Flow Preferences of Upstream Migrating Atlantic Salmon (*Salmo salar*)

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Cover: Swimming fish generate vortices; a vortex can generate thrust for swimming fish; a mathematical model for swimming fish treats them in the same way as a vortex; another mathematical model for swimming fish treats them as a wave; a wave always travels to minimize resistance; rivers flow in a meandering way because they find the path of least resistance; salmon find their way up rivers along paths of least resistance; salmon migration is a flow of fish through a river which flows with water.

(illustration: Dan-Erik Lindberg)

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Upstream Migration of Atlantic Salmon (Salmo salar).

Abstract

On their way from the sea to their spawning grounds in rivers, Atlantic salmon are often delayed or hindered by dams or other obstructions. Building a fishway can save a population that would otherwise go extinct. But even when there is a fishway present, sometimes the fish will have difficulties finding the entrance or navigating through the fishway. Understanding fish preferences during their upstream migration can help us improve fishway design so we can help the fish move upstream.

The main goal of my studies was to find hydrodynamic preferences of salmon. We were able to show a preference for high turbulence intensity ($I \sim 0.7$). We also found a preference for lower water velocity. In my last study, I found most salmon near the highest available water velocity, which in light of previous results was interpreted as the salmon seeking out the turbulent areas in the boundary layer of the high velocity jet in the center of the river.

There were several indications that Atlantic salmon prefer to save energy, and that they are able to utilize turbulent structures to save energy during their active migration. However, much of the proof was circumstantial and requires further investigation. As a main source of error, the instruments used to measure hydrodynamics were not precise enough. More focus should be put on developing better instruments, for example the newly invented artificial lateral lines.

Keywords: Atlantic salmon, *Salmo salar*, migration, ecology, behavior, path selection

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Dedication

To all the fish that were never allowed to live
With hopes of a better tomorrow
For all the rest

Fiskare hafva ofta råkat lax-stegar up i älfven så store, at de bårttagit hela noten, som skedt på Bergören och Edsforssen i Ångerman-älfven, då de i en sådan ordning marcherat så starkt, att gnyet deraf har hörts på landet, likt et stormväder eller lindrig tordön, då ock laxen ibland går med halfva ryggen öfver,eller synes såsom vågor på vatnet.

Nils Gisler, 1751

Contents

List of Publications

This thesis is based on the work in the following papers, referred to by Roman numerals in the text:

I Andersson A. G., Lindberg D-E., Lindmark E. M., Leonardsson K., Andreasson P., Lundqvist H., Lundström T. S. (2012). A numerical study of the location and function of the entrance of a fishway in a regulated river. *Modelling and Simulation in Engineering* 2012.

II Lindberg D-E., Leonardsson K., Andersson A. G., Lundström T. S., Lundqvist H. (2013). Methods for locating the proper position of a planned fishway entrance near a hydropower tailrace. *Limnologica* 43(2013), 339-347.

III Lindberg D-E., Lundqvist H., Leonardsson K. (2015). Path selection of Atlantic salmon (*Salmo salar*) migrating through a fishway. *River Research and Applications* (Accepted 2015-04-02).

IV Lindberg D-E. (2015). Path selection of migrating Atlantic salmon (*Salmo salar*) along a river transect. (Submitted).

The contribution of Dan-Erik Lindberg to the papers included in this thesis was as follows:

I Participated in study design. In charge of field work. Joint analysis of collected data. Writing parts of the article, especially sections about field work.

II Participated in study design. In charge of hydroacoustics field work. Joint analysis of collected data. Writing most of the article.

III In charge of study design. In charge of field work. Independent analysis of data. Writing most of the article.

IV In charge of study design. In charge of field work. Independent analysis of data. Sole author of article text.

Abbreviations

ADCP	Acoustic Doppler Current Profiler
ADV	Acoustic Doppler Velocimeter
CFD	Computational Fluid Dynamics
LTU	Luleå Tekniska Universitet (Luleå University of Technology)
PIT	Passive Integrated Transponder
PIV	Particle Image Velocimetry
RFID	Radio Frequency Identification
SLU	Sveriges Lantbruksuniversitet (Swedish University of Agricultural Sciences)

Prologue

> You can not step twice into the same river.
>
> **Herakleitos, c. 500BC**

My master thesis was entitled “Attitudes toward brown bears (*Ursus arctos*) in Sweden”. At the time, my aim was to work with the five large predators in Sweden, including humans. But the job offer I got was to work with fish for a short time in a project based on problems at the Norrfors dam.

At that time, I knew the difference between a pike and a perch, but that was about as far as my knowledge of fish extended. I didn’t even eat fish, other than the occasional sushi or sashimi. There were plenty of things for me to learn. I had some really nice days in the sun on a raft in the middle of the river, accompanied by egrets and beavers and other animals, and of course the salmon jumping all around.

Well, here I am, seven years later. Somewhere along the way, that short period of field work turned into a PhD student position. One of my supervisors wanted me to dive into applied studies of the local area; the other wanted me to do some more general studies. In the end, I guess I tried to listen to both of them and ended up doing twice as much work as I should have. But they also gave me a lot of freedom to decide for myself and do my own thing. I have certainly been allowed to make many mistakes. And I have learned a lot from those mistakes.

