Technical University of Denmark

Rikke Lock Harvig

Density and habitat use of juvenile salmon (*Salmo salar*) in a lowland river

Master's thesis, December 2014

Supervisor: Niels Jepsen

DTU Aqua
National Institute of Aquatic Resources

Abstract

Currently, we lack knowledge on ideal habitat types for Atlantic salmon in Denmark. Hence, restauration of Danish water courses, re-creating salmon habitats, are based on knowledge on local physical parameters used by brown trout (Salmo trutta). Therefore this thesis sets out to identify which physical conditions are considered ideal for growth and survival of juvenile Atlantic salmon (Salmo salar) in Danish lowland rivers. The discussed results are based on data collected in the Danish rivers Kongeå and Ribe (Hjortvad) å. In spring 2014 we released 100,000 artificially bred fry in 15 individual stations in River Kongeå. These were following examined thoroughly in July 2014 using a variety of methods, including electrofishing. Through Principal Component Analyses of the recorded variables, the study identifies key factors determining density of Atlantic salmon parr in Danish lowland rivers. The overall most important positive physical factors in salmon parr habitats in Danish lowland rivers are velocity, coarse gravel, stone and variation in the vegetation (heterogeneity). Conversely, the most negative parameters are too high depths, abundant vegetation, abundance of organic material (CPOM) and substrates dominated by silt.

Table of content

Abstract **1**

Introduction **4**

Hypotheses 4

Background and problems **4**

Theory and Methods **6**

Physical characteristics 6

Life cycle 7

Freshwater habitat (*Spawning, Fry, Parr*) 8

Threats 11

Atlantic salmon in Denmark 11

The investigations in River Kongeå 12

Selecting the investigation sites 14

Setting out the fry 15

The investigations in Ribe (Hjortvad) å 17

Maintenance 18

Electrofishing 19

Habitat description 22

Calculations 25

Software 25

Density 25

Mean 26

Variance 26

PCA 26

Results and discussion **27**

Weight and length relationship 27

Salmon abundance for all stations 28

Temperature 29

Variance between stations 30

Density 32

Substrate 35
Vegetation 36
PCA – all data 37
PCA 2 – Data from River Kongeå 45
PCA 3 - important variables 48
Overall discussion of the PCA's (considerations, limitations) 51
Non-objective observations of territorial behaviour 52
Intra-habitat behaviour 52
Inter-habitat behaviour 53
Summary and conclusions 53
The ideal habitat for salmon parr in Danish lowland rivers 54
1st PCA (Both rivers, All variables) 54
2nd PCA (River Kongeå, All variables) 55
3rd PCA (River Kongeå, Important parameters exclusively) 55
Implications and future challenges 56
Acknowledgements 57
References 58
Appendix 1 – Stations
Appendix 2 – Mathematical derivations of population estimation methods

All illustrations (drawings and graphics) and photographs are the exclusive work and property of the author unless otherwise noted

Introduction

The current thesis sets out to identify and study the complexity of physical conditions considered ideal for growth and survival of juvenile Atlantic salmon (*Salmo salar*) in Danish lowland rivers. The discussed results are primarily based on data from the Danish River Kongeå. Here, we released 100,000 artificially bred fry in spring 2014 on 15 individual stations. These were following examined thoroughly in July 2014 using a variety of methods, including electrofishing. Besides the stations in River Kongeå, supplementary data from River Ribe å, or more specifically Hjortvad å is used for comparison (see materials and methods). Using these data, the current study identifies key factors determining density of Atlantic salmon parr in Danish lowland rivers.

Hypotheses

The thesis sets out to confirm or reject the following 6 hypotheses, which were partly proposed during the initial stage of the project, based on experience and knowledge from the literature (see background and problems), collaborative partners and fellow researchers (i.e. researchers at DTU Aqua, Danish Centre for Wild Salmon (DCV) and employees at the Danish Nature Agency) and then revised based on observations from and experience with electrofishing gained during summer 2014 in the rivers Kongeå and Ribe å:

1) *Juvenile salmon density increases with physical variation of the habitat.*
2) *Too much vegetation is a negative habitat parameter.*
3) *Juvenile salmon are basically stationary.*
4) *Juvenile salmon reside in open water with high water velocity, only to seek shelter when necessary*.
5) *Juvenile salmon tend to use gravel of varying sizes.*
6) *Juvenile salmon are reluctant towards inhabiting (too) deep areas in the stream*.

Background and problems

Currently, we lack knowledge on ideal habitat types for Atlantic salmon in Denmark. Hence, restauration of Danish water courses, re-creating salmon habitats, are based on knowledge on local physical parameters used by brown trout (*Salmo trutta*) (e.g. Clausen *et al.* 2006; Pedersen *et al.* 2009; Kristensen *et al.* 2014). However, already in 1990, Heggenes and Saltveit could demonstrate that Atlantic salmon and brown trout in Norway did in fact have markedly different behaviours, each tolerating different environments: the brown trout used the slow-flowing and shallower areas of the stream, whereas Atlantic salmon tolerated several water velocities and depths (Heggenes and Saltveit 1990; Scruton *et al.* 1998). This was later supplemented with more studies on the behaviour of the two species including Arctic charr (*Salvelinus alpinus*) (Heggenes and Saltveit 2007), confirming the importance of studying species individually, despite similarities in habitat use (see also Heggenes 1996).

Both biological, geological, cultural and historical factors influence living conditions of all aquatic organisms in streams and rivers on cultivated lands (see for instance 'National Forvaltningsplan for Laks', Danish Ministry of the Environment; and Kristensen *et al.* 2014). Although many physical factors have been proposed as ideal for habituating Atlantic salmon (e.g. Heggenes 1990), little is known about the physical conditions (e.g. substrate and plant species, sediments, water flow, depth and temperature) that are to be considered ideal for spawning and optimal survival of fry and parr, particularly in Danish lowland rivers with their unique and characteristic physical conditions (i.e. low elevation and abundant macrophyte cover). Particularly, we lack knowledge on the complexity of factors affecting the survival of Atlantic salmon during the first year of life.

In other cases, physical conditions considered critical for the survival of salmon in Danish waters, are based on data on the behaviour of Atlantic salmon in Northern Scandinavian rivers or in sub-arctic climates (e.g. Heggenes 1991; Heggenes and Borgstrøm 1991; Heggenes *et al*. 1991; Heggenes *et al*. 1996; Payne and Lapointe 1997; Heggenes and Saltveit 2007; Orell *et al.* 2007), which clearly differ markedly from the Danish water courses (i.e. temperate climate zone, lowland geology). Studies conducted in the UK may be more relevant (e.g. Moir *et al*. 1998; 2002; Heggenes *et al.* 2002; Moir *et al.* 2004; Moir *et al.* 2005), however, streams are truly extremely heterogeneous eco-systems (e.g. Heggenes 1996), and even within smaller geographical areas in similar landscape settings, comparison may be difficult (see however McGinnity *et al.* 2012).

Habitat modelling has given much information about critical conditions for both species, but the complexity of eco-systems, variability and the many uncontrollable factors are difficult to predict (e.g. Heggenes *et al*. 1996; Scruton *et al.* 1998; Moir *et al.* 2005; Clausen *et al.* 2006; McGinnity *et al.* 2012; Habersack *et al.* 2014; Kristensen *et al.* 2014). Ideally, species-specific studies over longer time spans, identifying life cycles, diversity and variability in the life histories of particular fish populations, appear to be the most beneficial for our understanding of their behaviour in certain environments (e.g. Klemetsen *et al.* 2003). However, such studies are resource-demanding and, for obvious reasons, difficult to conduct.

Lastly, variation in habitat use correlated with age and size within species and, for example, competitive interaction between species, need to be considered (Thomassen 1995:25; Heggenes *et al*. 1996; Heggenes *et al.* 2002; Heggenes and Saltveit 2007).

Theory and Methods

Physical characteristics

The Atlantic salmon has a large mouth with numerous medium-sized teeth placed both in upper and lower jaws. The colour of the body varies over cream, light brown, silvery to silver-blue with dark brown and/or black, including darker spots on each side on the body. Parr marks (camouflage) are visible as a thick vertical bar on the juveniles after the first year of life. The fins (pectoral, pelvic and anal) are homogenous, varying in shades of light brown. Intra-species size is sex dependent. A female Atlantic salmon maximum reaches 20 kg and 120 cm. The male maximum size is 40 kg and 150 cm (Christensen 2010). In Denmark, the largest salmon ever caught weighed 26.5 kg and was captured in River Skjern in 1954. Today, salmon weighing more than 20 kg are rarely found. Salmon and trout share several physical characteristics, and distinguishing one from the other can be difficult when they are young. However, particular features in their outer appearance are distinct (Figure 1).

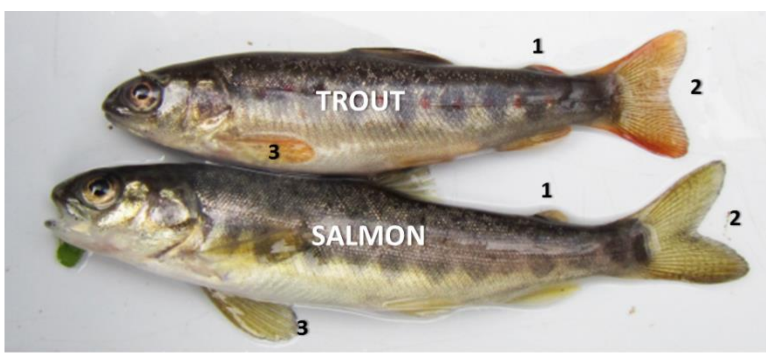


Figure 1: Salmon and brown trout parr (5–6 cm). The most distinguishable feature is that the gill rakers in salmon are more rod shaped. However, this is not identifiable in the field. Hereafter, the most pronounced differences are: 1) The brown trout has an orange adipose fin whereas the adipose fin on salmon are characteristic light brown; 2) The salmon tail fin is deep forked whereas the brown trout has more rounded tail fins. 3) Salmon have larger pectoral fins compared to the brown trout and the salmon tend to "rest" on the pectoral fins. Besides these three distinguishable features, there are several characteristics which, however, tend to be more unsecure. For

example, salmon has a thinner and more streamlined body morphology and a smaller mouth. Salmon often only have one large spot on the gill cover, and the red dots on the brown trout are often more well defined. Hence, characteristics nos. 1, 2 and 3 are the most practical and easy to use in the field.

Life cycle

Atlantic salmon are predominantly anadromous, i.e. they spend their juvenile phase in fresh water, migrate to the ocean to feed (spending most of their adult life here growing) and then they return to the fresh water to spawn (see for example Netboy 1980:24).

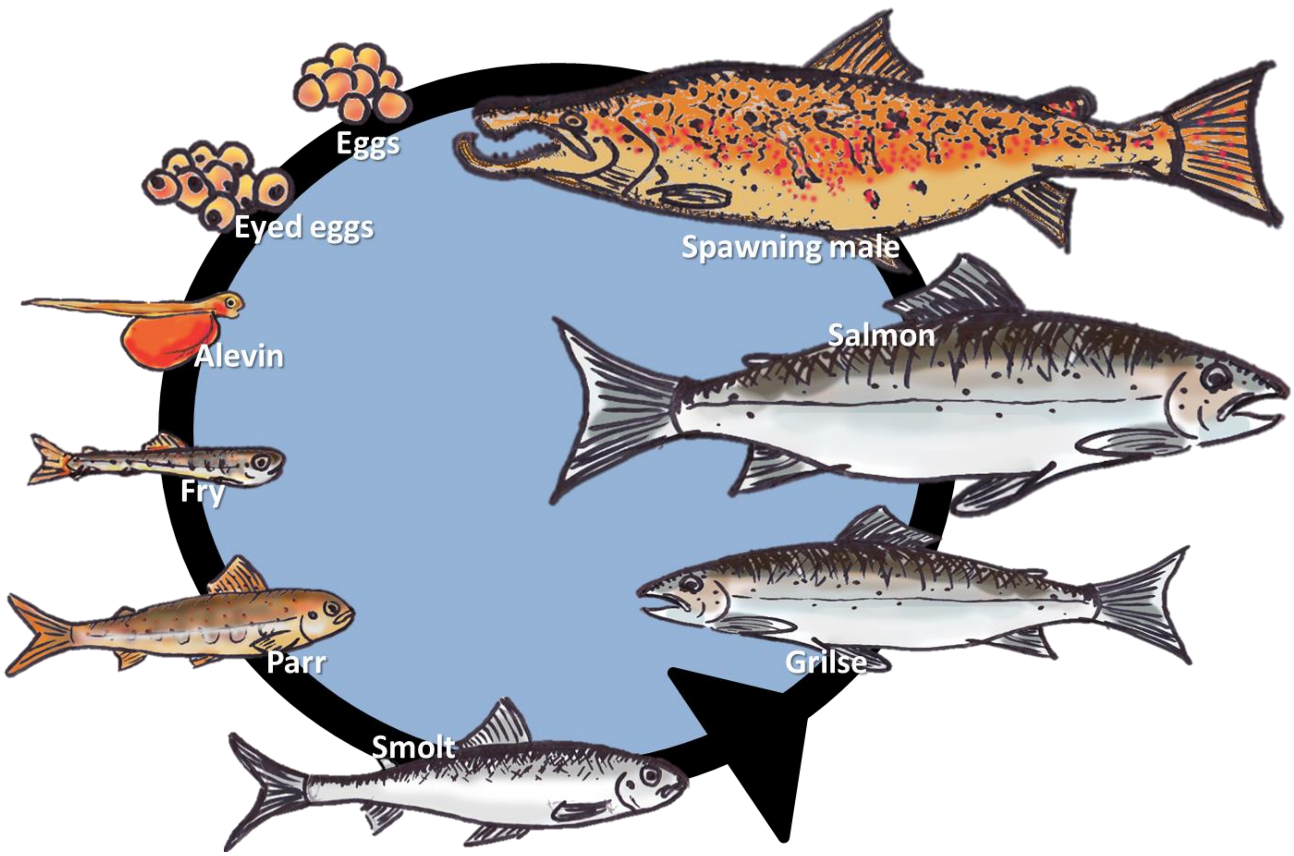


Figure 2: Life cycle of the Atlantic salmon (Salmo salar)

The Atlantic salmon has seven life stages (Figure 2). The first three (alevin, fry and parr) are the primary stages discussed in this thesis. These are exclusively fresh water stages. The following four stages (smolt, post-smolt, salmon and kelt) are found both in fresh water and in salt water (Shearer 1992:6).

The life cycle of Atlantic salmon begins in fresh water, where the adult Atlantic salmon female (in breeding dress) creates up to several redds in the spawning ground, often a riffle with suitable variation of velocity, depth and gravel ensuring the right amount of fresh oxygen saturated water. Here the female will release a (relatively) small quantity of large eggs, and the adult male (also in a breeding dress) covers the eggs with his sperm, fertilizing the eggs. From here, the embryos will develop for months in the redd (e.g. Bardonnet and Baglinière 2000:499; Hansen *et al.* 2013).

In their initial life stage, the alevins hatch from the egg, equipped with a yolk sac, after an incubation period of 50–110 days depending on temperature (Netboy 1980:24). In this entire stage, their yolk sac provides sufficient nutrition. The alevins stay buried in the gravel until their yolk sac is used, and hereafter, they emerge from the gravel to hunt and find feed, still close to the redd (fry). Fry will mostly find abundance of food in the river such as microscopic plankton, insect larvae and nymphs (Netboy 1980:25).

In the following stage (parr), they move from the redd. For both Atlantic salmon and brown trout, variable proportions of the males mature as parr and never leave the river. Parr feed on mayflies, stoneflies, insects, insect larvae, worms, mussels and snails. Parr have many natural enemies such as larger salmon, brown trout, pike, perch, eel, roach and predatory birds, and therefore the population needs to be large, to contribute to the adult salmon population (Netboy 1980:25).

The parr stage lasts until they begin migrating (smolt) and become silvered. During the smolt phase they slowly begin to move downstream and migrate into the sea. During the first years' time in the sea, and until after the first winter and the formation of a wide annulus (post-smolt), some return to the fresh water to spawn after only a year in the sea (grilse). However, the majority will stay in the sea (salmon) for several years until they return to the fresh water to spawn. When spawning salmon enter fresh water they do not feed until after spawning when they reach salt water again. Obviously, this exhausts the spawning salmon and drains its energy resources resulting in a marked weight reduction (kelt). Little is known about the behaviour of post-spawning salmon, but mortality is high, and those that do survive seek to slow waters to mend (Bardonnet and Baglinière 2000:499). Some return to the river to spawn a second time and only very few spawn more than twice. Scottish studies indicate that less than 5% will survive to spawn a second time (Shearer 1992: 5ff).

Freshwater habitat (*Spawning, Fry, Parr*)

Although fry and parr of Atlantic salmon tend to use habitats near the spawning habitat, the alevin population can settle up to several kilometres from the redd. Generally, this distance is however less than 200 m (Bardonnet and Baglinière 2000:500). It is easier to define which physical characteristics salmon reject exclusively, than which they prefer, because the ranges are so broad and availability of suitable spawning places sets (various) limits (Heggenes 1991; Bardonnet and Baglinière 2000:499). In the literature, ideal spawning sites are defined as shallow areas of the stream with high water velocities and coarse substrates (Gibson 1993:41f; Louhi *et al*. 2008: 333–336). In larger rivers parr are more abundant upstream where the width does not exceed 30 m. Outside of Denmark, parr are commonly found in rapids (high velocity and steep gradient) often made of large stone, stone and various sizes of gravel (Gibson 1993:41). Ideal spawning areas and juvenile habitats are riffles and shallow pools where water velocity is fast (the *rhithron* zone). Although colder temperatures are tolerated, salmon still feed in temperature ranges between 7 and 22.5 °C. Moreover, salmon parr requires high oxygen saturated water (Gibson 1993:42).

