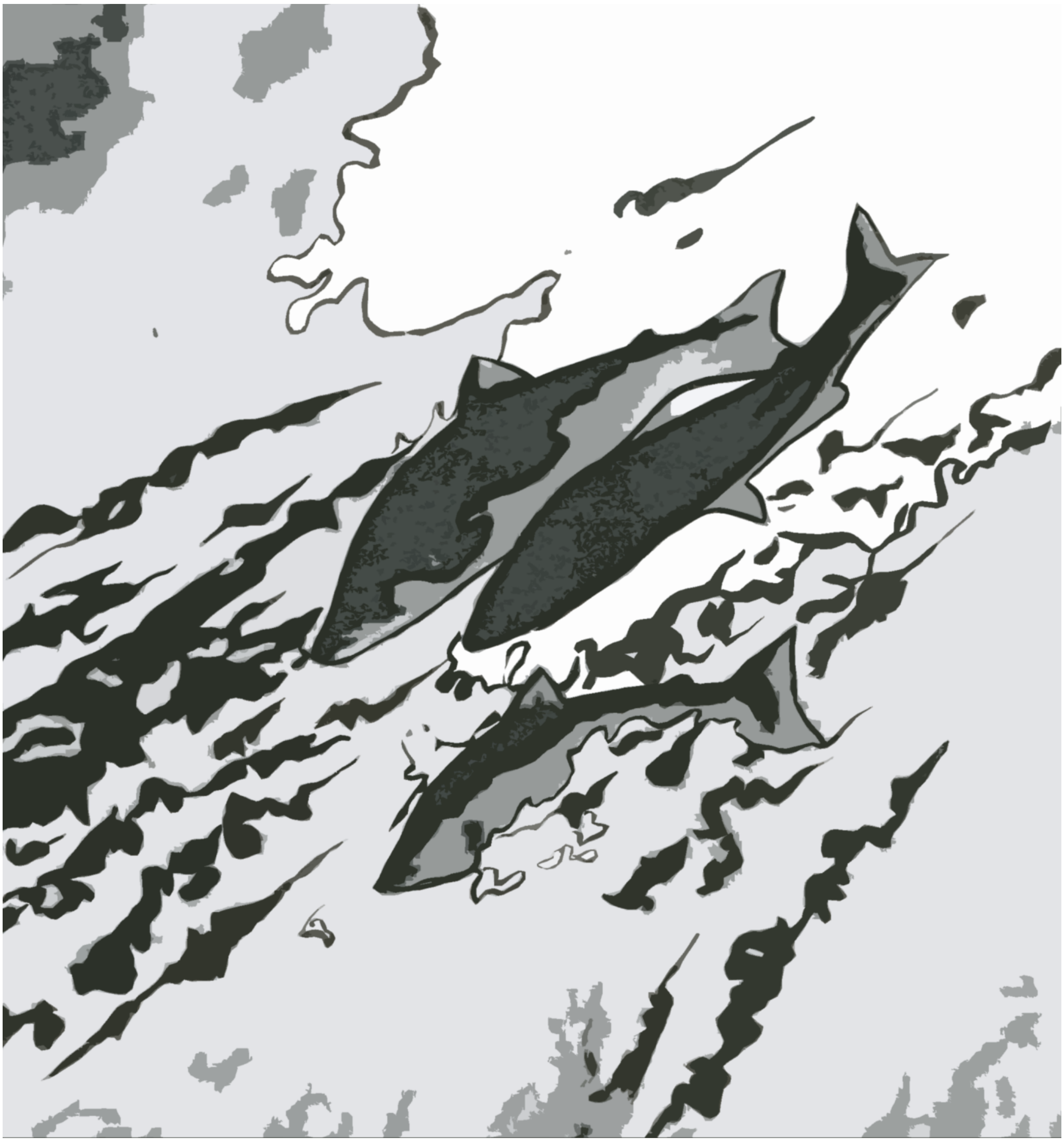


# Paper III

# Paper IV



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