> Much learning does not teach understanding.
>
> **Herakleitos, c. 500BC**

1 Introduction

> The real problem in speech is not precise language. The problem is clear language. The desire is to have the idea clearly communicated to the other person. It is only necessary to be precise when there is some doubt as to the meaning of a phrase, and then the precision should be put in the place where the doubt exists.
>
> **Richard Feynman, 1965**

Wildlife corridors are often used to connect habitats; with the purpose of allowing or increasing genetic flow between populations. Fishways are wildlife corridors for aquatic organisms; usually intended for fish. Terrestrial animals commonly use eyesight to orient and find a path through their habitat. Fish have a complimentary sense in their lateral line, which is especially beneficial in water with high turbidity or when navigating in darkness. The lateral line senses water movement, through which the fish are also able to sense other organisms and structures in the water. Since humans rely almost entirely on eyesight for orientation, understanding fish orientation requires an entirely novel way of thinking. Thus, while creating wildlife corridors for terrestrial animals appear to come natural for us, fishway constructions have failed many times due to a lack of understanding of how the fish sense their environment and orient themselves to find alternative passages when something blocks their path. Achieving a higher understanding of fish path finding is therefore essential for construction of efficient fishways.

Photographic techniques were developed around year 1800, but even before photography humans used art to describe their surroundings for thousands of years. Meanwhile, there have been precious few attempts to describe the world as a fish would see it; through pressure changes. Only very recently have there been some attempts at studying how the fish lateral line functions and what type of information the fish are able to gain from it. Some recent developments make use of Nano-technology to create artificial lateral lines (e.g. Fan et al., 2002). Perhaps those will provide a better understanding of how fish experience their surroundings, but that technology is not fully developed yet. In fact, there is no instrument at all available today that can measure water movement with any precision. The only measurements we are able to take are movement of particles suspended in the water, and use the assumption that the water around the particle moves in a similar fashion. Particle measurements can be taken with light receptors, which is called Particle Image Velocimetry (PIV), or with sound receptors through sonar technology. Sonar technology can be used to listen towards a single central cell, which is called Acoustic Doppler Velocimetry (ADV), or listening directionally along an axis with a long chain of time-differentiated cells, which is called Acoustic Doppler Current Profiling (ADCP). The ADCP is often used to create a transect with many points of measurement and from that calculate total river discharge or similar parameters. The ADV is often used stationary to measure how hydrodynamics change over time at a certain point of measurement. PIV is mainly used in a laboratory environment to get detailed measurements on a finer scale. Finally, when there is a desire to understand water movements over a larger area where it is impractical to take measurements, Computational Fluid Dynamics (CFD) modelling is commonly used to estimate an average flow model when flow has stabilized over a longer period of time.

While we lack the instruments to make precise measurements of how the fish experience their environment and what type of hydrodynamics they prefer, we can still make some observations on general patterns. By studying fish behavior we can see that Atlantic salmon prefer to swim near the surface and near the center of rivers. By studying general water velocity distributions we can see that near the center of a river there is often a high velocity jet forming. We also know that where there is a difference in water velocity, turbulent structures form as a result of friction. So then the question becomes; are the salmon attracted by the high velocity jet, or by the turbulent structures which form next to the high velocity jet? Or something else entirely?

Given the difficulties involved in accurately measuring hydrodynamics with chaotic turbulence and persistent turbulent structures, the classical approach is to ignore the particulars and focus on the general pattern; that salmon can be find in or near high velocity jets. Therefore, it is recommended that a fishway entrance is close to the main river flow, and that attraction water from the fishway is sufficient to compete with the main river flow as a high velocity jet. By fulfilling those simple basic requirements, you can be sure to attract salmon into your fishway.

Once the fish enter the fishway, they should also encounter favorable hydrodynamics so that they are encouraged to stay in the fishway and continue upstream, rather than fall back and leave the fishway. Even though salmonids have been shown to take advantage of turbulent structures and save energy that way, they have also shown a preference for the less turbulent environment of a submerged orifice fishway rather than the highly turbulent counter current fishway (McLeod and Nemenyi, 1941). So to maximize the efficiency of the fishway, we need a better understanding of when turbulence is favorable for the fish, and when turbulence is costly for the fish.

The efficiency of a fishway will depend on how well the fishway design is adapted to fish behavior and fish preferences (Williams et al., 2012). However, humans also have some preferences, such as minimizing cost of construction or maximizing the utility of the energy in the water. Since human preferences are usually of highest priority, fishway efficiency is rarely maximized. Therefore, if we use existing literature about fishway design to find fish preferences then we need to take the bias of human preferences into account.

The aim of this thesis is to discover path selection preferences of upstream migrating Atlantic salmon. This will be accomplished by using available methods to measure and calculate hydrodynamics and connect the measurements with fish behavior. These results can be used to improve fishway design and increase efficiency when guiding and transporting fish upstream to their spawning grounds.

1.1 What is a fishway?

Fishways, fish passes, and fish ladders are different names for the same thing; a wildlife corridor for aquatic organisms. These names are of historic origin from American English, British English, and International English. The Brits have ancient laws, possibly up to 900 years old, requiring dam owners to leave a “king’s pass” or “queen’s pass” open in their dam during the time of fish spawning migrations, but have modernized their name for this structure to “fish pass”. In Sweden, there was a similar law as in Britain about leaving a “king’s vein” in the middle of all rivers for the fish, but when technical constructions designed to retard water velocity started to be used, a new name was introduced due to the stepwise progression; “fish staircase” (fisktrappa). Other languages have names like fischtreppe (German), kalaporras (Finnish), etc; which also translate to “fish staircase”. Non-native English speakers have therefore made up an on-the-fly translation to “fish ladder”, which has become commonly used in International English. The first American fishways were a series of pools connected to allow passage around dams; in other words a way for the fish around the dam, and they labelled it fishway. For the sake of consistency, I will use the word fishway throughout the rest of this document, and I will be using it to refer to any wildlife corridor intended for use by aquatic organisms. However, the words fishway, fish pass, and fish ladder are entirely interchangeable.