Overall, heterogeneity of the habitat plays an important role and seasonal variation seems only to be relevant in areas with harsh winter climates (Bardonnet and Baglinière 2000:499f;502). Spatial variation in habitat use is suggested to depend on habitat availabilities such as substrate, vegetation and river morphology, whereas temporal variations depend on water flows and temperature (e.g. Heggenes and Saltveit 1996). However, spatial investigations of salmon habitats are often restricted to small-scale investigations of microhabitats or of meso-habitats within a few square metres (see Bardonnet and Baglinière 2000:498). Nonetheless, certain species-specific parameters have been proposed, which should be mentioned here:

Water velocity

Heggenes and colleagues have proposed that Atlantic salmon parr tolerate a wide range of water velocities and depths (Heggenes and Saltveit 1990). Nevertheless, water velocity is considered the primary variable (Heggenes 1991), where parr tend to avoid water velocities below 10 cm s^{-1} (mean) and above 60 cm s^{-1}, depending on individual size (Heggenes 1990; 1991; Heggenes *et al*. 1999:4). Ideal velocities for spawning are suggested to be 40–50 cm s–1 (Moir *et al.* 1998). Studies have suggested that parr are more depending on sufficient water velocity than sufficient depth during winter and are often seen in large schools in pools. Furthermore, the limitation in habitat during winter time reduces intra- and inter-species competition and thus more species co-exist during winter (Whalen and Parrish 1999:1547f). In an in-door controlled experiment with parr where plenty of food was provided and flow velocity was changed artificially, parr preferred the high velocity and constantly moved towards areas with high velocity (19.5–25.2 cm s^{-1}) where they immediately tracked changes in flow (low velocity: 7.2–10 cm s^{-1})(Kemp *et al. 2*003: 572f). This indicates that parr generally do not need to optimize net energy uptake (i.e. in that case they would prefer low velocity). However, it is suggested that the traditional variable velocity may be too simple and that a range of turbulence variables should be taken into consideration. As such, parr are more often observed in areas with lower Froude number (low resistance) (Enders *et al.* 2009:1824). Turbulence is primarily controlled by river morphology rather than substrate even in riffles with a coarse gravel bed. Similar turbulence is found in rivers with more or less the same morphology, regardless of substrate (Legleiter *et al.* 2006:242ff). Hence, ideal habitat variables may vary from one river to another.

Depth

It is suggested that Atlantic salmon parr are reluctant to stay in both too shallow (<10 cm) and too deep (>60 cm) areas of the stream (Heggenes 1991; Heggenes *et al.* 1999:4). Small parr tend to stay in shallow waters (<50 cm). Ideal depths for spawning are suggested to be 20–30 cm (Moir *et al.* 1998). Highest density of parr is often found in larger areas with shallow waters (Gibson 1993:41).

Substrate

Salmon are generally reluctant to stay in areas with fine substrates (sand and silt) (Heggenes 1991; Halvorsen *et al*. 1997:71f). Ideal spawning beds contain large quantities of gravel and smaller stones in different sizes (Heggenes *et al*. 1999:4; Bardonnet and Bagliniêre 2000:499). Gravel facilitates water flow through the pores and thus provides an oxygen source, which is highly important around the red. Conversely, silt appears to form a membrane around the eggs, preventing oxygen diffusion into the egg, resulting in low embryo survival (Levasseur *et al. 2*006). Good habitats are often associated with coarse substrates, which are positively correlated with gradient (on substrates as cover, see under vegetation below). In channelized streams, significant positive correlation is found between density of parr and proportion of stone >10 cm. It has been proposed that high turbulence can cause erosion and suspension of sand (Kostaschuk and Villard 1999:10). However, the process behind suspension of sand in rivers is not well understood. Concentration of sand and velocity can vary over short time in meandering rivers, changing the river bed noticeably. Hence, the general understanding of optimal substrates in parr habitats is still limited.

Vegetation

It is suggested that Atlantic salmon parr are reluctant to reside in areas of the stream without macrophyte cover (Heggenes 1991). However, salmon can utilize surface turbulence as cover in rivers with little instream cover (e.g. Armstrong *et al*. 2003:158f). Parr do not occupy areas with dense covers of vegetation. Instead, they are more often seen in areas with moderate vegetation, using gravel in various sizes as cover, depending on their own sizes (Heggenes *et al*. 1999:5). In lack of gravel as shelter, parr can utilize the roots of the plants, e.g.

in sand-dominated substrates (Beland *et al. 2*004:531). Altogether, covers provided by stone, large substrates, vegetation, roots and debris allow for co-existence of more individual fish because territorial species will be isolated from each other (Armstrong *et al*. 2003:158f).

Threats

The Atlantic salmon is a threatened species. Ocean temperature is generally considered an important factor for survival and size of the spawning population (Scarnecchia 1984). However, because of the anadromous nature of the wild Atlantic salmon, it is of similar importance that adults have a place to spawn in fresh water streams of a good quality. Lack of good salmon habitats is an urgent problem currently preventing increase in salmon populations (Bardonnet and Baglinière 2000:497). However, it has recently been discussed that the most prominent problem may well be the low return rates to the fresh water of the adult salmon. The high mortality in the ocean could possibly be due to shortage of food, salmon lice, cormorant (*Phalacrocorax carbo*), seals and overfishing.

Until recently, pollution of rivers has been considered one of the most serious problems in fresh water, preventing a good ecological state. However, lack of connectivity (e.g. due to constructions of dams or weirs), preventing the mature adults to reach their suitable spawning areas upstream, is currently imposing the largest threat to all anadromous species and studies have indicated that Atlantic salmon can be delayed for weeks in man-made dams, weirs, inefficient fishways and other barriers hindering passage (Thorstad *et al.* 2008). However, also downstream migration is associated with high smolt mortality (e.g. Jepsen *et al.* 1998:353; Aarestrup and Koed 2003:174), resulting in a marked decline in return rates for the spawning population.

For decades, maintenance has heavily affected the rivers in Europe (e.g. Kristensen *et al.* 2014). In many rivers, weed cutting, where both bankside vegetation and underwater vegetation is removed, is conducted by the local authorities several times annually, ensuring water flow and drainage of the surrounding agriculture fields. In addition, the rivers have been deepened and straightened mechanically, allowing for cultivation of more uniform field systems and hence also use of fertilizers nearer to the river banks which have destroyed many of the original salmon habitats.

Atlantic salmon in Denmark

Salmon found in Danish watercourses are of the species Atlantic salmon (*Salmo salar*), within the Salmonid family (*Salmonidae*). Until recently, physical changes of the Danish watercourses over the last century had left the large Danish rivers unsuitable for the Atlantic salmon, resulting in marked reduction (or extinction) of the total population. However, after extensive river-restoration projects, the salmon have returned and the annual run in the largest river (Skjern) currently reaches 3000–5000 individuals whereof the majority are naturally reproduced (i.e. wild).

Historically, Atlantic salmon has habituated at least 9 Danish rivers in Jutland: River Varde å; River Storå; River Gudenå; River Skjern å; River Sneum å; River Kongeå; River Ribe (Hjortvad) å; River Brede å; and River Vidå (Hansen *et al.* 2013). In each river, the original population of Atlantic salmon had its distinct fingerprint in the genome. Howvever, in the late 1980'ties the original Atlantic salmon populations were considered extinct (e.g. WWF 2001). Primarily therefore, restoration and improvement of river quality including a large Atlantic salmon release program (with adult Atlantic salmon from Ireland, Sweden and Scotland) began in the early 1990'ties. In River Skjern å restoration of the remaining (original) Atlantic salmon population was launched since it was discovered that some of the remaining salmon did in fact descend directly from the original salmon population in River Skjern å. Hence, the release program was immediately ended, and only bred on the original salmon from River Skjern å. Because the salmon from River Skjern å differed genetically from those found in other rivers in Western Jutland, a large project, analysing the genome from the 9 rivers, was conducted by DTU Aqua on material collected over a century, revealing that the original Atlantic salmon population was still present in four of these: River Skjern å, River Varde å, River Storå and River Ribe å (Hjortvad) å(Hansen *et al.* 2013). Today the population of Atlantic salmon increases. However, it is still not entirely self-reproductive and release programs are ongoing (Hansen *et al.* 2013).

The investigations in River Kongeå

River Kongeå is one of the few larger rivers in Denmark, flowing into the Wadden Sea in Western Jutland (the North Sea). The catchment area of River Kongeå is 455 km^2. Most of the river is unregulated and meanders naturally. The river has a naturally varying bottom, width and depth. The width of the stations investigated in the current study varies between 10 and 25 m, and the depth from many shallow riffles to deep water pools. Riffles (in various sizes) are spread along the river, providing spawning habitats in different qualities.

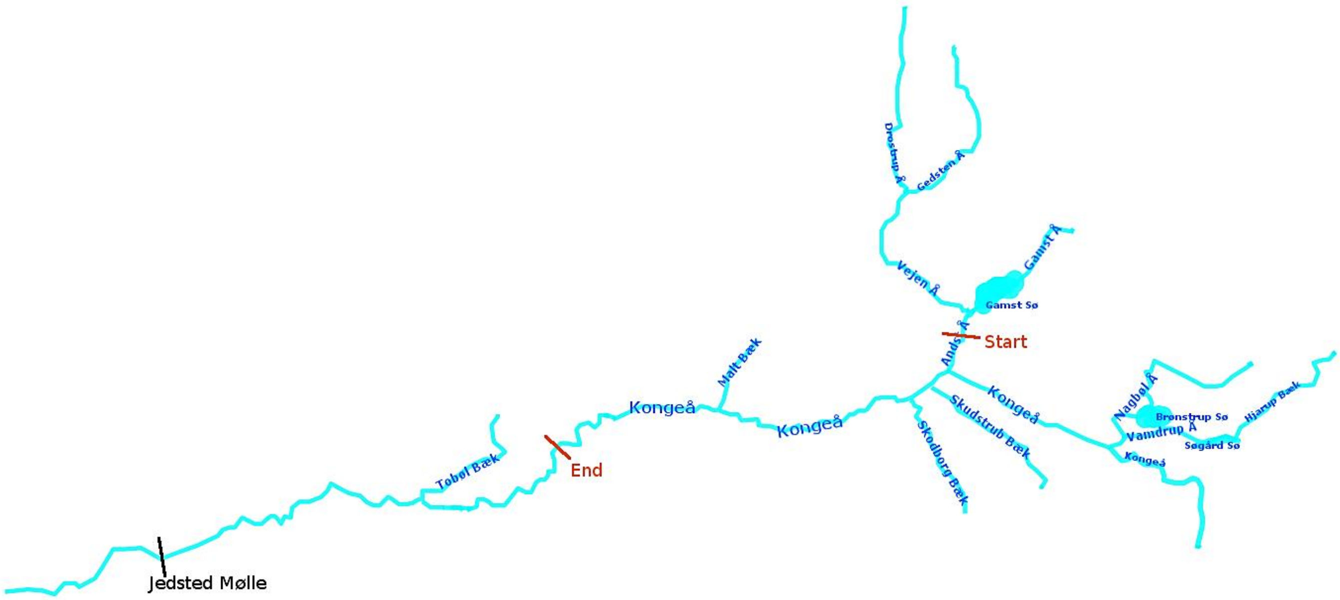


Figure 3: River Kongeå running from East to West, flowing into the Wadden Sea. The black line indicates the location of Jedsted Mølle Weir and Aquaculture. There are other aquaculture farms, however, these are recirculated. The analyzed investigation sites are located between the two red lines.

In the lower end of the river, downstream, between Grestedbro and the river mouth at the Wadden Sea, the river is regulated and sandy with little coarse substrate. Here, the natural hydrology is heavily influenced by the weir and fish farm at Jedsted Mølle (Figure 3). Whereas all other aquaculture farms in River Kongeå are recirculated, Jedsted Mølle has water intake from and discharge to River Kongeå and the weir prevents connectivity and water flow more than 1 km upstream (Naturstyrelsen 2006). It is suggested that the average population of fry is 60–82% and for parr 44–62% lower in rivers with fish farms (Butler and Watt 2003:103; Mills 2003). Furthermore, the fish farm can increase smolt mortality and, hence, the entire salmon population is in increased risk of depletion (Mills 2003; Butler and Watt 2003:109; Olesen and Aastrup 2006).

Figure 4

Figure 5

Figure 6

Figure 7

Figure 4: Upstream of Jedsted Mølle Weir and aquaculture, preventing connectivity and water flow, which is the main reason for the low number of natural breeding in River Kongeå. The stream is heavily affected, appearing like a (polluted) lake with a characteristic smell. Figure 5: Rainbow trout escaped from Jedsted Mølle fish farm found downstream of the weir. Figure 6: Polluted water discharged from Jedsted Mølle weir and fish farm. Figure 7: The artifical redirection of the stream, where the fish are supposed to migrate upstream. The water appears polluted with little flow and high turbidity.

Selecting the investigation sites

In April 2014, the investigation sites for the project were selected and defined. For each of the sites, the following demands had to be fulfilled:

1. A suitable spawning place for the *Salmo salar*
2. Variability in physical variables
3. Accessible (i.e. accessible with the equipment walking or by boat)

Initially, 15 individual sites in River Kongeå were selected based on experience and knowledge about the characteristics of the stream from Michal Deacon (from the Danish Nature Agency and head of the local angling union: *Vejen og Omegns sportsfiskerforening*). On a field trip on April 9th, Michael Deacon introduced us to the 15 sites and informed us on advantages and disadvantages for each of the sites. Each site was examined in waders. Due to rain, high flow and much turbulence, it was difficult to see material on the bottom. However, it was possible to distinguish between different sizes of sand, gravel and spawning material by walking through the spawning distance in the water. Geographical positions were recorded for all 15 sites using GPS and visualized using Google Maps Engine (see Figure 8).

On April 12th, only a few days later, I examined all 15 sites in clear weather, using a Kayak for accessing each of the sites over a distance of approximately 25 kilometres. The spawning sites were recognized from the kayak based on their GPS position. On this day, it was possible to see bottom material and to identify the spawning areas. This gave practical knowledge on how to identify spawning redds in lowland rivers.

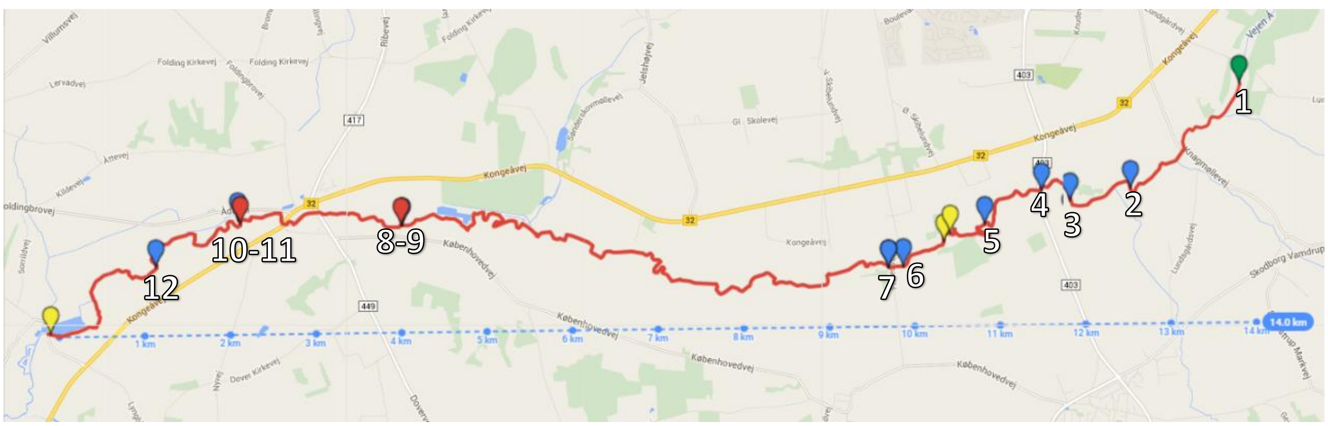


Figure 8: The 15 stations, nos. 1–12 seen from East. The red line indicates the investigation area. In stations marked with yellow, it was not possible to wade-fish during the period where the electrofishing and habitat description was performed. The green station is the only artificially manipulated station (added gravel and a very high gradient).

Setting out the fry

On May 20th, the 100,000 fry of *Salmo salar* spec. were released on the respective sites using a small motorboat for accessing the sites. This was done in collaboration with Danmarks Center for Vildlaks (DCV), who also provided the gear. The fry were 2 cm on average and bred at DCV. DCV produces juvenile salmon from wild salmon which are returned and caught in the rivers of western Jutland. The different salmon stocks are kept and bred in separately recirculated units (see the website for DCV: http://www.vildlaks.dk/). However, DCV had not previously released fry into natural water habitats at such an early stage (information from Kim Iversen, DCV). The reason to set out fry at such an early stage in this project was primarily to minimize costs.

Under the artificial conditions, prior to the date of release, the temperature was monitored stringently and was gradually increased from 7.5 C° to 14.5 C° over 4 days. As such, the fry were habituated to the temperature in River Kongeå. On the day of release, the temperature in River Kongeå was 16.5 C° (see Figure 30). The fry were kept in a tank with oxygen supply and brought to River Kongeå by DCV. DCV brought a boat with an additional tank which was filled up with fry 3 times during the release, going downstream the river. On average 6000–7000 fry were released in each riffle (see Appendix 1 for details on each station).

Figure 9

Figure 10

Figure 11

Figure 12

Figure 13

Figure 14

Figure 9: The large tank with oxygen supply was placed in the trunk of the vehicle and transported from Skjern to River Kongeå. Figures 10–11: The fry were moved with a small net from the large tank behind the vehicle to a smaller tank at the boat. Figure 12: The state of the fry was monitored visually at each station and the water was changed continuously with a bucket. Figure 13: The fry were transferred to a 1 Litre bucket with an estimated capacity of 1000 fry. Figure 14: The fry were released throuh a PVC-tube, which ensured that the fry were released into suitable shelters e.g. Sium latifolium and Ranunculus (based on the practical experience by Kim Iversen, DCV).