When the first fishways were constructed, the fishing industry was very important. Some of the first fishways were designed to let fish pass over a natural migration obstacle, so that a river that never before had salmon spawning could develop a new population for the fishery industry to exploit. This was done for example at Ballisodare, Ireland (Francis, 1870). When America was colonized, European immigrants constructed dams in rivers to power sawmills and similar industries. This caused a lot of conflicts with the natives who depended on the fish stocks for food. Thus, America very quickly developed laws that demanded fishways to be built around dams, to prevent war with the natives. When hydropower was developed to produce electricity, it was considered a more important industry than the fishery industry. Therefore, the fish stocks of many rivers were allowed to die out in favor of building a hydropower dam. Even where the fish were still considered a valuable resource, it was common to construct a fish hatchery for stocking of fish instead of constructing well-functioning fishways. Modern studies have revealed many secondary benefits from allowing access to spawning grounds; for example increased forestry production due to an influx of marine nutrients to forest streams (Hocking and Reynolds, 2011). Due to these secondary benefits, fishways appear to be a better solution than fish hatcheries.

Early fishway constructions are evidence that even then people knew how to attract fish into a channel and how to design the channel to allow safe passage upstream for the fish (US Bureau of Fisheries, 1873). The physics involved in retardation of water velocity was also known, as evidenced from early patents (Livermore, 1866). But even though they had the knowledge early on, they did not always make use of it (Prince, 1902). Constructing fishways where total discharge was limited only became common practice when hydropower became an important industry. Let me illustrate the vast differences in fishway design which were introduced with hydropower by comparing an old fishway in a water reservoir dam with a newly constructed fishway at a hydropower station.

1.1.1 Susquehanna River (1867) versus River Umeälven (2010)

When Colonel James Worrall incorporated a fishway into the Columbia Dam in the Susquehanna River (Pennsylvania, USA; possibly identified as the Wrightsville Dam), he made the narrowest part 6 m wide, stating that the wider a fishway is the better it functions (US Bureau of Fisheries, 1873). 142 years later, when a fishway was designed for the Stornorrfors dam in the River Umeälven (Västerbotten, Sweden), the narrowest passage was only 0.4 m wide and the maximum height of water pillar was also 0.4 m. The differences between these two constructions are here used as an introduction to how the combination of fish preferences and human preferences work to determine fishway design.

Area description

Both rivers have a similar discharge that averages around 800-1000 m^3s^{-1} but will drop as low as 100 m^3s^{-1} in dry periods (or much higher flows during spring floods). The fishway in the Stornorrfors dam has a drop of about 30 m over 300 m total length while the dam at Columbia only dropped 1 m over 15 m total length. So it seems that the rivers are quite similar, but the dam site in Sweden has a steeper incline than the Pennsylvania site. It should be noted that the Swedish dam had a much smaller drop when it was first constructed in 1924, but has since then been raised and extended over a couple of dam reconstructions. Nevertheless, even the first fishways built at Stornorrfors dam were constructed with passages less than 1 m wide (e.g. Ljungdahl, 1935).

Fishway design

Since migrating salmon follow the main current, it is important to place the entrance of a fishway as close as possible to where the migration obstacle and main current interact. By placing the entrance where it is no longer possible for the fish to continue in the main current, the fishway immediately presents itself as an alternative route upstream. If the fish have to fall back to find the fishway entrance, long delays in migration will be the result. This was well known when Colonel Worrall constructed his fishway (US Bureau of Fisheries, 1873) and it was well known when the new fishway was constructed in Stornorrfors in 2009 (Williams et al., 2012). Indeed, the Susquehanna fishway was situated in line with the spill water release from the dam. However, the Stornorrfors fishway entrance is some 100 m downstream from the spill bays.

I have not been able to identify any reason for locating the Stornorrfors fishway entrance at this downstream location, other than the fact that the elevation drop is doubled. Since most of the attraction water to the Stornorrfors fishway passes through a turbine, having a higher drop means that twice the energy can be extracted from the water and the power company can turn the fishway into a profitable investment. To maximize monetary profit from this auxiliary turbine, spill water flow through the fishway should be minimized. The Stornorrfors fishway was modelled after the Ice Harbor fishway (Perkins, 1974). But it is not an exact copy; it is cut in half (thus halving the discharge through the fishway) and the bottom orifice is reduced by 5 cm in width and 5 cm in height. By making these changes in fishway design, discharge through the fishway may have dropped from 3 m^3s^{-1} to around 0.5 m^3s^{-1} (Paper III). It may seem like a small change, but the additional water available to the turbines amounts to around 33 million m^3 per year. Because of the entrance being placed downstream of the spill bays, those additional masses of water plus the obligatory 21 m^3s^{-1} of attraction water has twice the drop, which means higher profits from the turbine installation. It should be noted that the spill bays are closed in some parts of the year with low river flow, which means the entire bypass channel flow goes through the fishway.

At Columbia there was no profit to gain for reducing spill water. The main purpose of the Susquehanna dam was to keep the water level high enough for boat traffic on the river even during low flow. They did not care how much water was spilled, as long as it did not mean too low water levels for boats, so they had no reason to reduce the dimensions of the fishway. Additionally, they did not have any reason to increase the drop, so they kept the fishway entrance close to where the main current was.

Other considerations

Susquehanna River was a very important transportation route with heavy boat traffic. Consideration to boat traffic was incorporated in other American fishway designs as well, such as the McDonald fishway (McDonald, 1879) and the Brewer fishway (Brewer, 1872). What they realized was that power can be gained through utilizing turbulent kinetic energy. Therefore, Colonel Worrall intentionally built the sides of the fishway as a horizontal staircase, so that the narrowest part at the upstream end was 6 m wide and then stepwise increasing 1 m in width on both sides in three steps until it reached 12 m width at the downstream end. These steps produced large vortices along the edges of the fishway. Further developments like the McDonald fishway had two straight lines of counter-currents instead of the staircase with expanding distance. By using straight rows a catamaran with one hull in each current could glide upstream without any force applied other than that of the turbulent kinetic energy from the vortices created by the fishway (Mather, 1887). It was assumed that the fish would be able to utilize the counter-currents in a similar fashion as the catamaran, but it was never confirmed.

Observations from fishways with large eddies showed that the vortices seemed to confuse the fish (US Bureau of Fisheries, 1873 p. 603) while it was generally observed that migratory fish adapt a positive rheotaxis and are attracted to strong flow. Perhaps these observations contributed to the reason for why the Cail fishway (and its evolved derivatives such as the one at Stornorrfors) became dominant. The ones who picked up on the counter current concept were the Belgians and French (e.g. Denil, 1909; Larinier, 2002), who also denied knowledge of any previous American constructions despite them being well documented (e.g. Brewer, 1872; Francis, 1870; US Bureau of Fisheries, 1873; von Bayer, 1908). Therefore, the counter-current fishway is commonly known as the "Denil fishway" to this day.

A comparison between pool-and-weir fishways with Denil fishways showed that cyprinids preferred the counter current fishway while salmonids preferred the pool-and-weir types (McLeod and Nemenyi, 1941). Salmonids are economically important fish, while cyprinids are usually not. Therefore, the main priority in most projects was to find a fishway that was well suited for enabling salmonid migration. There was only one single comparison study ever made, and there was no attempt at quantifying turbulent structures or compare hydrodynamic parameters or how the fish reacted to each parameter. Additionally, the study was done using juvenile fish, because of the small scale models used for fishways.

Concluding remarks

Both of these sites had a very small fish population to start with. In the case of Stornorrfors, the salmon population was decimated from many thousands, possibly even millions, of fish (c.f. Gisler, 1751) to 5-6 individuals passing the new fishway per day (Ljungdahl, 1935) due to the dam construction completely blocking upstream passage and after heavy fishery. A fish hatchery was built at Stornorrfors to stock the river with Atlantic salmon and brown trout. At Susquehanna extensive work was done to stock the river with shad (*Alosa spp.*). So there is no doubt that both sites had some willingness to spend money in benefit of the fish population. But fish benefit was only the secondary goal for both of these operations. The primary goal of operation at Susquehanna was to allow boat traffic, while the primary goal of operation at Stornorrfors was to maximize monetary profits from hydropower generation.

We do not know what the passage success was at Susquehanna. Their tools of evaluation were too crude to provide any reliable estimate. But it seems unlikely that any fish would have difficulties in transcending their fishway. Even the weaker swimmers should be able to burst-swim through such a short distance.

From Stornorrfors, we know from telemetry studies that the average passage success is around 30 %, if the entire bypass channel is included as a definition of the fishway (Leonardsson et al., 2005; Lundqvist et al., 2008; Rivinoja et al., 2006, 2001). Most of the salmon fail to find the fishway, and a lot of the salmon that do find the fishway turn around and never make it through. This poor result comes from the primary goal of increasing monetary gains, reducing water spill that is necessary to attract fish upstream. After a lengthy conflict with fishermen and local residents, the power company has agreed to release freshets of higher flow occasionally. Those freshets have increased success rate in finding the fishway, but there are still many fish that never successfully make it through the fishway.

In conclusion, this comparison shows us that when human preferences do not act to minimize discharge through a fishway, then it is easy to build a fishway that mimics river flow and acts as a habitat corridor. When, on the other hand, human preferences act in favor of minimizing discharge, many of the fish will have difficulties finding a way through.

1.2 Discovering salmon preferences

Human preferences usually act to override fish preferences (e.g. Prince, 1914). Even so, it is useful to study fish preferences and try to include them in fishway construction, as much as human preferences will allow. By considering fish preferences in the fishway design, passage time can be reduced and overall passage success can be increased (Williams et al., 2012). Increasing fish passage success can lead to substantial financial gains (Håkansson et al., 2004).

Atlantic salmon are famous for their tremendous ability of climbing rapids, leaping through the air to pass vertical waterfalls as high as 5 m (US Bureau of Fisheries, 1873, p. 593). But it is important to realize that ability is not the same as preference.

Preference can only be studied when there is a choice between two or more options. In order to study preferences, there should optimally be a gradient where the fish can position themselves. Such a gradient could be, for example, a gradient of water velocity.

Migrating Atlantic salmon alternate between a state of active migration and a state of resting. Therefore, a study of preferences should make sure to separate these two states to avoid bias.

1.2.1 Preferences during active migration

Salmon have been observed to swim in high velocity water near the center of the river, even when lower velocity water is available (Gisler, 1751; Karppinen et al., 2002). At first glance, it appears that this behavior is pessimal in terms of energy consumption. During their passage through rapids, Atlantic salmon have been observed to move their tails a surprisingly small amount, making the ascendance look easy (Gisler, 1751). Pacific salmon have also been observed to have a surprisingly low tail beat frequency, and the hypothesis is that this is possible because the fish utilize turbulent structures in high velocity water (Standen et al., 2004). If a fish positions itself correctly when swimming through a vortex, it can gain a considerable amount of propulsion upstream. Therefore, the salmon appear to have a preference for saving energy by utilizing turbulent structures.