The investigations in Ribe (Hjortvad) å

The supplementary data from the nearby and morphologically similar river Ribe (Hjortvad) å (Figure 15), today habituating only naturally bred fry of both Atlantic salmon and brown trout, are an indispensable reference. The populations of salmon in Ribe å partly stem from artificially added populations (DCV ended the salmon release project in 2012 and the population is now considered self-sustainable). Also river morphology and substrate has been artificially manipulated (i.e. various gravel sizes have been added by excavators) (Naturstyrelsen 2012). Nevertheless, River Ribe (Hjortvad) å is an eco-system both geographically and geologically fairly similar to River Kongeå, i.e. east-west oriented and located on the sandy soils just southwest of the late glacial maximum (Weichsel) (see Figure 15). Both rivers were originally functioning as drainage for the ice sheet, which covered most of Scandinavia in the period approx. 13.000–10.000 BC (Krüger 1989). Since the last glaciation, both rivers have (as any other Danish watercourse) been subject to several artificial changes for either historical, cultural or practical reasons (e.g. artificially constructed spawning areas, channelization, dredging, construction of dams, maintenance etc.) (e.g. Brookes 1987). Nevertheless, the analyzed data from the two rivers must be considered both spatially and temporally comparable (i.e. data from both were collected within the two same weeks in July 2014).

Figure 15: Map of Southern Jutland and location of the two rivers, River Kongeå and River Ribe å, where the investigations were performed in July 2014. Both rivers were originally functioning as drainage for the ice sheet during the late glaciation (13–10.000 BC). The dotted line indicates the approximate location of the ice sheet at its maximum.

Maintenance

Rivers in Denmark are generally maintained by weed cutting one or several times annually. This is done to ensure sufficient water flow and thereby drainage of the surrounding cultivated lands. However, recent studies have demonstrated that the long-term effect of weed cutting is directly opposite, and weed cutting cause severe biological damage by reducing biodiversity distinctly (Moeslund 2007). In River Kongeå weed is cut twice annually by the respective municipalities (Vejen Kommune and Esbjerg Kommune). The section of River Kongeå analyzed in the current investigation was within the responsibility of Vejen Kommune. Despite the EU water framework and multiple national water plans, Vejen municipality have not changed their regulations since 1993. However, they are presently working on new regulations. According to their regulations they are controlling the rivers capacity for optimal water flow at least twice annually, which is often associated with weed cutting done by boat (see Ribe Amt 1993). It was decided to contact the municipality to prevent weed cutting between medium May and August 1st when the investigations were performed to ensure that this factor would not influence the results. Vejen municipality kindly agreed to those conditions. In addition, they provided a boat and one of their employees to participate in a shared review of all the spawning areas where fry were released.

Figure 16: Map with the borders of each municipality. Vejen Kommune cut weed twice annually and has the full responsibility for the entire investigation area. The black line illustrates the border of the municipality. Vejen Kommune is within the white area. The area of investigation is between the two red lines (Edited GIS map, Geocortex, Vejen Kommune).

Figure 17: Field trip on June 2nd with "Frede", employee at "Vej og Park", Vejen Municipality, and partly responsible for maintenance of River Kongeå. The river is (in practice) maintained with the main purpose of sufficient water flow to ensure drainage of the surrounding fields and to prevent flooding of cultivated lands. Although habitats were identified in the regulations, cutting methods were not adjusted to prevent destruction of these (see Ribe Amt 1993). Occasionally, the municipality performed additional cutting to meet extraordinary requirements from the landowners.

Electrofishing

The standardized sampling method for fish in rivers (CEN-standard) is electrofishing. To perform electrofishing, a safety course and permission from the Danish Ministry of the Environment is required, specifying the exact area(s) where electrofishing is allowed. The equipment used for electrofishing was a generator, a transformer and two electrodes, a positive and a negative. The generator creates a voltage drop between the two. An alternating current is converted into a signal which is close to direct current. The negative electrode is set out upstream of the investigation area, whereas the positive (which attracts the fish) is handheld and used for manually dragging the fish into a net of proper size. Voltage is highest nearest to the positive electrode creating an attraction zone around it and—even closer—an immobilization zone (see Figure 18; and Geertz-Hansen *et al.* 2013:12ff). Because the current creates a voltage drop over the fish, it is the size (length) of the fish that determines how much it is affected by the current. Small fish are more difficult to catch than larger ones. However, the small fish (e.g. 6 cm juvenile salmon) are less affected because they are not immobilized that easy. In larger streams with much vegetation, this is a huge advantage because they are easier to hold in the attraction zone. It is more difficult to catch fish in vegetation when they are immobilized because they will often get stuck in the vegetation. However, the small salmon could be seen swimming actively out of the vegetation towards the positive electrode and did not get stuck since they were not close enough to be immobilized.

To perform the investigation, I depended on several voluntary helpers. In each case, the selected station was marked with surveyor sticks and electrofished in a standardized way by the same person (me). Each area was electrofished twice. One area (station 1) was electrofished thrice and again one area (station 5) was fished four times to verify the efficiency (see Appendix 2).

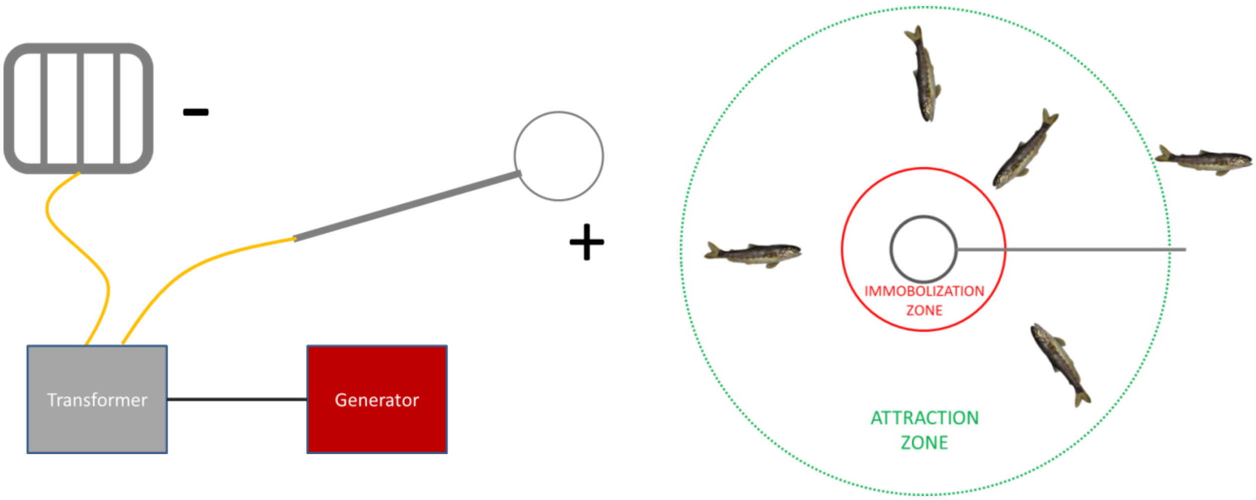


Figure 18: The electrical fishing kit (left) receives power from a generator. The generator is connected to the transformer which transforms the current from alternating to a current close to direct current. The positive electrode is shaped as a round circle with a handle and used for fishing. The negative electrode has a surface as large as possible for a larger voltage drop. This is placed upstream of the investigation and creates a voltage drop from the negative to the positive electrode. The electrical field is highest close to the positive electrode, and the zone in which the fish are affected is illustrated in the circle (right). If the positive electrode is not close enough to the fish, particularly the small (parr) will register the current and seek shelter. If the fish are in the immobilization zone, they will be paralyzed which is not preferable because water current often will lead them away. Therefore it is important to keep the fish only in the attraction zone. This requires some technique and is done by moving the electrode in a precisely adjusted speed similar to that of the attracted fish, and then dragging them gently into the net.

Figure 19

Figure 20

Figure 21

Figure 22

Figures 19–22: A boat was used to access the stations we could not access by car. However, the boat was also brought for each investigation, serving as a floating working station. A negative electrode was put in the water few meters upstream of the investigations area. The entire area was marked by surveyor sticks. The electrofishing started downstream of the investigation area. All fish were registered. For station 5, salmon and brown trout were weighed and measured. For the rest of the stations, only lengths were recorded.

All fish for each electrofishing sample were kept in separate tanks until counting and measurements were done separately (i.e. meeting the demands of the *removal methods* (Appendix 2)). Individuals of all species were registered and counted; however, all these data are not included in the analysis. Salmon and brown trout was anesthetized with Benzocaine. From a mixture of 20 gram Benzocaine and 1 L 96% ethanol, 8 ml was dissolved in 5 L water according to the official recommendations (Geertz-Hansen *et al.* 2013:24).

Although 15 stations were initially included in the investigation in River Kongeå, data were only collected from 12 of these because the water was too deep for electrofishing in the remaining 3 stations during July 2014. Hence, these were excluded from the analysis (see also Appendix 1).

Habitat description

Habitat descriptions in this study were drawn from experience with habitat recordings by The Danish Nature Agency, DTU and DCV, who kindly trained me in each of their standards. The variables chosen here were result of an evaluation and optimization of the three different standards, adjusted to the current project, primarily focusing on variability within the sites in River Kongeå.

Transects

Depending on the width of the station, two (or three) transects were described thoroughly to ensure sufficient data on physical characteristics of the stream. In most cases, transects were placed in each end of the investigated area of approx. 100 m^2. However, in narrow stations three transects were needed to ensure enough descriptive points. In these cases, the third transect was placed exactly between the two transects in each of the ends. Hence, the selection of transects meet the criteria of a random selection. For every square metre across each transect (approximately 25–35 values per station), 22 individual physical variables were recorded in detail using laminated data sheets (see list below and Figures 23–25). In this investigation we did not distinguish between runs, riffles or pools. Instead, these can be identified in the graphs displaying depth, vegetation and velocity in Appendix 1. However, the majority of the stations were riffles.

Figure 23

Figure 24:

Figure 25

Figure 23: Each transect was marked with visible land markers (red-white surveyor sticks). Figure 24: Across the transect gravel was grouped per square meter (by feeling the substrate with the feet and through visual identification). This approach is relatively fast after some training. Figure 25: Depth was measured with a ruler added to a board.

Photographs and video records

Each site was filmed and photographed using a digital underwater camera for observations of the bottom and the sediments (gravel, etc.) and a digital video camera was used for filming each investigation area with a voice-over description of the characteristics of the stream and immediate observations made at the site. These visual recordings were an invaluable supplement to the written records from each of the sites.

Recorded variables

The recorded variables at each station were:

1. **Width**: a 30 meter band was used to measure the width of each transect
2. **Velocity**: a *Valeport* 801 (flat) returned the mean from 3 measurements, repeated once every meter across each transect. The velocity was measured in 60% of the depth from the water surface giving the mean velocity (Figure 26).

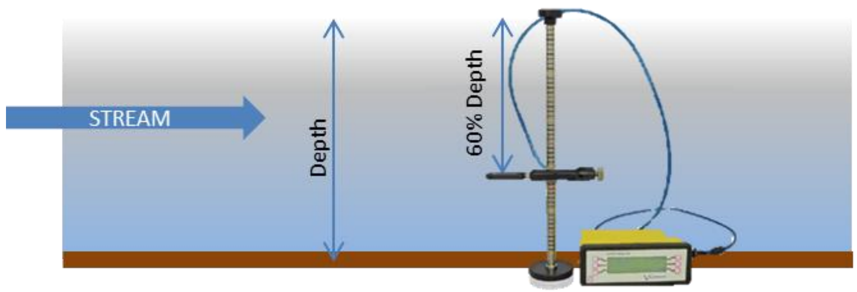


Figure 26: Valeport 801 (flat) placed in 60% of the depth with the "duckbill" pointing up against the stream.

3. **Depth**: Depth was measured every meter across each transect.
4. **Substrate**: Each square meter across each transect was systematically described for each of the following subgroups (in percentages):
    a. CPOM – Coarse Particulate Organic Matter
    b. Silt – substrate < 0.25 mm
    c. Sand – 0.25–2 mm
    d. Fine gravel – 2–16 mm
    e. Medium gravel – 16–32 mm
    f. Coarse gravel – 32–64 mm
    g. Stone – 64–128 mm
    h. Large stone > 128 mm
5. **Vegetation**: Vegetation was recorded in percentages for each square meter across all transects.
    a. Emergent vegetation was recorded in percentages.
    b. Submerged plant species were registered for the most abundant water plants;
        i. Ranunculus sp.
        ii. Sium latifolium
        iii. Eloda sp.

iv. *Sparganium sp.*
v. *Lemna sp.*
vi. *Potamogeton sp.*
vii. *Zannichellia sp. (only observed in one station but in large quantities, and therefore included in the analysis)*

c. Veg/no veg: Vegetation-free zones where substrate was visible were recorded in each transect.

6. **Trees**: The amount of shelter provided by trees was registered in percentages for each transect.
7. **Undercut bank**: undercut banks, providing shelter if needed, were recorded for each transect.

Temperature was recorded using a *TidbiT v2* Water Temperature Data Logger. This was attached to a brick at the bottom in station 4. Temperature was logged every hour for 216 hours (9 days), covering variation in weather conditions within the investigation period sufficiently, e.g. still warm days and windy days with heavy rain and thunder.

Calculations

Software

XLSTAT 2014 (an add-in for *Microsoft Excel*) was used to perform the statistical analyses.

Density

Estimating a given animal population is a recurrent mathematical problem in biological sciences. The two commonly used methods are the *mark-recapture* method and the *removal method* (Zippin 1956; 1958; Bohlin *et al.* 1989), also called *the effect on the population of catches of random size but known effort* (see Appendix 2). For each station (except no. 5) density was calculated using: 1) the formula derived according to the *removal method* with 2 samples; 2) the corresponding standard error; and 3) efficiency.

The estimates are calculated using the formulas below:

$$\widehat{N} = \frac{{C_2}^2}{C_2 - C_1}$$

$$\hat{p} = \frac{C_1 - C_2}{C_1} \quad , \qquad \hat{q} = \frac{C_2}{C_1}$$

$$SE(\widehat{N}) = \sqrt{\frac{Nq^2(1+q)}{p^3}}$$

where $\widehat{N}$ is the estimated fish density, C_1 is the amount of fish in the first run and C_2 is the amount of fish in the second run. The probability of being caught (or the electrofishing efficiency) is $\hat{p}$ (see Figure 34). The probability of not getting caught in the first run is called $\hat{q}$. The 95% confidence interval for the density can be calculated by multiplying standard error with 2 and is valid if the inequality below is true (Seber and Le Cren 1967).

$$Np^3 > 16q^2(1+q)$$

For using these formulas, the efficiency must be above 0.5 or the density must be higher than 200 fish per $100m^2$ (Zippin 1958; Geertz-Hansen 2013:32f).

The calculations were performed on both salmon and brown trout in lengths ≤10 cm and ≤15 cm. The catch of large salmon and brown trout was limited (see Figure 29).

For more comprehensive derivations, formulas, specification of efficiency in the field work conducted for this thesis, see Appendix 2. Calculations for station 5 are also found in Appendix 2.

Mean

Mean values were calculated for the variables depth, velocity, vegetation, trees, silt, CPOM, sand, fine gravel, medium gravel, coarse gravel, stone and large stone.

Variance

Because the classic ANOVA test is incapable of handling variations in the amount of measurements, the *Kruskal Walis one-way-analysis of variance*, also referred to as the *non-parametric* ANOVA, was performed on all stations for depth and velocity. This was done to ensure difference between stations.

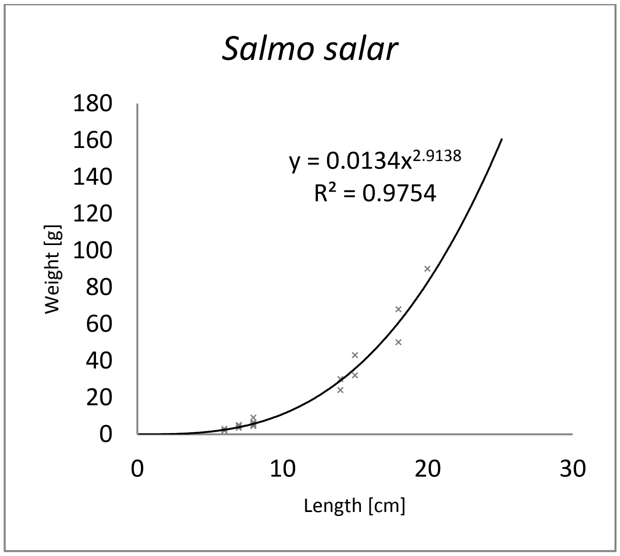
PCA

Three different *Principal Component Analyses* (PCA) were performed on the 28 variables (24 variables for habitat and 4 for salmon and brown trout) for all stations in different tempi and contexts (see results and discussion). In the *XLSTAT* PCA tool, all data were normally distributed. The PCA is optimal for finding structure in and thereby interpreting significant variation between the variables within high-dimensional data sets. Because at least some of the variables are correlated (some highly correlated) the PCA is both capable of explaining less variance or more variance, depending on the level of explanation we request. The vectors of principal component score (eigenvectors of the correlation matrix) are uncorrelated linear combinations of weighted variables and explain the maximum amount of variance in the dataset. The PCA reduces the dataset into a set of independent principal components (PC) which we can look at separately to explain the maximal variance. All variables in the PCA are standardized with a mean (equal to zero) and a standard deviation (equal to 1). The first PC explains the largest amount of variance in the data set, whereas the second PC explains the second highest amount of variance, and so on. The eigenvalues of the correlation matrix are used for estimating the percentage of variance explained by each PC. The corresponding eigenvectors are used for obtaining the scores in the PC (for further details on PCA, see Ersbøll and Conradsen 2002:287–322).

Results and discussion

Weight and length relationship

At station 5 where the *mark/recapture method* was used (see Appendix 2), fishing efficiency had linear growth over time, reflecting the gradually increased experience with electrofishing. These initial results are therefore biased and not used in this thesis. However, the weight and length correlation used for Atlantic salmon and brown trout is gained from data on these species (82 salmon and 19 brown trout) recorded at station 5.