Salmon follow the current by maintaining positive rheotaxis (Stuart, 1962). By following the current, the fish make sure that they are traveling upstream towards their natal site. Therefore, they avoid large eddies, even though such large scale turbulent structures could potentially transport them upstream with much lower energy cost. On the other hand, if a vortice or similar turbulent structure is too small, then it does not provide enough kinetic energy to push the fish forward. Minimum turbulence scale to provide forward propulsion would be such that it covers two thirds of the fish length (Lacey et al., 2012), but a long chain of turbulent structures might be used by the fish instead of finding just one large vortex. In any case, there should be a preference of scale for turbulent structures so that the vortex is small enough that the fish are able to recognize positive rheotaxis but the vortex is still large enough to enable the fish to utilize kinetic energy for forward propulsion. However, there are no studies yet that can confirm this preference of scale, most likely due to the difficulties of measuring scale of turbulent structures.

Atlantic salmon migrate upstream near the surface and near the center of the river, where water velocity is usually highest. It is possible that the fish accept the higher cost of moving through high velocity water because that ensures that their olfactory organs encounter molecules at a higher rate so that they can recognize their natal stream. There are indications that olfactory cues influence path selection (Keefer et al., 2006). But other migratory fish like sturgeon have been found to migrate close to the bottom (McElroy et al., 2012), so this alternative explanation might not be very credible. Since the sturgeon can find their natal spawning site while migrating along the bottom, salmon should not need to swim near the surface in high velocity water to find their way. Instead, it seems more likely that the salmon prefer surface water due to the energy saving potential of turbulent structures.

1.2.2 Preferences during resting

Even early observers noted that salmon would occasionally sit still in the wake behind a rock for half a day before continuing its journey upstream (Gisler, 1751). The area downstream of rocks and other protruding objects produce chains of vortices, otherwise known as Kármán streets, which enable the fish to hold position without expending any energy. Vortices and turbulent structures were used to enhance fishways (e.g. Brewer, 1872; Landmark, 1884; Mather, 1887; McDonald, 1879; US Bureau of Fisheries, 1873; von Bayer, 1908) but there were no tools available to describe water characteristics in any detail. Not until recently there was a study published where Particle Image Velocimetry (PIV) was used to describe hydrodynamics around a fish body resting behind an object (Liao et al., 2003). In that study, they also used advanced telemetry to confirm that the fish had reduced muscle activity.

The problem with using PIV is that it is laboratory equipment. Pumps are used to transport water, and even high capacity pumps will only circulate 1 m^3s^{-1} or even less. Compared to a river with 1000 m^3s^{-1}, the laboratory can never reproduce natural conditions for free swimmers. Even adult fish with sizes around 1 m body length will be exceedingly difficult to study in a laboratory environment. Thus, laboratory studies are done on juvenile fish in small streams, which may not be comparable to adult fish in a river. Additionally, a natural river bed consists of a multitude of rocks and pebbles, causing a complex flow when all the turbulent motions interact to create even more turbulence. Even for a small stream, such a setup is rarely reproduced as a copy of natural conditions in the laboratory. Instead, one single rock or artificial object is used to study simple stream characteristics. This means that even for resting fish, we cannot be entirely sure that the results in the laboratory translate well to natural conditions.

1.3 Laboratory versus on site studies

To take accurate measurements and find fish preferences it is important that we eliminate any sources of bias. This is why we set up a laboratory where the environment can be manipulated in detail. One manipulation that is usually done is to create uniformity. For example, if you study how fish react to turbulent structures, then in the laboratory you create a Kármán street of repeating vortices that behaves uniformly and predictably (Liao et al., 2003). Thus, some evidence can be presented that fish prefer to utilize turbulent structures to reduce energy expenditure, because the fish prefer to spend time in that area. But there is no case in nature where water in a stream produces such straight Kármán streets of vortices like the lab produces. Turbulence is created by every single protrusion along the bottom, and turbulent structures interact with one another in a chaotic evolution of flow. While a uniform environment can give us solid proof that the fish prefer to save energy in turbulent structures, it does not prove that the fish are able to seek out turbulent structures in natural river flow.

We know that river dwelling fish will stand behind rocks to rest, because we can see them move their body significantly less when holding position there. We know that objects in streaming water create turbulent structures, and the turbulent structures can provide forward propulsion, which is what fish use to maintain a state of rest (Liao et al., 2003). So we know that at a certain scale of turbulent structures, at a small enough turbulence intensity, salmonid fish are able to find and utilize turbulent structures both in a laboratory setting and on site in the river, in order to save energy. But what happens when the water velocity increases toward 1 ms^{-1} or more in deep water, like in the middle of the river where salmon migrate upstream? We cannot reproduce those conditions in the laboratory. Furthermore, all laboratory studies use small or even juvenile fish, due to size restrictions of the flume. Can we really say that a 20 kg fish will react in the same way as a 0.5 kg fish? There are many uncertainties that arise from the restrictions we have in the laboratory. Therefore, it is necessary to do some studies on site in the river, despite the many other uncertainties that arise from the many sources of bias that are introduced in an uncontrolled environment.

2 Objectives

> However far man may extend himself with his knowledge, however objective he may appear to himself - ultimately he reaps nothing but his own biography.
>
> **Friedrich Nietzche, 1878**

The aim of this thesis was to find fish preferences by measuring hydrodynamics and locating fish within the measured body of water. The specific objectives for each paper were:

I Investigate if a small high velocity jet can compete with the main flow in a turbine tailrace so that it is noticeable by fish. A secondary aim was to compare CFD modelling with ADCP measurements.

II Investigate if any fish would encounter the high velocity jet from Paper I, if a fishway was constructed in that manner. A secondary aim of this paper was to compare hydroacoustic positioning with telemetry detections.

III Identify hydrodynamic preferences of salmon migrating through a fishway.

IV Identify hydrodynamic preferences of salmon migrating past a river transect.

In Paper II there was an indication of a preference for some turbulent properties in active migrants; which had only been shown for resting fish before that. Therefore, the focus of the remaining work was put towards finding methods to provide stronger evidence of this preference.

A secondary aim was to investigate the reliability of measurements.

3 Material and Methods

If you learn "indoor" techniques, you will think narrowly and forget the true way. Thus you will have difficulty in actual encounters.

Miyamoto Musashi, 1645

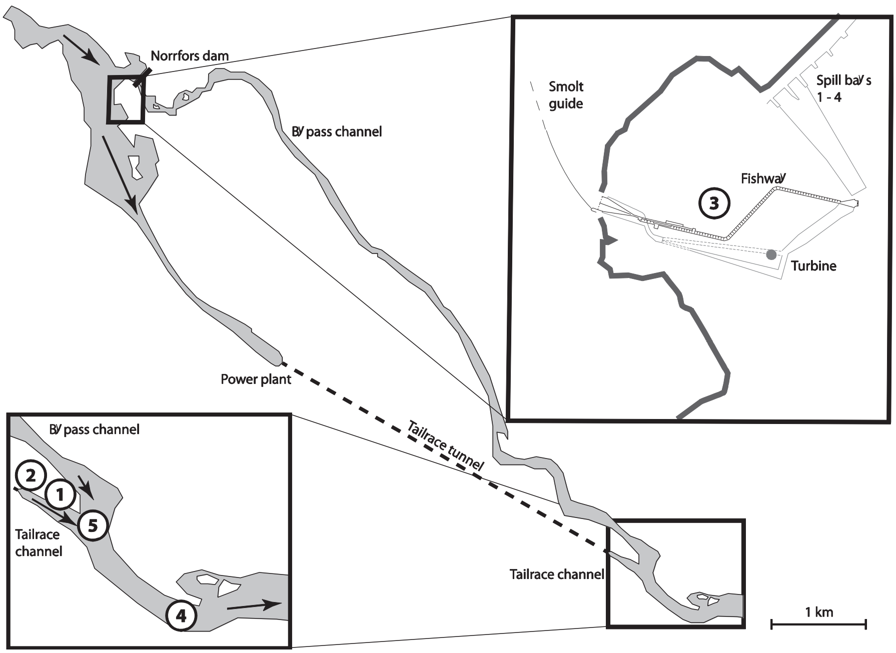

Figure 1. Study area, with the focus area for each manuscript denoted with numbers. (*Illustration: Dan-Erik Lindberg*)

3.1 Study area

My study area was in River Umeälven, Sweden (Figure 1). Fish migrating from the sea start their freshwater journey at the estuary (63.40 E, 20.20 N). For the first 25 km, the water flows slowly and there is little resistance for the fish. Then they arrive at the confluence area between the hydropower tailrace and the bypass channel, which was the focus area for most of my studies.

Around 1 km of the river was bulldozed to create a tailrace channel which joins the old river bed. From the hydropower turbines, a 4 km tailrace tunnel leads to the tailrace channel after which the main river continues (Montén, 1985). To allow fish passage past the turbines, an eight kilometer stretch of the old river bed is used as a natural bypass for fish. At the upstream end of the bypass channel, a fishway enables fish to ascend the dam. However, the attraction water flow from the bypass is too low in relation to turbine flow (< 10 % of turbine flow over a 270 m wide confluence) to effectively guide fish upstream. With poor attraction from the bypass channel, many fish are detained or delayed in the tailrace channel or tailrace tunnel where they display "yo-yo migration" behavior (Lundqvist et al., 2008).

At the Norrfors Dam there is a 1.7 km long headrace channel which diverts the main river flow to the turbines. There is also a reservoir above the dam, but only 1 m variation of depth is allowed so most of the water reserves are stored upstream. The unregulated tributary Vindelälven connects to Umeälven about 10 km upstream from the Norrfors Dam and this tributary is where all the salmon go to spawn. In the main River Umeälven, there are 18 additional hydropower plants and this entire part of the river is in effect closed for all fish migration.

3.1.1 Stornorrfors Fishway

When the Norrfors Dam was first built in 1924, there was no fishway. Instead, some of the salmon were caught in a trap and transported by truck to an upstream location. After some dispute with local fishermen, a fishway was finally installed in the dam (Ljungdahl, 1935) and the dam owners even put in an electronic and automatic fish counter (Ljungdahl, 1934). When the dam was extended with a new hydropower station and the tailrace tunnel in 1960, a new fishway was also installed. Following some high floods in the 1990's, a risk assessment demanded that a new spill bay must be installed in the Norrfors Dam. It was decided that the only reasonable place to put this new spill bay was where the fishway was located, so there was a need to replace it with a new fishway. This work was finished in the winter 2009/2010.

The 2010 fishway is a modified version of the Ice Harbor fishway, on Snake River, Washington, USA (Perkins, 1974). The modifications include making the bottom orifice smaller and cutting the fishway in half lengthwise, so that the discharge through the fishway is reduced. Auxiliary water flows through a turbine and 22 m^3s^{-1} is released into a diffusor at the fishway entrance. Sometimes, this auxiliary water accounts for all the spill water going through the bypass channel, but there are also freshets released from the spill bays to increase attraction.

Individual data, such as species, weight, length, and gender, on all fish migrating through the Norrfors fishway between 1960 and 2009 has been collected by Vattenfall Vattenkraft AB through trapping all fish at the top of the fishway and manually handling each fish. After closing the fishway on 30th September every year, the spill to the bypass is shut down. Then gillnet fishing is performed to remove as much as possible of remaining salmon and brown trout from the pools just downstream the fishway. Individual data for these fish is also collected by Vattenfall Vattenkraft AB.