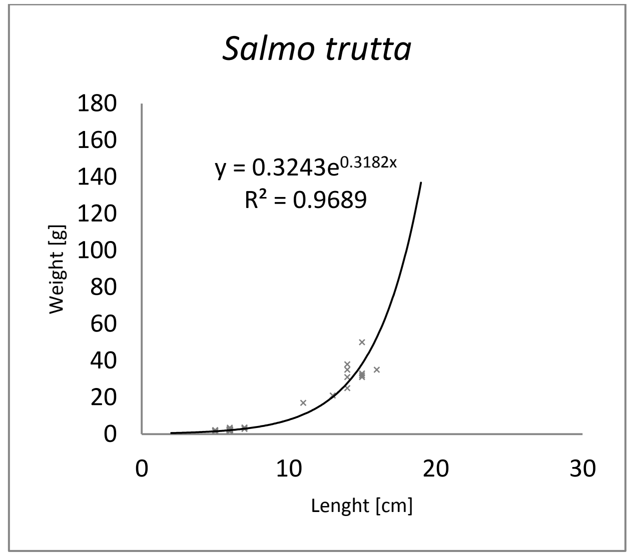


Figure 27: Correlation of length and weight for Atlantic salmon (Salmo salar) registered in station 5 (n=82).

Figure 28: Correlation of length and weight for brown trout (Salmo trutta) registered in station 5 (n=19).

For both species, the regression grows exponentially with an expected high correlation between length and weight: for Atlantic salmon an R^2- value of 0.9754 was obtained, and for brown trout and R^2- value of 0.9689 (Figures 27–28). However, the relationship between the two species is not expected to continue throughout the growth period. According to the model based on the graphs, brown trout obtain higher weights than salmon. The average weight of a mature salmon ranges between 3.5–5.5 kg and average lengths 70–75 cm. Thus, it will result in a more linear relationship between weight and length over time. These results indicate that parr of both species gain weight fast in their initial life stage. When salmon and brown trout fry grows into parr, the territorial borders are beginning to be established. Dominant individuals generally grow faster than subdominant ones. Moreover, salmon parr grow slow in high densities, even when food is abundant because of interactions with other individuals (Refstie and Kittelsen 1976:325f). Notice that the released parr in River Kongeå have gained the same sizes as the natural bread individuals in River Hjortvad.

Salmon abundance for all stations

The released salmon had grown from approximately 2 cm into 6–8 cm at the time of investigation, estimated from the abundance of these lengths for all stations. Remarkably higher quantities of parr were found within this length range (Figure 29).

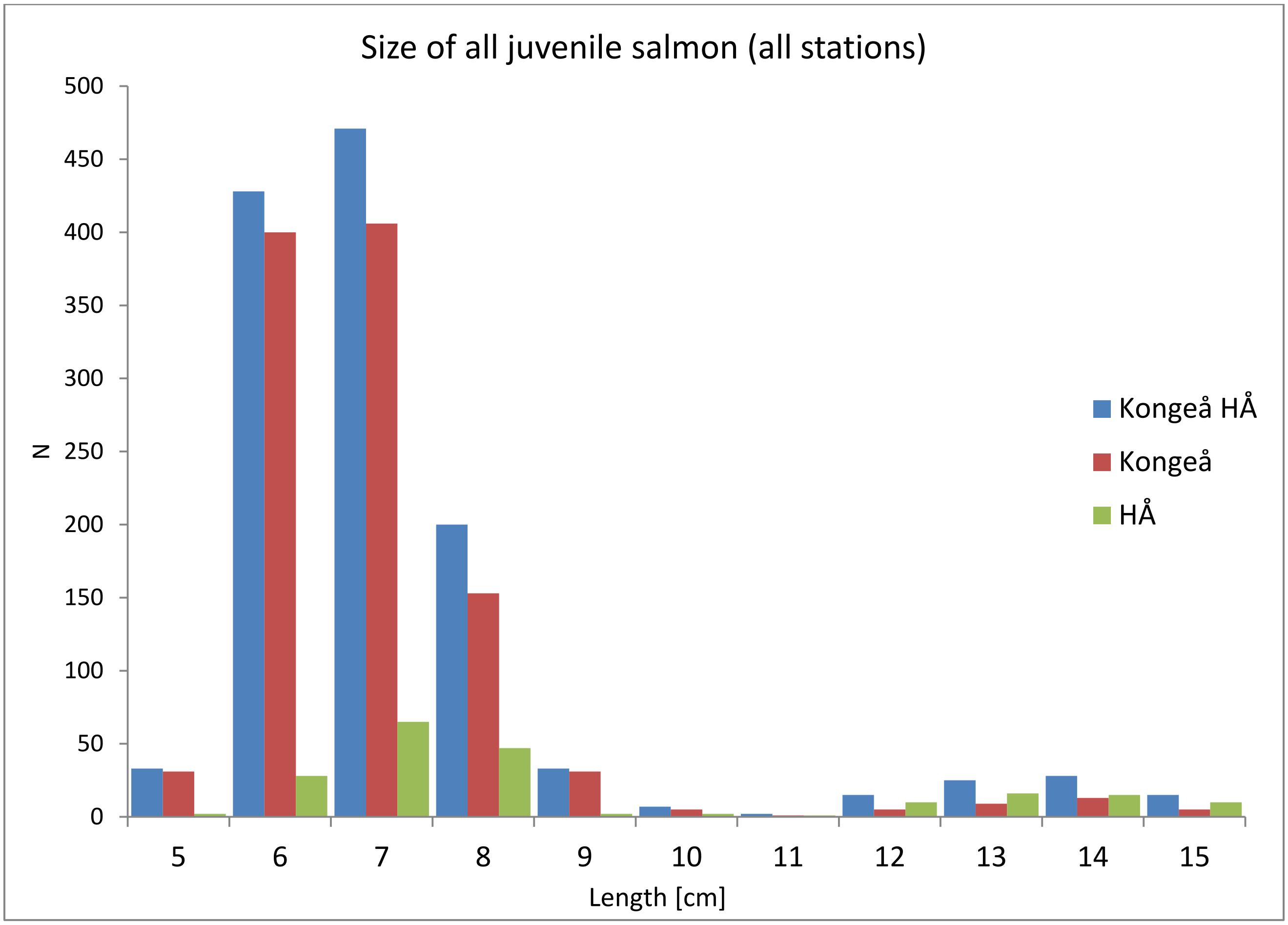


Figure 29: The high abundance of parr of 6–8 cm are presumably the released salmon, corresponding well to the growth of natural fry in River Hjortvad. Salmon bred in 2014 (0+) are set to ≤10 cm. Salmon bred in 2013 (1+) are set to ≤15 cm. The catch over this size was limited. The abundance of brown trout was also limited.

Temperature

A Canadian study from a river somewhat smaller than River Kongeå and thus more affected by temperature (i.e. width: 1.5–5.0 m / temp: 11.0–19.5°C) has demonstrated that salmon parr-habitats are dependent on temperature and density (Bult *et al.* 1999). According to the study, salmon parr shift habitat from pools and riffles to runs at higher temperature. They use high-quality habitats (primary habitat) when density is low but can also use habitats of lower quality (secondary habitats) when density is high (Bult *et al. 1*999). In our investigations, width varied from 7.5 to 21 metres. Temperature fluctuations at the time of investigation are illustrated in Figure 30, varying maximum 2.7°C from lowest night-temperature to highest day-temperature within 24 hours. The maximum difference between the highest temperature and the lowest in the entire period is 3.7°C. Hence, temperature fluctuations during the investigation period were fairly constant and within ideal ranges for the species, based on studies suggesting that temperatures are optimal around 16°C with minimum critical limits below 6°C and maximum critical limits beyond 25°C (Elliot and Hurley 1997:597; Elliot *et al*. 1998:273; Armstrong *et al.* 2003:162).

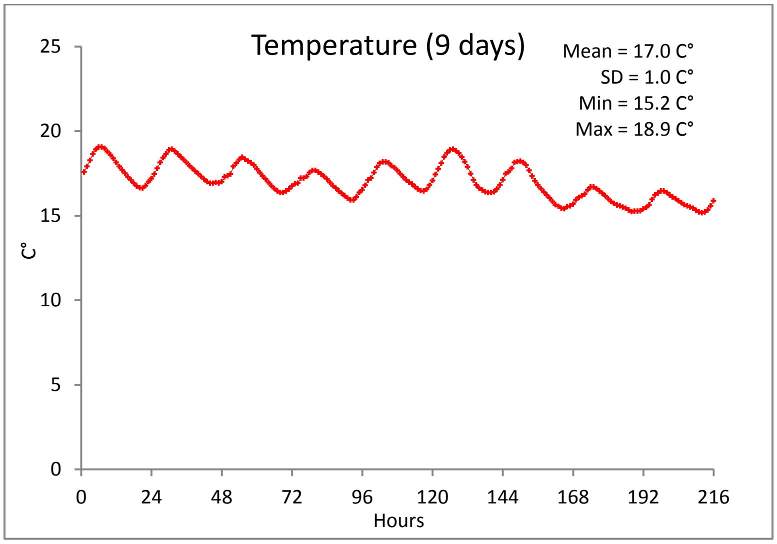


Figure 30: Water temperatures from July 24th 2014 – August 2nd 2014. The highest temperature span between night and day (24 h) was 2.7 C°. Water temperature was generally high with a maximum day temperature of 18.9 C°.

Variance between stations

For all 12 stations in River Kongeå, 28 variables were recorded. Station 5 was excluded from the analyses, partly because the station was investigated by the *mark-recapture method* and therefore not meeting the demands of the method, i.e. that recordings should be standardized. Moreover, station 5 was the first station we electrofished and therefore efficiency was low here (see Appendix 2). The 13 analyzed stations are thus 11 in River Kongeå and 2 in River Ribe (Hjortvad) å (see Appendix 1). Data were collected from 395 points (each one square metre) in River Kongeå and 38 points in River Ribe (Hjortvad) å.

To ensure that data from each station were in fact compatible, several tests were performed on all data recorded on velocity and depth. *Kruskal Walis one-way-analysis of variance* (equivalent with ANOVA) was used. For both velocity and depth, the test demonstrated that the observations came from different populations with a significance level at 0.05.

In each station, the size of the recorded area varied significantly. Hence, it was necessary to standardize (extrapolate) the recorded data from all stations to 100 m^2. The entire area in which we had released salmon was huge, and therefore it was only meaningful to investigate smaller areas in average of 184±36 m^2 at each station (see table 1.1 in appendix 1:ii).

There was no correlation between the released salmon per 100 m^2 and the number of salmon electrofished two months later. A linear regression analysis gave a correlation of only 0.0001% (R^2) at significance level 0.05, reflecting that although the amount of released salmon varied between 516–667 pr. 100 m^2 for all stations, this difference in number of released fry did not influence the results (see Table 1).

Station	Mean width [m]	Length [m]	Total areal [m^2]	Released per 100 m^2	Estimated survival per 100 m^2	Density: 0+ per 100 m^2
1	7.5	120	900	667	350	62
2	14.0	80	1120	536	281	12
3	15.5	75	1163	516	271	36
4	12.5	70	875	686	361	82
6	15.3	70	1071	560	294	73
7	15.5	60	930	645	339	26
8	19.0	60	1140	526	277	41
9	15.5	70	1085	553	291	31
10	18.5	100	1850	540	284	106
11	17.5	100	1750	571	300	81
12	18.0	180	3240	525	276	121
HÅ 1	8.0	125	1000	-	-	94
HÅ 2	7.5	125	938	-	-	48

Table 1: Mean width and total size of the investigated areas at the 11 stations in River Kongeå and the two stations in River Ribe (Hjortvad) å (HÅ 1 and HÅ 2). The lengths are measured with an in-build tool on a map provided from www.Krak.dk. From this estimate the total areas of all stations are calculated. The 0+ (≤10 cm) estimated density based on the removal method. For all stations it is assumed that the maximum capacity per 100 m^2 is reached

Salmon fry are exposed to many threats and mortality is high during the early (fragile) stage of life. The estimated survival rates in Table 1 are calculated from the assumption that the mortality rate during the first year is 1% per day (Shearer 1992:45). It has not been possible to obtain data on mortality and survival rates for fry from hatcheries compared to natural fry. However, studies on pacific salmon indicate that the “fitness to survive” is less pronounced among fish from hatcheries compared to wild fish (Unwin 1997:1252). Hence, it is possible that the maximum survival on each station is lower than the estimated numbers in Table 1.

Despite uncertainties and disagreements within the study, the average carrying capacity pr. 100 m^2 for parr (1+) in larger rivers was estimated to 12 per 100 m^2 (mean) by Gustafson and colleagues in 1984 (Gustafson *et al.* 1984:715). However, Danish recommendations for brown trout parr (0+) suggest up to 250 pr. 100 m in water courses wider than 2 m for the best ecological state (DCE 2014).

Density

Apart from Station 5, results from electrofishing were calculated for each of the other stations using *the removal method* with 2 samples (see Appendix 2). Figures 30 and 31 display results of juvenile salmon gained for each of the sites. Each bar indicates the estimated density N±SE for 0+ and 1+ at the given station. Figure 33 displays the total catch of both salmon and brown trout.

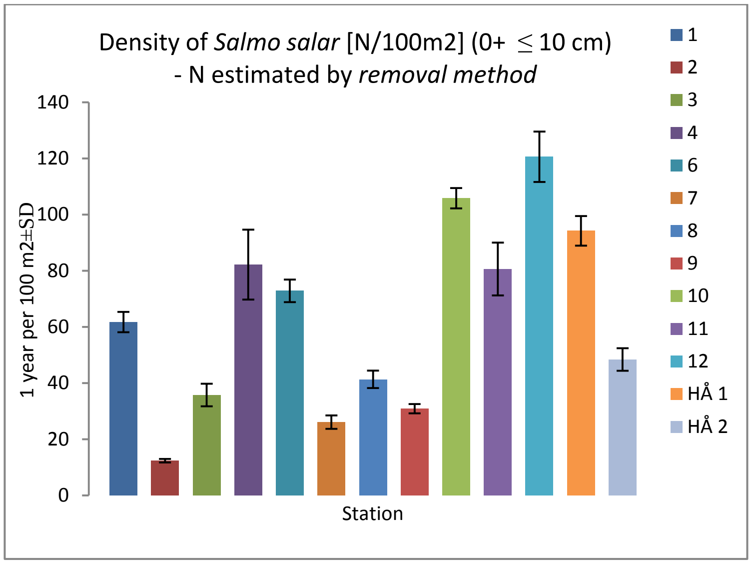


Figure 31: Histogram giving an overview of the salmon 0+ density for each of the 11 stations in River Kongeå and the two in River Ribe (Hjortvad) å. The black bar indicates Standard Error.

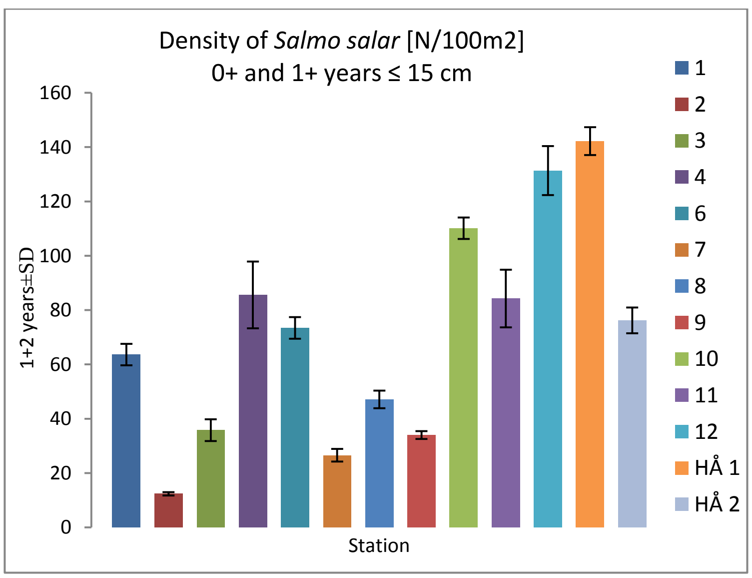


Figure 32: Histogram with both salmon groups up until 15 cm. The density N is estimated with the removal method. The histogram reflects almost the exact same pattern as in Figure 31. The black bar indicates Standard Error.

In Figures 31–32, the highest densities for 0+ and 1+ are found in station 12. The lowest density is found in station 2. Particularly stations 10, 12 and HÅ 1 have remarkably higher densities than the remaining stations. Stations 1, 4, 6, 11, and HÅ 2 fall in the middle density group and stations 3, 4, 7, 8, and 9 in the low density group. In stations 1 and 2 in River Ribe (Hjortvad) å (HÅ 1 and HÅ 2), the group of salmon ranging from 10 cm to 15 cm is very large, reflecting that the river had a large population of salmon spawning in 2013 (natural spawning). The two stations in River Ribe (Hjortvad) å were also the best of the brown trout habitats, with a significant higher density than the 11 stations in River Kongeå. However, there is no indication of interspecies competition between brown trout and Atlantic salmon. Conversely, good habitats had relatively large densities of both species, particularly in River Ribe (Hjortvad) å.

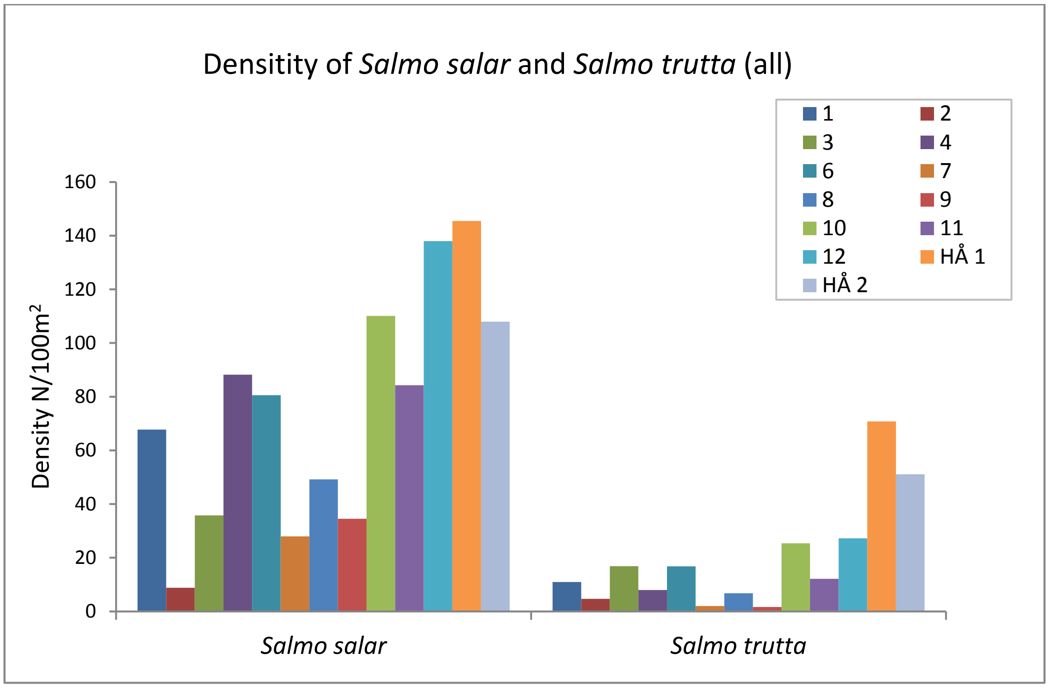


Figure 33: Density of young and older salmon and brown trout for the 11 sites in River Kongeå and the two in River Ribe (Hjortvad) å. Brown trout density was remarkably higher at the two stations in River Hjortvad. This is presumably partly because the connectivity is better in River Ribe (Hjortvad) å compared to River Kongeå and due to artificial adding of gravel into River Ribe (Hjortvad) å by the Danish Nature Agency. Moreover, there was more bank vegetation in River Ribe (Hjortvad) å (e.g. trees) providing shadow and thereby preventing too much submerged vegetation. Presumably for these reasons, the salmon population has been self-sustainable since 2012 (Naturstyrelsen 2012).