For the new fishway that was first used in the 2010 season, VAKI automatic fish counters were installed. These were later fitted with PIT-tag antennas for detection of tagged fish. Twelve other PIT-tag antennas were also installed in the fishway to monitor passage success and fish behavior in the fishway. No manual handling of fish is done in the new fishway, except for when some spawners are selected for brood stock to the hatchery.

3.2 Hydroacoustic systems

Sonar works by emitting an acoustic signal ("ping") and listening to the echo. Echoes are produced by rapid density changes, for example an air bubble in water or a solid object in air. If we know the sound velocity we can use the time from emitting a ping to when we hear an echo to determine the distance to the object. Movement from detected objects can be determined by analyzing the Doppler effect; where a moving object generates an echo with slightly different frequency than the original ping (Figure 2).

Signal frequency of the ping determines the minimum size an object can have and still return an echo, where a higher frequency signal will generate echoes from smaller objects. Differing echo generation from different transducers at varying ping frequency can be used to determine fish species since a combination of frequency responses can give some sense of the air bladder size and shape. For an ADV and ADCP, higher signal frequency can be better because there are more moving objects that can be used to estimate velocity. For fish detection sonar, too high frequency will yield echoes from plankton or other small objects in the water so that the fish disappear in noise from other echoes.

Sonar detection can be compared to a flashlight in a dark room. Just like the light extends like a cone from the flashlight, the ping and echoes are detected in a cone from the hydroacoustic transducer. Because of this, if several transducers are used together, they need to be angled away from each other so as to not cause interference. For applications such as the ADCP, this setup causes an increasing area of measurement for each bin with increasing distance from the ADCP (Figure 3, left). For an ADV, only one speaker (or signal emitter) is used but three microphones are mounted on extended arms and aimed at a central point (Figure 3, right). So the ADCP can measure at any distance but with increasing bias, and the ADV can measure without increasing bias but with limitation to one single point.

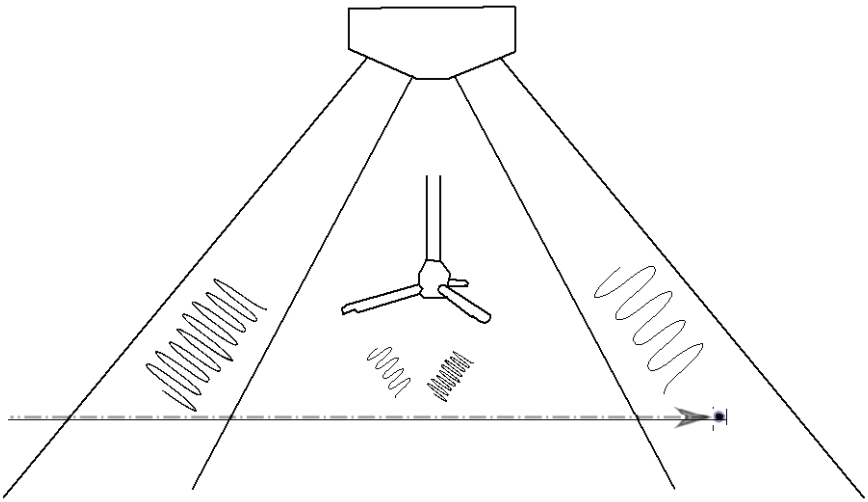

Figure 2. An object (small black dot) moving through detection areas of an ADCP (top) and ADV (center) will cause a Doppler effect where the echo changes frequency compared to the frequency of the ping. Illustration: Dan-Erik Lindberg

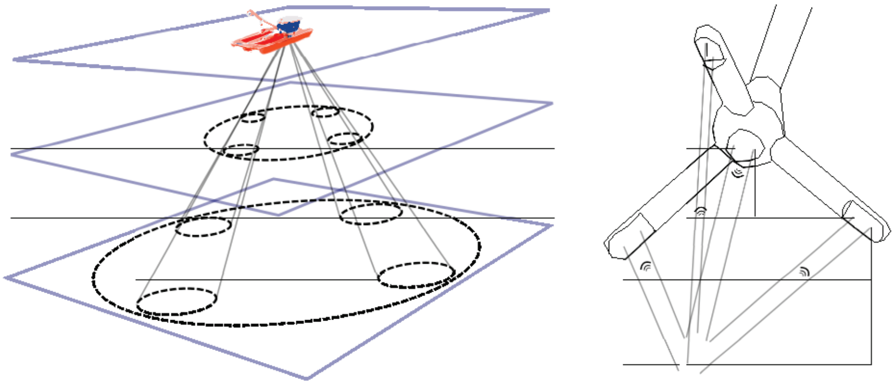

Figure 3. ADCP (left) with four lobes listening in opposite directions and calculates velocity as an average between the four measurements. ADV (right) on the contrary listens to echoes from a single point from three outer positions. Illustration: Dan-Erik Lindberg

3.2.1 SIMRAD

We used a SIMRAD EK60 echo sounder system with an ES120-7C split beam transducer (7 ° viewing angle) to detect fish in the river. This transducer operates at 120 kHz and 300 W. The resulting data files were analyzed in Sonar5-Pro (Balk and Lindem, 2004) and exported to text files for post-processing.

3.2.2 ADV

Our Acoustic Doppler Velocimeter (ADV) was a SonTek Argonaut. This ADV has a sampling frequency of 1 Hz, which is very slow, and an even slower output frequency of 0.1 Hz. The slow sampling frequency is compensated by an affordable price tag and a very high signal frequency at 10 MHz, which enables very small objects to be detected.