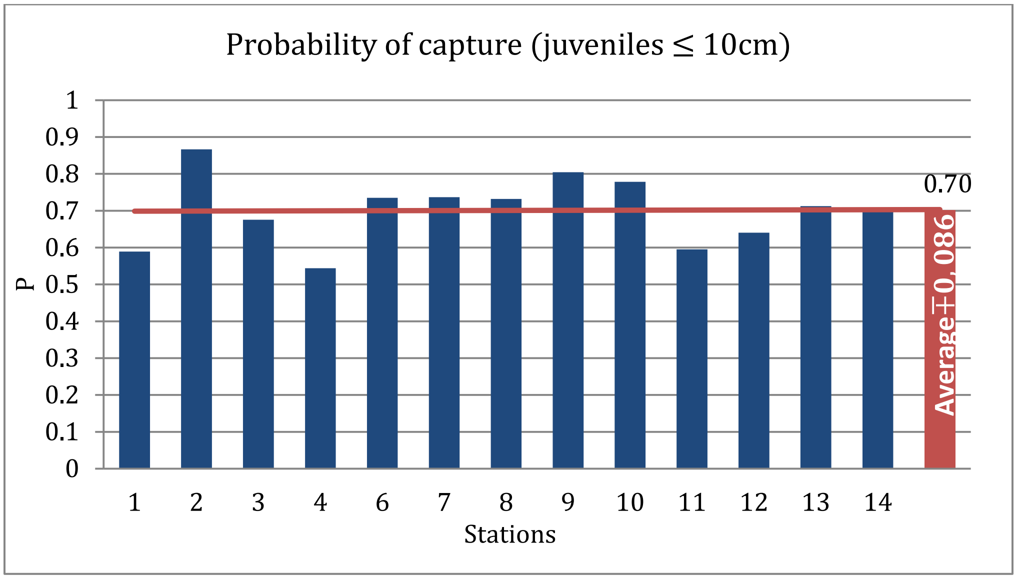


Figure 34: Electrofishing efficiency in all stations. The average efficiency was 0.70±0.086 (±Standard deviations calculated for each of the 14 stations – the standard errors of the efficiency for each station are not included in the analysis). The efficiency was fairly constant throughout the investigations (except from station 5) (for comprehensive mathematical details see Appendix 2).

Although density in all stations is low for brown trout and in some stations also for salmon, the results are considered valid because of the high and known constant efficiency rate at 0.7±0.086 (see Appendix 2). The specific reason for the density pattern for natural bread individuals may well be the weir further downstream of the investigated area, reducing access for spawners.

Substrate

Mean values for substrate types for each of the stations is illustrated in Figure 35 in percentages. On average 33 points of 1 m^2 were described, depending on the width of the station. HÅ 1 and HÅ 2 (River Ribe (Hjortvad) å) are particularly rich in stone because these two stations are artificially created. However, sand is also dominant in these stations.

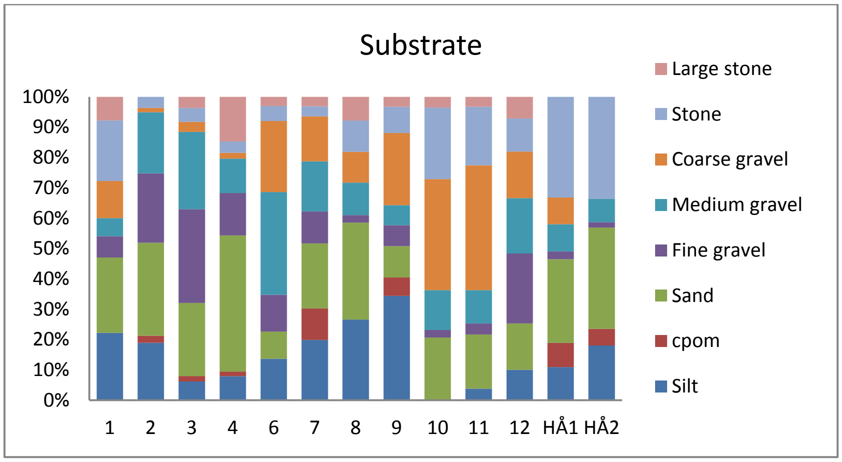


Figure 35: Percentages of substrate types in each station. Compared to the 11 stations in River Kongeå, the two stations in River Ribe (Hjortvad) å (HÅ1 and HÅ2) stand out because of many stones (64–128 mm). Relatively large amounts of sand were identified in all stations including the two in River Ribe (Hjortvad) å.

Vegetation

Figure 36 illustrates the relative amount of vegetation in each station combined with vegetation types (plant species). It is immediately observed that station 2 has the highest proportion of overall vegetation, dominated by *Lemna sp.* This is consistent with the observation that almost no salmon or brown trout were found in the areas covered with *Lemna sp.* (often associated with low water velocity and the co-existence of several other vegetation species). For the two stations in River Ribe (Hjortvad) å (HÅ 1 and HÅ 2), fewer species were present and the overall amount of vegetation reaches beyond 50%, dominated by *Sparganium sp.* and *Ranunculus sp.* Perch, pike and eel were often found in areas with large amounts of *Sparganium sp.* and *Lemna sp.* (associated with slow waters and substrates dominated by sand and silt). *Sparganium sp.* only stood out as a negative parameter if the vegetation was homogenous and large areas were covered with *Sparganium sp.* exclusively (and often also *Lemna sp.*). If the cover of *Sparganium sp.* was interrupted with vegetation-free zones, and substrates dominated by gravel in different sizes and sand (associated with higher water velocities), the appearance of *Sparganium sp.* did not seem to affect salmon density negatively. High water velocity comes (in most cases) naturally when the river is in a good ecological state (e.g. with a meandering morphology).

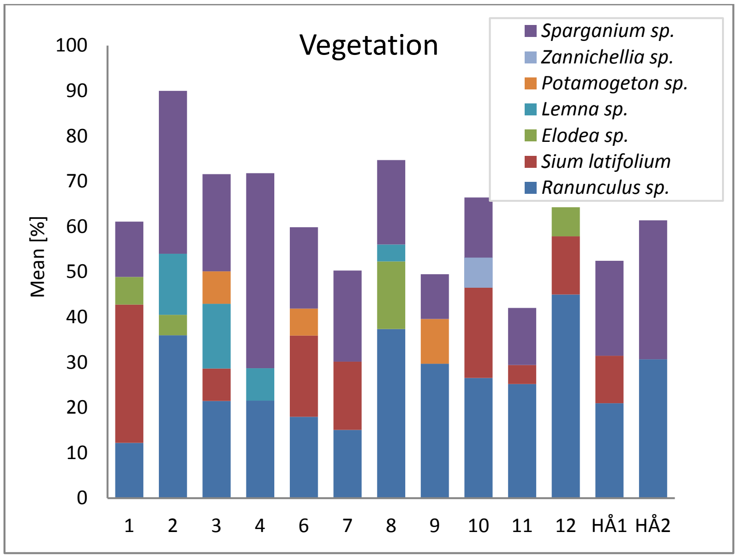


Figure 36: Histogram illustrating both the amount of vegetation in percentages in each transect and the fraction of each species. Ranunculus sp. and Sparganium sp. are the two species frequently represented. Lemna sp. was only represented in areas with slow water (often close to the bank and often with other types of vegetation beneath). However, neither salmon nor brown trout used areas with slow waters and the correlated high amounts of Lemna sp. and Sparganium sp. Instead, perch and pike were often found in these areas. Zannicehllia sp. was only found in station 10, however, in relatively high amounts.

PCA – all data

Principal Component Analyses were performed on three slightly different sets of data. The first analysis was on all stations including the two stations in River Ribe (Hjortvad) å. The second analysis was on the stations in River Kongeå exclusively, and the third analysis was performed with reduced (but more important) variables for River Kongeå. This last PCA was to investigate how the variables were considered important in relation to each other.

For all variables, a correlation matrix was calculated. In Table 2 only the correlation of all variables with salmon ≤10 cm; salmon ≤15 cm; and trout ≤15 cm is illustrated. Values in colour and bold differ significantly from zero. The matrix reflects a strong correlation between salmon, depth, velocity, stone, 'veg/no veg' (shifting vegetation) and silt. Furthermore, all variables are negatively correlated with depth.

Whereas small salmon ≤10 cm and velocity are positively correlated, trout ≤15 cm and salmon ≤15 cm are not significantly correlated with velocity, reflecting that salmon habitats differs from brown trout habitats, which is also suggested in other studies (Heggenes 1996; Heggenes and Saltveit 1990; 2007).

The matrix suggests a correlation between trout and trees; however this is uncertain because land vegetation in the size of trees was generally very limited. There also appear to be a correlation between width and trout, but also this result may be uncertain because the two stations in River Ribe (Hjortvad) å were broad and had higher densities of trout compared to River Kongeå. In general River Kongeå had low densities of natural salmon and trout.

Variables	Salmon ≤10 cm	Salmon ≤15 cm	Trout ≤15 cm
Salmon 1	**1**	**0.941**	0.273
Salmon 2	**0.941**	**1**	0.536
Salmon old	0.095	0.177	0.477
Trout young	0.273	0.536	**1**
Trout old	0.532	0.548	0.410
Depth	**-0.585**	**-0.722**	**-0.696**
Velocity	**0.647**	0.412	-0.362
Vegetation	-0.250	-0.333	-0.237
Trees	0.064	0.272	**0.690**
Silt	**-0.610**	-0.513	-0.206
cpom	-0.360	-0.111	0.396
Sand	-0.087	-0.057	0.136
Fine gravel	-0.147	-0.221	-0.309
Medium gravel	-0.009	-0.137	-0.143
Coarse gravel	0.395	0.284	-0.152
Stone	0.432	**0.601**	**0.745**
Large stone	0.284	0.091	-0.505
Veg/no veg	0.478	**0.609**	**0.614**
Width	0.083	-0.139	**-0.625**
Bank undercut	0.462	0.381	0.188
Ranunculus sp.	0.103	0.108	-0.124
Sium latifolium	0.368	0.262	-0.015
Elodea sp.	-0.097	-0.205	-0.329
Sparganium sp.	-0.386	-0.324	0.128
Lemna sp.	-0.472	-0.512	-0.225
Potamogeton sp.	-0.320	-0.285	-0.116
Zannichellia sp.	0.391	0.281	-0.046
Emergent	0.188	0.343	0.525

Table 2

Table 2: Correlation matrix used to extract information to the principal component. Normally, the correlation matrix is symmetric, with all variables displayed in both rows and columns. However, in this table only the correlation between the variables we want to study further is shown. Only the correlated values with a significance level of 0.05 are marked with yellow (if they are negatively correlated) and green (if they are positively correlated with salmon). The rest of the values are insignificant and cannot be excluded from a value of zero correlation. Thus, salmon ≤10 cm and salmon ≤15 cm are m positively correlated with velocity and negatively correlated with depth and silt. A slightly different scenario is seen for salmon ≤15 cm which is significantly correlated with stone and the variable 'veg/no veg'. Salmon ≤15 cm has (similarly to salmon ≤10 cm) a significant negative correlation with depth. For trout ≤15 cm, it is uncertain whether they are correlated with salmon with any statistical significance. However, trout is significantly positively correlated with trees, stone and 'veg/no veg' and significantly negatively correlated with width (which was insignificant for both groups of salmon in the correlation matrix).

The first PCA was done for all stations in River Kongeå and the two in River Ribe (Hjortvad) å.

The eigenvalues in a PCA give information about the principal components (PC) and how much of the variability is explained in each of these by percentages of the entire variability within the variables in all stations. In Table

3, the eigenvalues for all of the five components together are shown (explaining the highest amount of the variability). It is important to keep in mind that the PCA does not only give information about one variable but about all variables and how the vary with each other (with a significance level of 0.05). The eigenvalue for the first eigenvector (i.e. principal component (F1)) explains 26.8% of the variability. As such, the first five eigenvalues together explain 77.1% of all variability on all stations.

Eigenvalues:

	F1	F2	F3	F4	F5
Eigenvalue	7.492	5.273	3.706	3.002	2.121
Variability (%)	26.757	18.833	13.236	10.723	7.575
Cumulative %	26.757	45.590	58.826	69.549	77.123

Table 3: Eigenvalues for the first five principal components F1–F5. The eigenvalues reflect exactly how much of the variability the principal components explain. The first eigenvalue (corresponding to the first principal component (F1)) explain 26.8% of the variability, the next eigenvalue explain 18.8% of the variability, etc. The last principal component (F5) only explains 2.1% of the variation, and is therefore practically irrelevant (contributing with too little information).

The Scree plot in Figure 37 illustrates the cumulative variability as a red curve adding up to 100%. The bars reflect the eigenvalues. The first PCs are listed according to their proportion of information about the variables. Hence, the first PC will always contain the most information.

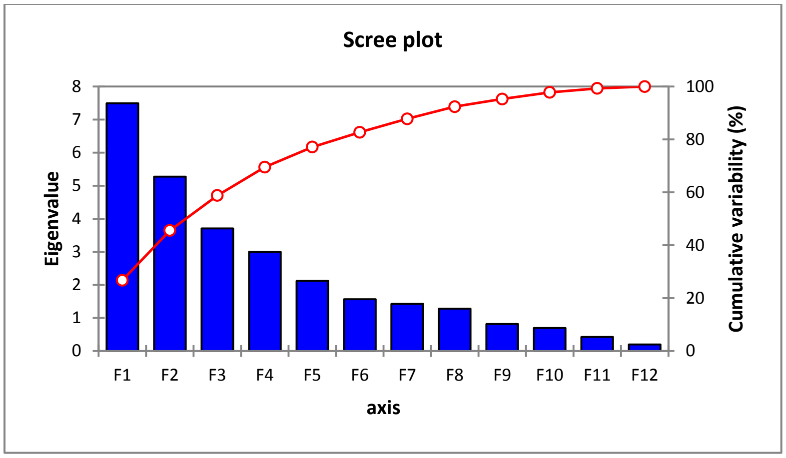


Figure 37: Scree plot for the eigenvalues. In the actual PCA, all variables and the data from River Ribe (Hjortvad) å are included. In Table 3 the first five eigenvalues are examined. However, in the PCA the results yield 12 eigenvalues and 12 corresponding principal components (eigenvectors). The Scree plot displays the eigenvalues in the blue bars, with the proportion of explanation in the left y-axis. The red curve illustrates the cumulative percentage (the right y-axis).

	F1	F2	F3	F4	F5
Salmon 1	-0.257	0.190	0.116	-0.030	-0.211
Salmon 2	-0.293	0.074	0.110	0.025	-0.126
Salmon old	-0.085	-0.081	-0.255	0.277	-0.157
Trout young	-0.236	-0.237	0.075	0.234	0.050
Trout old	-0.212	0.157	0.209	0.095	0.174
Depth	0.325	0.063	-0.163	0.005	-0.099
Velocity	-0.110	0.377	0.076	-0.039	-0.151
Vegetation	0.206	0.036	0.357	0.059	0.001
Trees	-0.190	-0.311	0.057	-0.051	-0.071
Silt	0.148	-0.178	-0.239	-0.247	0.254
cpom	-0.022	-0.287	-0.187	0.103	0.113
Sand	0.060	-0.206	0.366	-0.163	-0.179
Fine gravel	0.210	0.115	0.110	0.294	-0.113
Medium gravel	0.110	0.193	-0.095	0.388	-0.142
Coarse gravel	-0.190	0.253	-0.232	-0.075	0.112
Stone	-0.324	-0.135	0.095	-0.055	0.105
Large stone	0.107	0.102	0.102	-0.343	-0.378
Veg/no veg	-0.314	-0.127	-0.056	-0.073	-0.018
Width	0.097	0.362	-0.044	-0.042	0.200
Bank undercut	-0.189	0.215	0.030	0.117	0.157
Ranunculus sp.	0.033	0.128	0.234	-0.064	0.476
Sium latifolium	-0.135	0.107	-0.150	-0.021	-0.393
Elodea sp.	0.099	0.062	0.147	-0.342	0.166
Sparganium sp.	0.143	-0.227	0.222	0.108	-0.153
Lemna sp.	0.257	-0.006	0.268	0.224	-0.006
Potamogeton sp.	0.125	0.043	-0.285	0.200	0.123
Zannichellia sp.	-0.142	0.219	0.094	-0.010	-0.015
Emergent	-0.116	-0.041	0.247	0.380	0.153

Table 4

Table 4: The first five principal components, explaining 77% of the total variation. Because of the high numerical values for salmon 1 (0.257) and salmon 2 (0.293), F1 is considered to contain most information on salmon parr (≤15 cm). Salmon 1 (≤10 cm) and salmon 2 (≤15 cm) vary together with velocity and silt (in particular). Because they vary in all of the first 3 principal components F1–F3, they are considered important.

Too high depth, vegetation, fine gravel and Lemna sp. vary negatively with salmon in F1 (counting for 27% of the variability). Stone and 'veg/no veg' instead have a positive effect on salmon habitats, whereas sand does not contribute with any information (obtained the lowest numerical score (0.060)).

Although F2 explains 19% of the variation, the score for salmon in this component is relatively low (<200) because other factors than primarily salmon dominate the component explanation. For example, trout obtains a high numerical value here, and therefore this information is more relevant for trout than for salmon, indicating that there are in fact differences between salmon and trout habitats.

In F2 it is seen that when velocity is too high and the river too wide, then the effect on trout is negative. Even though factors such as coarse gravel and 'bank undercut' are present. This is, however, not the case with salmon 1 and 2. Similar results have been found by Heggenes and Salveit (1990).

Only the first five PC's are shown in Table 4. Together they explain 77.1% of the total variation in all stations, including the two in River Ribe (Hjortvad) å. Each PC (F1–F5) is independent, and each value contributes with information about the variable. All variables with large numerical values vary together. When variables are positively correlated, they are all either positive or negative and *vice versa*. Values close to 0 have no importance in the particular component but may still vary with other variables in other components. A high value reflects that the PC's contain much information about the actual variable (e.g. gravel). The first PC (F1) gives information about the variability of the variables in 27% of all stations. In Table 4 it is evident that both salmon and trout vary with each other (and are all negative in F1). They are all positively correlated with stone, ‘veg/no veg’ and *lemna sp.* (yellow) and negatively correlated with depth and vegetation (green). All numerical values above 0.200 are considered of high importance. However, although velocity and silt do not have numerical values above 0.200, they are still considered important factors because they vary with salmon in all of the first three PC’s (F1, F2 and F3) together explaining 59% of the overall variance, indicating that these are highly related variables. That silt and velocity are two of the most important variables are verified in the correlation matrix by a 95% confidence interval (see Table 2).

In this analysis, young parr (≤10 cm) varied negatively with fine gravel, depth and vegetation and positively with stone and variance in vegetation (veg/no veg). Sand, medium- and coarse gravel did not contribute much to explaining the variance in the first component (which explained the most of the variance for young parr (≤10 cm)). However, in the second PC (explaining 18% of the variance) trout ≤15 cm varied negatively with coarse gravel and positively with CPOM and sand, i.e. demonstrating the exact opposite as what we normally associate with trout parr.

The PC’s tell us that there are different ways of seeing it. The first PC counts for the highest level of variance. In Figure 38 the first PC is plotted against the second, explaining 46% of the overall variation. The closer the variables are to origo (0.0), the less they vary with the other variables. The plot displays how the variables group: Velocity, coarse gravel, ‘bank undercut’ and *Zannichellia sp*. group with salmon parr and are thus positive physical factors in salmon habitats in this analysis. Trout have similar behaviour in the first component, however, not in the second. Hence, trout and salmon cluster differently. The blue lines indicate how the variables spread with salmon ≤10 cm and ≤15 cm. The variables on the opposite site (close to the blue line) are associated with poor habitat quality, whereas the variables close to the blue line on the salmon site are positive qualities. Hence, we can also see that ‘veg/no veg’ and stone both have a positive effect. These variables will also vary with each other, and if they increase the amount of salmon will decrease. Sand, silt and *Sparganium sp*. are grouped as negative variables in the plot. However, we also see variables close to the blue line opposite of salmon (*Lemna sp.*, vegetation, fine gravel and depth) and these also have a negative influence on the habitat.

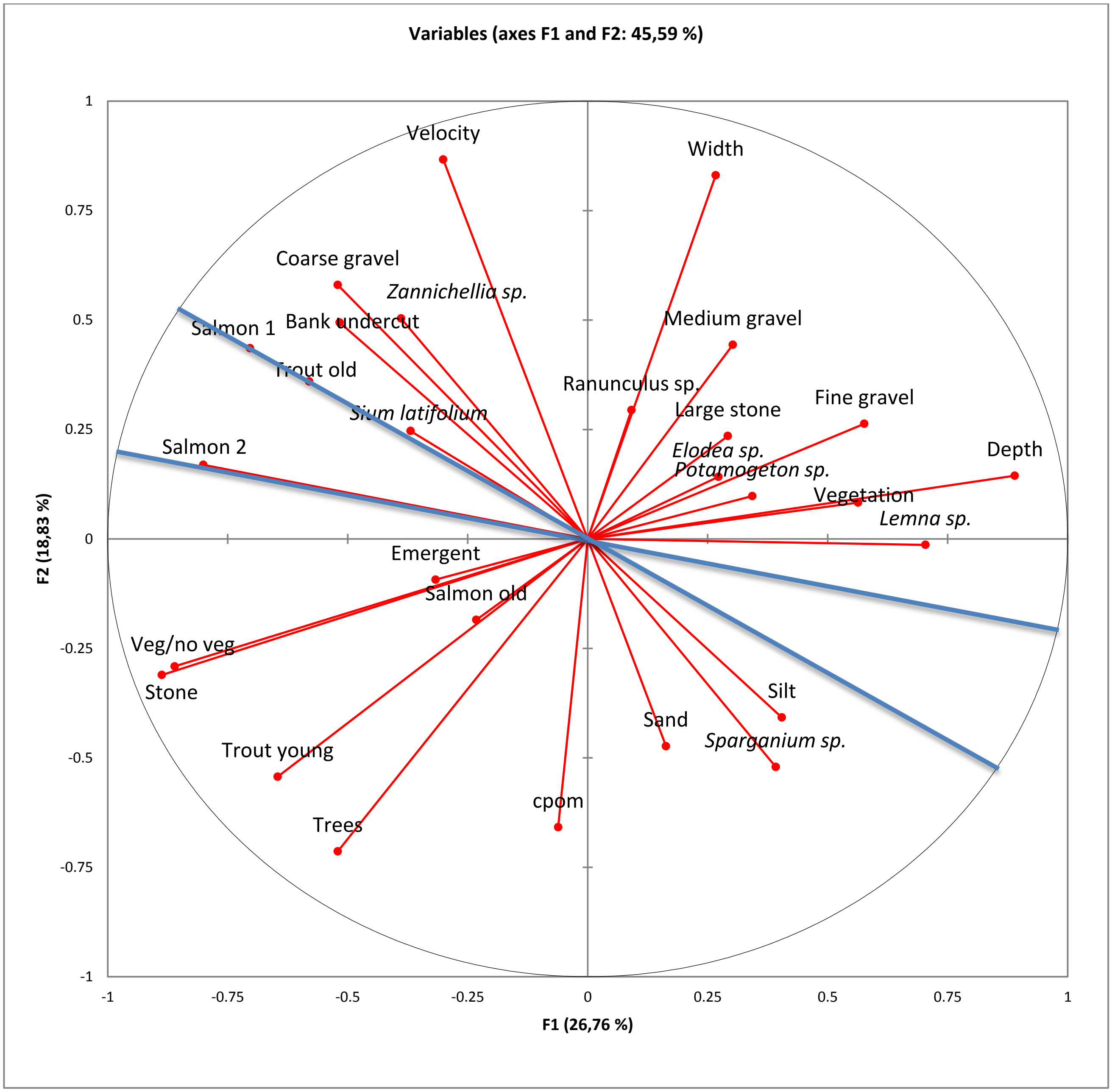


Figure 38: PCA 1. Plot illustrating the first principal component (F1) plotted against the second (F2). If the variable is close to origo (0.0) it is not considered important. Because the plot is a projection of information from the first 2 components, it is twice as informative than intepreting only one component. The blue line indicates the importance of the variables in relation to salmon 1 (≤10 cm) and salmon 2 (≤15 cm). The more important a varible is in both F1 and F2, related to salmon, the closer it (the value) will be to (the value for) salmon on this line. If it has a negative effect on salmon it will be in the opposite direction. The plot indicates that stone, 'veg/no veg' and coarse gravel are important variables in salmon habitats. On the other hand, Sparganium sp. and Lemna sp. are negative factors. Sand obtains a low score and is therefore considered less important, together with, for example, emergent vegetion and large stones.

In Figure 39 it is seen how the stations are related to each other in the two first components. Stations 10, 11 and 12 are grouped. Particularly in stations 11 and 12, salmon density is high. Stations 1, HÅ 1 and HÅ 2 also group and have similar characteristics. These three stations are also the only artificially constructed spawning sites represented in the analysis. During our investigations, we observed low salmon density in stations 2, 7 and 9. In the plot, we can also see that these three group with similar physical characteristics.

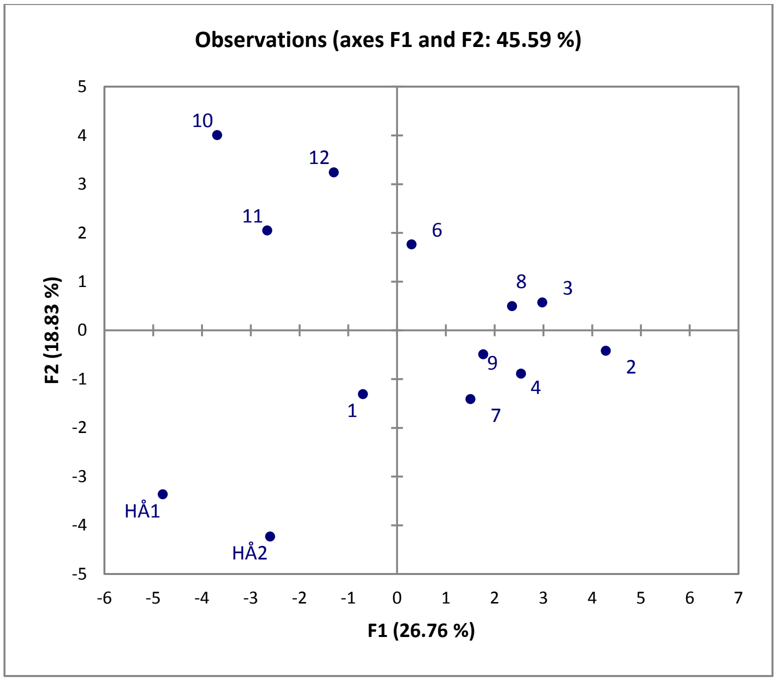


Figure 39: The first principal component plotted against the second. River Ribe (Hjortvad) å groups slightly with station 1 which was also an artificially constructed riffle. However, the values for Station 1 are not as high as the values in the first and second component for River Ribe (Hjortvad) å. The rest of the stations group because they have almost similar features.

This particular analysis contributes with the highest level of information because it includes data from River Ribe (Hjortvad) å, which were slightly different from data recorded in River Kongeå, i.e. the artificially constructed stations in River Ribe (Hjortvad) å are narrow and shallow compared to the stations in River Kongeå. Moreover, River Ribe (Hjortvad) å had the highest densities of trout, whereas the abundance of trout in River Kongeå was indeed limited. The low density of natural occurring trout and salmon in River Kongeå is presumably due to the dam and fish farm Jedsted Mølle downstream of the investigation area (e.g. Figures 4–7).

PCA 2 – Data from River Kongeå

The highest densities of trout were recorded in River Ribe (Hjortvad) å, reflecting the characteristic attributes of these two sites (i.e. both stations are artificially constructed, narrow and shallow). Therefore a PCA containing only data from the stations in River Kongeå was performed. The correlation matrix for this analysis reflected the same significant correlation between salmon, velocity, depth and silt. The eigenvalues in Table 5 reflect that the first PC (F1) explains 32% of the total variation, the second 17% (the two in combination describe 42% of the total variation), etc.

	F1	F2	F3	F4	F5
Eigenvalue	7.976	4.181	3.586	2.562	1.811
Variability (%)	31.906	16.722	14.343	10.249	7.245
Cumulative %	31.906	48.628	62.971	73.219	80.465

Table 5: Percentages of the explained variablity in each component. The first component (F1) explains 32% of the overall variation. All together, the five components explain 80% of the total variation.

In Table 6, the first three principal components are shown, all three with positive values in Salmon (Salmon 1 and 2) and velocity, reflecting that velocity is to be considered one of the most important variables in salmon habitats, which is also proposed by Heggenes (1990). In contrast, depth is a negative variable together with silt and CPOM (Coarse Particulate Organic Matter).

	F1	F2	F3
Salmon 1	0.289	0.130	0.137
Salmon 2	0.282	0.121	0.102
Depth	-0.312	-0.085	-0.108
Velocity	0.312	0.182	0.076
Vegetation	-0.178	0.282	0.249
Trees	0.043	-0.284	0.257
Silt	-0.166	-0.314	-0.074
cpom	-0.145	-0.206	-0.243
Sand	-0.140	0.049	0.429
Fine gravel	-0.154	0.292	-0.043
Medium gravel	-0.046	0.245	-0.241
Coarse gravel	0.290	-0.076	-0.224
Stone	0.297	-0.091	0.125
Large stone	0.007	-0.078	0.394
Veg/no veg	0.283	-0.178	0.003
Width	0.108	0.237	-0.211
Bank undercut	0.217	0.194	-0.115
Ranunculus sp.	0.016	0.274	0.017
Sium latifolium	0.179	-0.160	0.056
Elodea sp.	-0.034	-0.017	0.261
Sparganium sp.	-0.240	0.097	0.175
Lemna sp.	-0.249	0.277	0.089
Potamogeton sp.	-0.099	-0.047	-0.350
Zannichellia sp.	0.200	0.113	0.022
Emergent	0.028	0.362	-0.076

Table 6

Table 6: Scores from the first 3 components containing information on 63% of the total variation. Firstly, salmon varies positively with velocity and negatively with depth, silt and CPOM in all 3 components. F1 (32%) contains most of the information regarding salmon, reflected in the high numerical value (0.289). Here, salmon varies positively with velocity, coarse gravel, stone, veg/no veg, 'bank undercut' and Zannichellia sp and negatively with depth, Sparganium sp. and Lemna sp. The rest of the information in the component is less important and does not vary much with salmon (low scores for salmon in F2 and F3).

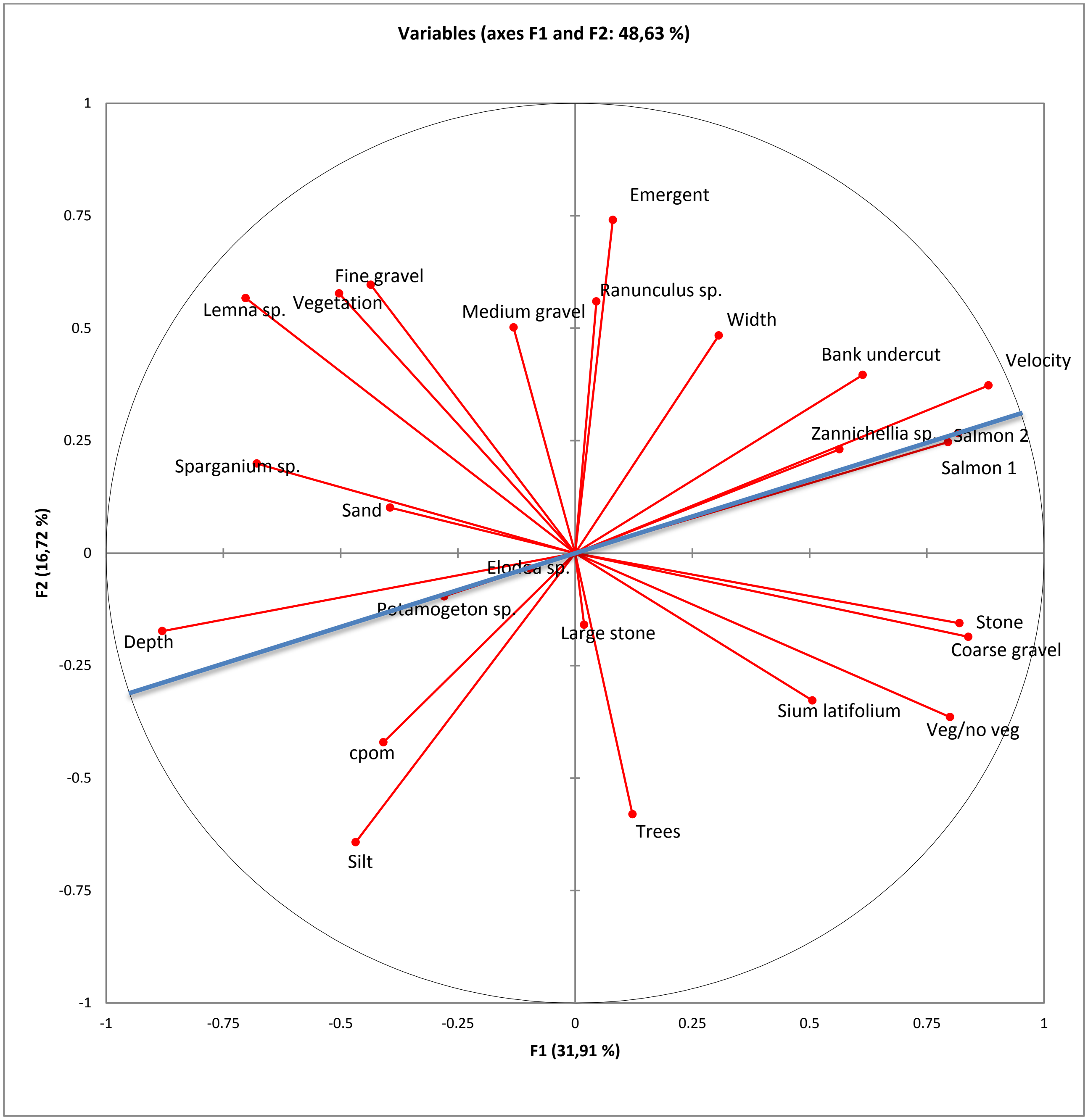


Figure 40: PCA 2. The first principal component plotted against the second. As also reflected in Figure 38, salmon does not have a high numerical value in the second component, and therefore the information on salmon is less important. However, the plot counts for 49% of the total variation (e.g. Table 5). Velocity is seen in the almost same postion as salmon, being the most significant positive variable. Depth is directly opposite (see the blue line), and therefore regarded as the most negative variable.

In the plot of the first two PC's in PCA 2 (Figure 40), depth is almost directly opposite of salmon (close to the blue line) grouping with CPOM and silt. Similarly, *Sparganium sp.* and sand both have negative effects. Conversely, velocity and 'bank undercut' both group near Salmon (1 and 2). *Zannichella sp.* was only found in one station, and the positive result for this specific species is uncertain. Stone, coarse gravel and 'veg/no veg' all have positive effects on the salmon habitat. Compared to the full dataset in PCA 1 (from all stations including River Ribe (Hjortvad) å), CPOM is more negatively correlated with Salmon in River Kongeå. Otherwise the general pattern within the variables is similar.

PCA 3 - important variables

Based on these findings we can perform a third PCA, however, on a reduced dataset reflecting which of the variables from the two first PCAs are considered truly negative or positive in salmon habitats. Again, the correlation matrix for this analysis reflected the same significant correlation between salmon, velocity, depth and silt as the correlation matrix for PCA 1 and PCA 2.

The eigenvalues in Table 7 reflect that the first PC explains as much as 46.9% of the total variation.

	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10
Eigenvalue	7.044	2.858	1.676	1.082	0.874	0.666	0.277	0.236	0.158	0.129
Variability (%)	46.961	19.051	11.173	7.214	5.829	4.438	1.847	1.574	1.055	0.859
Cumulative %	46.961	66.011	77.184	84.398	90.227	94.665	96.512	98.085	99.141	100.000

Table 7: All eigenvectors (100% information). Notice that the first principal component explains as much as 47% of the total variation.

Looking more closely at the variables combined with all PC's in Table 8, we can see that the first PC does in fact contain all the relevant information related to salmon. Conversely, salmon has almost no effect on components 3 and 4, instead holding (other) information that has little effect on salmon. The fifth component counts for only 5.8% of the overall variation (see table 5) and holds little information on overall variation which is also the case for the remaining PC's (F6–F10).

	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10
Salmon 1	0.321	0.161	-0.143	-0.132	-0.256	0.356	0.091	-0.049	-0.008	0.179
Salmon 2	0.313	0.130	-0.110	-0.194	-0.320	0.368	0.089	-0.168	-0.249	0.017
Depth	-0.336	-0.075	0.037	0.160	0.091	0.453	-0.145	-0.151	-0.125	-0.054
Velocity	0.337	0.185	-0.132	-0.045	-0.066	-0.229	-0.065	-0.313	0.083	-0.186
Silt	-0.191	-0.324	0.286	-0.425	0.306	0.191	0.106	0.053	-0.020	0.109
Cpom	-0.171	-0.383	0.152	0.149	-0.455	-0.233	0.398	-0.379	0.182	-0.289
Coarse gravel	0.300	-0.196	0.151	0.346	0.218	-0.003	0.127	-0.200	-0.448	-0.064
Stone	0.299	-0.047	-0.123	-0.135	0.464	-0.326	0.437	0.011	-0.141	0.150
Veg/no veg	0.299	-0.270	-0.134	0.028	-0.121	-0.034	-0.076	0.631	0.320	-0.242
Bank undercut	0.237	0.186	0.214	0.451	0.377	0.273	-0.088	-0.087	0.318	-0.333
Ranunculus sp.	0.047	0.306	0.557	-0.344	-0.084	0.015	0.167	0.221	-0.222	-0.517
Sparganium sp.	-0.255	0.212	-0.256	0.358	-0.058	0.182	0.614	0.365	-0.158	-0.032
Lemna sp.	-0.248	0.367	-0.086	0.106	-0.047	-0.397	-0.298	0.080	-0.372	-0.109
Width	0.139	0.141	0.599	0.294	-0.242	-0.123	0.023	0.151	0.079	0.594
Vegetation	-0.183	0.473	-0.011	-0.167	0.164	-0.027	0.270	-0.211	0.489	0.077

Table 8: All principal components (all information about the total variation). Salmon scores the third highest numerical value, very close to the two highest values: velocity and depth. Hence, F1 primarily explains these three variables. By extracting the important information from the two first PCA's above, we are able to distingush a higher level of importance for the variables: Variables with numerical values higher than 300 are considered highly important, e.g. velocity, stone, coarse gravel, 'veg/no veg'. Depth is the only negative parameter which is also considered highly important. Similarly, 'bank undercut' is also an important positive factor, and Sparganium sp. and Lemna sp. are both considered (negatively) important, although less pronounced. The remaining varibles in the analysis are less important. The principal component F5 only explains 4.5% of the variation, but is still interesting because salmon has a high numerical value here. Thus, F6 reflects that the generel assumumptions on salmon behaviour are not true in all cases, i.e. here we can see that salmon can be present in larger depths (e.g. pools) with less velocity if an undercut bank is available. In these cases Lemna sp., larger stone and CPOM are not present. If the negative paramenters were present, salmon density would decline. This could either be because of too high velocity, but could also indicate that turbulence is a more explanatory factor than velocity.

A biplot of all stations in River Kongeå (combining the scores of the variables in F1–F2 with each station) is illustrated in Figure 41. The biplot counts for 66% of the total variation (Table 7). The plot displays how salmon increases with velocity, stone, 'veg/no veg' and coarse gravel. 'Bank undercut', *Ranunculus sp*. and width are also considered positive. However, width and *Ranunculus sp*. do not have high values the first component. In addition 'Bank undercut' and Width both have small values in the second component, indicating that these two are less important than those with high values in the first component. The variable having the most negative effect on juvenile salmon is Depth. Silt, *Sparganium sp*., *Lemna sp*., Vegetation and CPOM also effect habitats negatively.

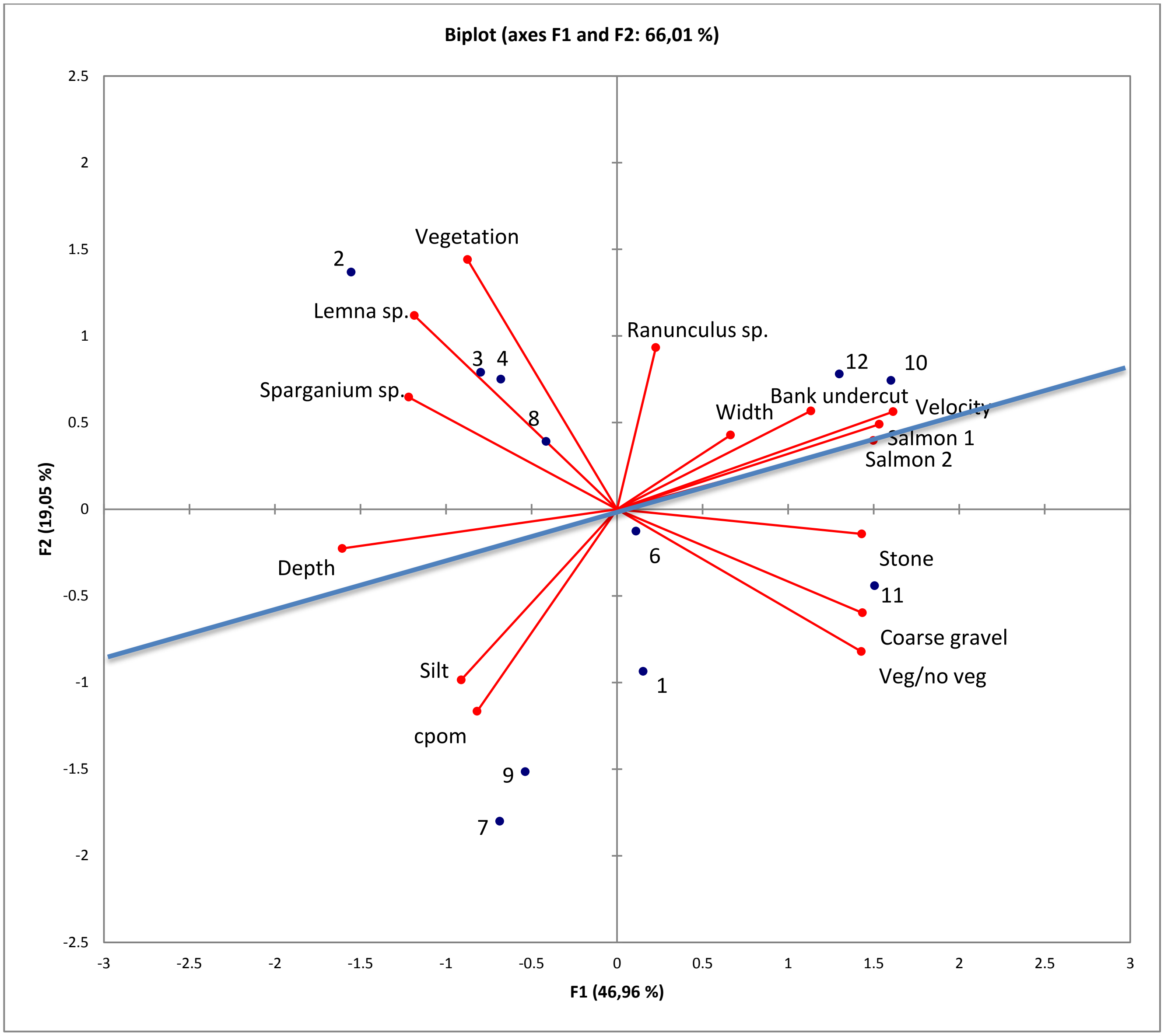


Figure 41: PCA 3. Plot based on Table 8, illustrating how the diffent stations are placed in relation to the variables within F1 and F2 (explaining 66% of the variation). Clusterings are seen with Lemna sp., Sparganium sp. and vegetation, all associated with stations 2, 3, 4 and to a less extend 8. Stations 10, 11 and 12 explain much of the high density for salmon, whereas station 2 is placed in the negative direction of F1, reflecting that salmon density was low. Generally, velocity and depth are two of the most important variables in River Kongeå. The plot also illustrates that there are no differences in ideal habitat types for salmon 1 and 2 for these variables (reduced dataset).

The biplot also illustrates groupings of stations and their relation to the variables in 66.0% (see Table 7). In stations 11 and 12, the highest densities of juvenile salmon were recorded. Stations 2, 3, 7, 8 and 9 all had low salmon densities which is also reflected in the biplot. Stations 6 and 8 do not contribute with much in neither PC 1 or 2, and their variation is instead explained by other components.

Overall discussion of the PCA's (considerations, limitations)

One of the disadvantages of using PCA's is the risk of drawing conclusions on a too simplified picture. To fully understand juvenile salmon (parr) habitats, several complex and immeasurable variables need to be considered, e.g. variation in velocities, seasonal changes, turbulence, overall hydrology, geomorphology, etc. When this is said, the PCA is a powerful tool for explaining variance within a large dataset, when variables are interpreted within their proper spatial and temporal context.

In the investigations conducted for this study, focus was on including as many variables as possible to understand variance within these. The most significant variables were highly correlated in the initial analysis (correlation matrix). The correlation was significantly positive for salmon ≤10 cm and velocity but negative for depth and silt. However, salmon ≤15 cm did not exhibit the same strong aversion towards silt. Neither did trout ≤15 cm. Salmon and trout were significantly positively correlated with stone and shifting vegetation (veg/no veg) which, however, could not be verified for salmon ≤10 cm in the correlation matrix. Large depths, e.g. pools, were not used by any of the groups (all significantly negatively correlated). Trout ≤15 cm was negatively correlated with large widths.

River Ribe (Hjortvad) å generally had high densities of parr of both species (trout and salmon). Furthermore, it differed in characteristics from most of the stations in River Kongeå (except from station 1, the only artificial riffle in River Kongeå). Hence, the inclusion of River Ribe (Hjortvad) å may influence the PCA regarding artificially added substrates. In general, the high densities in River Ribe (Hjortvad) å may be due to the full connectivity in this River rather than the coarse substrates (artificially added stone. Although, it is obvious that coarse substrates will increase oxygen-saturation, and thus be more suitable for spawning and nursery of eggs, it may not necessarily be a crucial variable for salmon parr. Instead, velocity appears to be the most dominant variable. However, even velocity may be too simple a parameter, which is indicated by studies that instead suggest that turbulence (which is more closely related to river morphology than substrate) is crucial. Hence, in supplement to substrates and velocity, turbulence and river morphology are two parameters that require more attention in the future.

Non-objective observations of territorial behaviour

In 1991 Heggenes and colleagues released 39,000 fry (mean total length 30 mm) in three different densities in habitats with slow, intermediate and fast water velocities. In several ways, this experiment is comparable to the current study. Heggenes made several observations which can also be confirmed in this study. For example, he observed avoidance of slow, deep habitat types in the absence of interspecies competition, and suggested that this was fixed behavioural response for salmon.

In this study, several observations were made on territorial behaviour of parr during the investigations in the two rivers (River Kongeå and River Ribe (Hjortvad) å) during summer 2014. Particularly the short underwater video films gave invaluable insight into variations in their behaviour during daytime. Based on these films and my own observations during electrofishing, it was evident that salmon parr were markedly stationary in daytime during the time of our investigations. When walking through the water, approaching the fish (even walking fast), the young parr (6–7 cm) were reluctant to change position when they had found a suitable area to stand. Generally salmon parr did not tend to shoal but were autonomously (individually) territorial, and stood still in open areas of the stream (in full sun-light) between areas with vegetation, with little if any shelter to hide in. They always stood above sand or gravel in certain (medium) water velocities, swimming against the current. In contrast to Heggenes and colleagues observations (Heggenes *et al*. 1999:5), we observed that parr ≤10 cm used sand without shelter or turbulence in River Ribe (Hjortvad) å (natural spawning) and that little inter-species competition was present. Hence, the non-objective observations made in both rivers confirm data from the performed PCA’s, indicating that velocity plays one of the most important roles in salmon habitats. As earlier mentioned, turbulence may however also have played an important role.

Intra-habitat behaviour

When electrofishing on each station, several observations were made on parr behaviour within the habitat, on both macro- and micro-habitat scale. Inter-species competition may have affected the location of parr and their (observed) stationary behaviour. However, when good habitat parameters were fulfilled, salmon parr were evenly spread across the riffle. It was evident that salmon parr were not reluctant to reside in open and shallow areas of the stream (in open sunlight) without vegetation, which contrasts what has hitherto been proposed as typical parr behavior in streams and rivers. They did not tend to use undercut banks. Neither did they tend to use stone shelters or areas covered with vegetation.

Inter-habitat behaviour

Similar behaviour was observed between habitats, even between the two rivers. Thus, salmon parr behaviour in the two Danish lowland rivers discussed here differs from behaviour observed in other contexts. Again, this may be due to turbulence, which is a generally underestimated factor.

Summary and conclusions

The thesis set out to identify and study the complexity of physical conditions considered ideal for growth and survival of juvenile Atlantic salmon (fry and parr) in Danish lowland rivers. 6 hypotheses were proposed, and in the following, these are discussed in relation to the results gained from the investigations in River Kongeå and Hjortvad å:

1) *Juvenile salmon density increases with physical variation of the habitat.*

This was generally true, particularly for geomorphology and water velocity. However, salmon parr did not use too deep areas or pools, nor did they use still waters. In areas where water velocity was narrowed down to certain areas of the stream, the young salmon mostly stood here. This was confirmed in the PCA's performed on data from the two rivers, exhibiting that velocity was significantly correlated with salmon. Coarse gravel, stone and variation in the vegetation (i.e. heterogeneity) also affected density positively.

2) *Too much vegetation is a negative habitat parameter.*

Again, heterogeneity was in general the most important factor for a good habitat, and too much uniform vegetation was truly a negative factor, generally associated with low salmon density. This was confirmed in the PCA's performed on data from the two rivers, exhibiting that 'vegetation' was a negative habitat parameter.

3) Juvenile salmon are basically stationary.

The observations made during daytime in summer 2014 in both River Kongeå and River Ribe (Hjortvad) å indicated that salmon parr were generally stationary, with little if any moving side-ways within the micro-habitat, unless confronted with obvious threats.

4) Juvenile salmon resides in open water with high stream velocity, only to seek shelter when necessary.

This was true at least during daytime in summer 2014 in both of the two investigated rivers, in areas shallower than 1 m. Parr did seek shelter when approached, but rapidly returned to their territory when danger had passed. This was partly confirmed in the PCA's performed on data from the two rivers, exhibiting that velocity was (significantly) positively correlated with salmon.

5) *Juvenile salmon tend to use gravel of varying sizes*

Gravel was only in some cases a positive parameter. This was partly observed during the investigations in summer 2014 (i.e. salmon parr often had territories in areas of the stream dominated by sand), and confirmed in the PCA's reflecting that small- and medium-sized gravel was less important. Instead, stone was a positive parameter.

6) *Juvenile salmon are reluctant towards inhabiting (too) deep areas in the stream*.

This was both observed during the investigations in July 2014 and confirmed in the PCA's all reflecting too high depths as negative parameters.

The ideal habitat for salmon parr in Danish lowland rivers

It becomes increasingly evident that no individual physical factors are ideal in spawning places and habitats for the Atlantic salmon. Conversely, few factors can be considered less suitable than others when evaluated on their own (see for example Moir *et al*. 2002; and Klemetsen *et al.* 2003). Instead it appears to be the combination of the different factors (i.e. heterogeneity), the general state of the eco-system and, not least, biological diversity which—in combination—make out the ideal spawning place and habitat for the Atlantic salmon (see discussion).

A river is a complex ecological system, and we still have much to learn, for example about the mechanisms behind the transport of eroded sand from one position to where it is deposited. However, the current study has identified several physical attributes that are to be considered ideal for the survival of salmon fry and parr in Danish lowland rivers. The following conclusions were gained from the three PCA's:

1st PCA (Both rivers, All variables)

The first PCA reflected that the habitat for salmon differs from the habitat for trout, which has also been suggested in previous studies. Trout was significantly negatively correlated with width and varied negatively with velocity, suggesting that trout often spawn further upstream. However, both species (salmon and trout) were positively correlated with stone, shifting vegetation and *Lemna sp.* and negatively correlated with depth and vegetation.

For salmon exclusively, the following results were gained from the initial PCA:

1) Velocity and silt varied with salmon in all of the first three components
2) Velocity, coarse gravel and 'bank undercut' are positive physical factors- 'veg/no veg' (shifting vegetation) and stone also have a positive effect
3) Sand, silt and *Sparganium sp*. as well as *Lemna sp.*, vegetation, fine gravel and depth are negative
4) Silt and velocity are two of the most important variables (with significant correlation of 0.05 in the correlation matrix)

2nd PCA (River Kongeå, All variables)

In both PCA's, salmon was significantly correlated with velocity, depth and silt. The following results were gained from the 2nd PCA:

1) Velocity must be considered the most important variable in salmon habitats
2) Depth, CPOM and silt as well as *Sparganium sp.* and sand all influence habitats negatively
3) Velocity and 'bank undercut' are positive physical factors
4) Stone, coarse gravel and 'veg/no veg' (shifting vegetation) are all positive factors

3rd PCA (River Kongeå, Important parameters exclusively)

In the third PCA, parameters important in the two first PCAs were analyzed exclusively. The following results were gained from the 3rd PCA:

1) Salmon increases with velocity, stone, 'veg/no veg' and coarse gravel
2) 'Bank undercut', *Ranunculus sp*. and width are also considered positive
3) However, 'Bank undercut' and width are less important
4) The variable having the most negative effect on juvenile salmon is depth
5) Silt, *Sparganium sp*., *Lemna sp*., Vegetation and CPOM also effect habitats negatively

In conclusion, the overall most **important positive physical factors** in salmon parr habitats in Danish lowland rivers are **velocity, coarse gravel, stone and variation in the vegetation (heterogeneity).** Conversely, the most

negative parameters are **too high depths, abundant vegetation, abundance of organic material (CPOM) and substrates dominated by silt.**

Implications and future challenges

Hitherto, focus has primarily been on gravel sizes and shelters as the most relevant factors in salmon habitats. However, rivers are complex ecological systems and we still have much to learn about them. To fully understand juvenile salmon habitats, several variables need to be considered besides the measurable and relatively simple parameters analyzed in the current study. For example, the analyses in River Ribe (Hjortvad) å found the artificially added substrates as positive attributes, reflected in the high densities of both salmon and trout. However, not only may the densities in River Ribe (Hjortvad) å be due to the full connectivity in this river (rather than the amount and quality of gravel), they may also be due to more immeasurable parameters such as turbulence, river morphology and other hydrological parameters. In a recent study, parr were more often observed in areas with lower Froude numbers (low resistance) (Enders *et al.* 2009), indicating that turbulence defines cost of energy rather than velocity. Hence, these are parameters that require much more attention in the future. Recorded variables in similar studies may therefore have to be more creative to embrace the full variation in salmon habitats. As already mentioned, the traditional variable velocity may be too simple. Instead, a range of turbulence variables should be taken into consideration. Lastly, although juvenile salmon (parr) may thrive in areas with sand and absence of vegetation, it is important to meet the demands of all salmon life stages in fresh-water before restoring water courses with the aim of improving habitat quality. For example, critical periods in the life cycle such as spawning may require more specific habitat qualities than suggested for parr in this study.

Acknowledgements

I owe a special thanks to all who have been helpful in the initial phase of the project and who have helped ease the project by discussing methods and results continuously. Particularly thank to: Supervisor Niels Jepsen, DTU Aqua; Stig Pedersen, DTU Aqua, for training in habitat descriptions, guidance and supervision and providing gear; Michael Deacon, the Danish Nature Agency, for identifying habitats, guidance and supervision during field work in spring and summer 2014; Kim Iversen, DCV, for substantial help when setting out the fry and for training in electrofishing skills and habitat description; Peter Geertz-Hansen, DTU Aqua, for guidance and supervision in electrofishing theory; Vejen Municipality (Vejen Kommune) for postponing weed cutting and being utmost cooperative; and last but not least to Maria Holm Larsen, Petter Astrup, Pia Astrup, Lise Harvig, Morten Nielsen and Tenna Astrup for physical constrains and extraordinary patience during field work in spring and summer 2014.

References

Armstrong, J.D., Kemp, P.S., Kennedy, G.J.A., Ladle, M. and Milner, N. J. (2003) Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries research* 62(2): 143–170.

Bardonnet, A., J. and Baglinière, J.-L. (2000) Freshwater habitat of Atlantic salmon (Salmo salar). *Canadian Journal of Fisheries and Aquatic Sciences* 57(2): 497–506.

Beland, K. F., Trial, J.G. and Kocik, J. F. (2004) Use of riffle and run habitats with aquatic vegetation by juvenile Atlantic salmon. *North American Journal of Fisheries Management* 24(2): 525–533.

Bohlin, T., Hamrin, S., Heggberget, T. G., Rasmussen, G. and Saltveit, S. J. (1989) Electrofishing - Theory and practice with special emphasis on salmonids. *Hydrobiologia* 173: 9–43.

Bult, T. P., Riley, S. C., Haedrich, R. L., R. J. Gibson, and Heggenes, J. (1999) *Canadian Journal of Fisheries and Aquatic Sciences 56*: 1298–1306.

Butler, J. R. A. and Watt, J. (2003). Assessing and managing the impacts of marine salmon farms on wild Atlantic salmon in Western Scotland: identifying priority Rivers for conservation. In: Mills, D. (Ed.) *Salmon at the edge*. Oxford, p. 93–118.

Brookes, A. 1987. The distribution and management of channelized streams in Denmark. *Regulated Rivers: Research and Management* 1: 3–16.

Christensen, G. H. (2010) *Danmarks ferskvandsfisk*. Nordisk Forlag, p. 27–59.

Clausen, B., Olsen, M., Pedersen, S. and Pedersen, M.L. (2006). *Habitatmodellering i Ledreborg Å. Effekten på ørred ved reduceret vandføring*. Faglig rapport fra DMU nr. 580. Danmarks miljøundersøgelser. Miljøministeriet.

DCE (2014) *Dansk fiskeindeks for vandløb (DFFV)*. Videnskabelig rapport fra DCE - Nationalt Center for Miljø og Energi, nr. 95. Aarhus Universitet.

Elliott, J. M., and Hurley, M. A. (1997) A functional model for maximum growth of atlantic salmon parr, salmo salar, from two populations in northwest England. *Functional ecology* 11(5): 592–603.

Elliott, S. R., Coe, T. A., Helfield, J. M. and Naiman, R. J. (1998) Spatial variation in environmental characteristics of Atlantic salmon (Salmo salar) rivers. *Canadian journal of fisheries and aquatic sciences* 55: 267–280.

Enders, E. C., Ovidio, U. M., Hallot, E. J., Philippart, J.-C., Petit, F., Roy, M. L., Boyer, C. and Roy, A. G. (2009) Can Turbulence Statistics reflect the meso-habitat choice of juvenile Salmonids? *Proceedings of the combined conference on Hydro-Informatics and Ecohydraulics, Concepcion, Chile, January 2009. Ecohydralics. International Symposium 7th 2009*. International Association for Hydro-Environment Engineering and Research.

Ersbøll, B. K. and Conradsen, K. (2012) *Multivariate Statistics – An introduction*. (8. ed.). DTU Informatics, Lyngby.

Geertz-Hansen, P., Koed, A. and Sivebæk, F. (2013) Manual til elektrofiskeri. Vejledning til elektrofiskeri ved bestandsanalyser og opfiskning af moderfisk. *DTU Aqua-rapport*: 272.
Gibson, R. J. (1993) The Atlantic salmon in fresh-water – spawning, rearing and production. *Reviews in fish Biology and Fisheries* 3(1):39–73.

Gustafson, I., Marjanen, K. and Moring. J. R. (1984) Construction of artificial redds for evaluating survival of Atlantic salmon eggs and alevins. *North American Journal of Fisheries Management* 4(4a): 455–456.

Habersack, H., Tritthart, M., Liedermann, M. and Hauer, C. (2014) Efficiency and uncertainties in micro- and mesoscale habitat modelling in large rivers. *Hydrobiologia* 729: 33–48.

Halvorsen, M., Jergensen, L., and Amundsen, P. A. (1997) Habitat Utilization Of Juvenile Atlantic Salmon (Salmo Salar L), Brown Trout (Salmo Trutta L) And Arctic Charr (Salvelinus Alpinus (L)) In Two Lakes In Northern Norway. *Ecology of freshwater fish* 6(2): 67–77.

Hansen, M. M., Sivebæk, F., Bekkevold, D., and Nielsen, E. E. (2013). Vandløbenes fisk. In: Sand-Jensen, K. (Ed.). *Naturen I Danmark. De Ferske Vande*. Naturen I Danmark, bind 5. Gyldendal, p. 179–219.

Heggenes, J. (1990) Habitat utilization and preferences in juvenile Atlantic salmon (salmo salar) in streams. *Regulated Rivers: Research & Management* 5: 341–354.

Heggenes, J. (1991) Comparisons of Habitat Availability and Habitat Use by an Allopatric Cohort of Juvenile Atlantic salmon Salmo salar under Conditions of Low Competition in a Norwegian Stream. *Holarctic Ecology* 14(1): 51–62.

Heggenes, J. (1996) Habitat selection by brown trout (*Salmo trutta*) and young Atlantic salmon (*S. salar)* in streams: static and dynamic hydraulic modelling. *Regulated rivers: Research and Management* 12: 155–169.

Heggenes, J., Bagliniere, J.L., and Cunjak, R. A. (1999) Spatial niche variability for young Atlantic salmon (salmo salar) and brown trout (s-trutta) in heterogeneous streams*.* *Ecology of freshwater fish* 8(1): 1–21.

Heggenes, J. and Borgstrøm, R. (1991) Effect of habitat types on survival, spatial distribution and production of an allopatric cohort of Atlantic salmon, *Salmo salar* L., under conditions of low competition. *Journal of Fish Biology* 38: 267–280.

Heggenes, J., Brabrand, Å. and Saltveit S. J. (1991) Microhabitat use by brown trout, *Salmo trutta* L. and Atlantic salmon, *S. salar* L., in a stream: a comparative study of underwater and river bank observations. *Journal of Fish Biology* 38: 259–266.

Heggenes, J. and Saltveit, S. J. (1990) Seasonal and spatial microhabitat selection and segregation in young Atlantic salmon, Salmo salar L., and brown trout, Salmo trutta L., in a Norwegian river. *Journal of Fish Biology* 36: 707–720.

Heggenes, J. and Saltveit, S. J. (2007) Summer stream habitat partitioning by sympatric Arctic charr, Atlantic salmon and brown trout in two sub-arctic rivers. *Journal of Fish Biology* 71: 1069–1081.

Heggenes, J., Saltveit, S. J., Bird, D. and Grew, R. (2002) Static habitat partitioning and dynamic selection by sympatric young Atlantic salmon and brown trout in south-west England streams. *Journal of Fish Biology* 60: 72–86.

Heggenes, J., Saltveit, S. J. and Lingaas, O. (1996) Predicting fish habitat use to changes in water flow: Modelling critical minimum flows for Atlantic Salmon, *Salmo salar*, and brown trout, *S. trutta*. *Regulated Rivers. Research and Management* 22: 331–344.

Jepsen, N., Aarestrup, K., Økland, F. and Rasmussen, G. (1998) Survival of radio-tagged Atlantic salmon (Salmo salar L.) and trout (Salmo trutta L.) smolts passing a reservoir during seaward migration. *Hydrobiologia* 371-372(0): 347–353.

Kemp, P.S., Gilvear, D. J. and Armstrong, J. D. (2003) Do juvenile Atlantic salmon parr track local changes in water velocity? *River Research and Applications* 19 (5–6): 569–575.

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

Kostaschuk, R. and Villard, P. (1999) Turbulent sand suspension over dunes. *Fluvial sedimentology* (28): 3–13.

Kristensen, E. A., Thodsen, H. Dehli, B. Kolbe, P. E. Q. K., Glismand, L. and Kronvang B. (2014) Comparison of active and passive stream restoration: effects on the physical habitats. *Geografisk Tidsskrift/Danish Journal of Geography* 113(2): 109–120.

Krüger, J. (1989). *Gletscheren og landskabet: i nutid og istid*. Gyldendal, København.

Legleiter, C. J., Phelps, T. L. and Wohl, E. E. (2007) Geostatistical analysis of the effects of stage and roughness on reach-scale spatial patterns of velocity and turbulence intensity. *Geomorphology* 83 (3-4): 322–345.

Levasseur, M., Bergeron, N. E., Lapointe, M. F. and Berube, F. (2006) Effects of silt and very fine sand dynamics in Atlantic salmon (salmo salar) redds on embryo hatching success. *Canadian Journal of Fisheries and Aquatic Sciences* 63(7): 1450–1459.

Louhi, P., Maki-Petays, A., and Erkinaro, J. (2008) Spawning habitat of atlantic salmon and brown trout: General criteria and intragravel factors. *River research and applications* 24(3): 330–339.

McGinnity, P., De Eyto, E., Gilbey, J., Gargan, P., Roche, W., Stafford, T., McGarrigle, M., O'maoileidigh N., and Mills, P. (2012) A predictive model for estimating river habitat area using GIS-derived catchment and river variables. *Fisheries management and ecology* 19: 69–77.

Moeslund, B. (2007) *Grødeskæring i vandløb - erfaringsopsamling af metoder, praksis og effekter*. Rapport, Skov- og Naturstyrelsen. ISBN: 978-87-7279-794-6

Moir, H. J., Gibbins, C.N., Soulsby, C. and Webb, J. (2004) Linking channel geomorphic characteristics to spatial patterns of spawning activity and discharge use by Atlantic salmon (*Salmo salar* L.). *Geomorphology* 60: 21–35.

Moir, H.J., Gibbins, C. N., Soulsby, C., and Youngson, A. F. (2005) PHABSIM modelling of Atlantic salmon spawning habitat in an upland stream: Testing the influence of habitat suitability indices on model output. *River research and applications* 21: 1021–1034.

Moir, H. J., Soulsby, C. and Youngson, A. (1998) Hydraulic and sedimentary characteristics of habitat utilized by Atlantic salmon for spawning in the Girnock Burn, Scotland. *Fisheries Management and Ecology* 5: 241–254.

Moir, H. J., Soulsby, C., and Youngson, A. F. (2002) Hydraulic and sedimentary controls on the availability and use of Atlantic salmon (*Salmo salar*) spawning habitat in the River Dee system, north-east Scotland. *Geomorphology* 45: 291–308.

Netboy, A. (1980) *Salmon the world's most harassed fish*. Winchester Press. Michigan.

Olesen, T. M. and Aarestrup, K. (2006) Fisks vandring forbi opstemninger i vandløb. *Vand og jord* 13(4): 142–146.

Orell, P., Erkinaro, J., Svenning, M. A., Davidsen, J. G., and Niemela, E. (2007) Synchrony in the downstream migration of smolts and upstream migration of adult Atlantic salmon in the subarctic River Utsjoki. *Journal of Fish Biology* 71: 1735–1750.

Payne, B. A. and Lapointe, M. F. (1997) Channel morphology and lateral stability: effects on distribution of spawning and rearing habitat for Atlantic salmon in a wandering cobble-bed river. *Canadian journal of fisheries and aquatic sciences* 54: 2627–2636.

Pedersen, M. L., Kristensen E. A., Kronvang, B. and Thodsen H. (2009) Ecological effects of re-introduction of salmonid spawning gravel in lowland Danish streams. *Wiley InterScience* 25: 626–638.

Refstie, T., and Kittelsen, A. (1976) Effect of density on growth and survival of artificially reared Atlantic salmon. *Aquaculture* 8(4): 319–326.

Scarnecchia, D. l. (1984) Climatic and oceanic variations affecting yield of icelandic stocks of Atlantic salmon (salmo-salar). *Canadian journal of fisheries and aquatic sciences* 41(6): 917–935.

Scruton, D. A., Heggenes, J., Valentin, S., Harby, A. and Bakken, T. H. (1998) Field sampling design and spatial scale in habitat-hydraulic modelling: comparison of three models. *Fisheries management and ecology* 5(3): 225–240.

Seber, G. A. F and Le Cren, E. D.(1967) Estimating Population Parameters from Catches Large Relative to the Population. *Journal of Animal Ecology* 36(3): 631–643.

Shearer, W. M. (1992) Ed. *The Atlantic salmon*. *Natural History, Exploitation and Future Management*. University Press, Cambridge.

Thorstad, E. B., Okland, F., Aarestrup, K. and Heggberget, T. G. (2008) Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries* 18(4): 345–371.

Unwin, M. J. (1997) Fry-to-adult survival of natural and hatchery-produced chinook salmon (oncorhynchus tshawytscha) from a common origin. *Canadian journal of fisheries and aquatic sciences*: 54(6): 1246-1254.

Whalen, K. G. and parrish, D. L. (1999) Nocturnal habitat use of Atlantic salmon parr in winter. *Canadian journal of fisheries and aquatic sciences*: 56(9): 1543–1550.

Zippin, C. (1956) An evaluation of the removal method of estimating animal populations. *Biometrics* 12(2): 163–189.

Zippin, C. (1958) The Removal Method of Population Estimation. *The Journal of Wildlife Management* 22(1):82–90.

Aarestrup, K. and Koed, A. (2003) Survival of migrating sea trout (Salmo trutta) and Atlantic salmon (Salmo salar) smolts negotiating weirs in small Danish rivers. *Ecology of Freshwater Fish* 12(3): 169–176.

Web content

Ribe Amt (1993) *Regulativ for Amtsvandløb nr. 6, Kongeåen fra sammenløb med Andst å til havet og amtsvandløb nr. 9, Andst å*: http://www.esbjergkommune.dk/Files/Filer/Borger/Natur,%20park,%20vandl%C3%B8b/Vandl%C3%B8bsregulativer/Konge%C3%A5en%20regulativ.pdf

Naturstyrelsen (2006) *Basisanalyse 2006. Habitatområde nr. 80. Kongeå. Ribe og Sønderjyllands Amter*: http://naturstyrelsen.dk/media/nst/Attachments/N91_H80_Kongeaa_bas.pdf

Naturstyrelsen (2012) *Første naturlige laksebestand i Danmark*: http://naturstyrelsen.dk/nyheder/2012/sep/foerste-naturlige-laksebestand-i-danmark/

World Wide Fund for Nature (2001) *The Status of Wild Atlantic salmon: A River by River Assessment*: http://wwf.panda.org/about_our_earth/blue_planet/publications/?3729/TheStatus-of-Wild-Atlantic-Salmon-A-River-by-River-Assessment