3.2.3 ADCP

For bathymetry and current profiling we used a RiverBoat WorkHorse RioGrande ADCP manufactured by Teledyne RD Instruments. This unit operates at 1200 kHz with a sampling rate of 1-2 Hz (depending on other settings).

3.3 Radio telemetry

ATS F1835 radio tags operating at 30 MHz were used to tag fish. The benefit of using 30 MHz radio tags is a slightly longer detection range, which brings the drawback of needing much larger antennas than other systems (e.g. 155 MHz used in some previous studies in this river).

To record data we used custom-built NOAA loggers capable of scanning all frequencies simultaneously. Each of these loggers can be connected to one antenna or two antennas through a MUX. Data is recorded to a text file, which can be used directly in post-processing and data analysis.

Each tag has a numerical identification code which is sent to the receiver and stored with time and signal strength information. Despite various methods of encoding data transfers, a lot of noise makes its way through. For example, if there is a tag with ID 4500 in the system then ID 4499 will often be detected. I guess this is caused by some bit error as a result from noise, but there are no instructions on how to handle this from the manufacturer. What is more worrying is that sometimes ID 4500 may be detected on a different data logger which is physically positioned so far away that the tag signal could impossibly reach it. In other words, sometimes random noise will appear in precisely the correct order to be identified as a tag signal and stored in the system. Moreover, these false detections happen fairly often. Standard praxis is therefore to ignore any signals unless at least 5 signals are received within a one minute period, where the tag sends a signal every second.

We also saw some occasions where the noise was so strong that it drowned out all actual tag signals and false signals were the only ones stored by the loggers. Fortunately, noise was rarely strong enough to have an impact on underwater antennas since the water dissipates the signal. Therefore, the data used for this thesis was not affected too much by noise or interference.

3.4 Software

3.4.1 Wolfram Mathematica

Mathematica is a powerful tool for quickly visualizing data and build mathematical models. We used it for several studies in post-processing, statistical analysis, and to produce graphs and charts (Wolfram, 2011).

3.4.2 R statistical software

R has quickly grown to be one of the most commonly used statistical software packages in both research and commercial applications. I used it in a couple of studies for both post-processing, statistical analysis, and to produce graphs and charts (R Core Team, 2013).

3.4.3 Python

Python is a programming language that is primarily used for fast prototyping. The syntax is made to make the code easily readable, so it is a great tool for collaboration (Python Software Foundation, 2011). I used Python scripts often throughout most of my studies for post-processing data, for example to restructure it from text files to database tables.

3.4.4 PostgreSQL

My database engine of choice has been PostgreSQL, which is a fast and scalable database with open source code (PostgreSQL, 2009). Using SQL is a fast way to access and restructure data, but I also used some functions to get means or other simple math operations.

3.4.5 Other

Most of the technical equipment had its own software to extract data. We used SIMRAD EK-60 and Sonar5-Pro for the sonar; WinRiver II for the ADCP, and some custom software for the radio telemetry loggers from NOAA. For the RFID system I wrote my own software called RiffDee, which was published as an open source project on GitHub.

4 Results

> The stream of life is maintained only in continuous flow of matter through all groups of organisms.
>
> **Ludwig von Bertalanffy, 1952**

4.1 Comparison between ADCP and CFD modelling

During my first summer, I spent a lot of time on the river, observing the salmon and observing the river flow. Later that year, the group from Luleå Technical University (LTU) presented their results from CFD modelling and my spontaneous reaction was “your results are entirely wrong”. Looking at the CFD modelling, it did not match my expectations in the least bit. The LTU group was still confident in their results, however. So we all went out to the river, where we agreed that some aspects of river flow were not represented clearly in the CFD results, but that the CFD modelling was still rather accurate. In the beginning of the tailrace channel, there is an upwelling and backwater from the tunnel exit where there is a lot of turbulence. The CFD model results presented water velocity, but not maximum velocity or any measure of variability. Instead, the results presented were just mean velocity magnitude over a long time period. Because of the long time period for the average, all of the turbulence “got lost”, so to speak. There was no indication that sometimes the velocity was 2 ms^{-1} and sometimes it dropped toward zero. This was the beginning of a lengthy discussion on how to include turbulence in our measurements and models.

I started this thesis with saying that it is exceedingly difficult for us terrestrial animals to understand the aquatic environment due to our lack of a lateral line or similar sense of water movements. This difficulty appears to be multiplied when discussing these topics, because each person has their own way of trying to make sense of it all. This discussion was how Paper I came to include a comparison of ADCP measurements with the CFD modelling. The ADCP measures over a relatively short amount of time (1 Hz), so it will capture more of the variability of the flow. The measurements are still not equivalent to what the human eye will experience, and most likely far from what the fish experience, but it adds a level of detail that the CFD modelling could not provide. There were also some other differences, as we shall see. But later studies also showed that even the ADCP results require some interpretation, where communication difficulties were introduced yet again.

4.1.1 Paper I. A numerical study of the location and function of the entrance of a fishway in a regulated river

We investigated the possible effect of placing a fishway in the inner parts of the tailrace channel, which would guide fish up into the bypass channel.

CFD modelling showed that a fishway should be placed in the innermost parts of the channel, if the flow should be able to reach across the entire channel (figure 4).

We set up three transects at 16, 23, and 32 meters from where the tailrace channel starts, and where the tailrace tunnel exits at 40 meters depth. At these transects, there was a significant difference between CFD modelling and ADCP measurements, where the ADCP measurements showed more instability of flow. CFD modelling showed a pronounced high velocity jet that was slowly moving closer to the surface as distance from the tunnel exit increased. ADCP measurements showed the same pattern, but less pronounced jet and faster rise toward the surface with highest velocities at the surface around 32 m where CFD modelling still showed the jet at 6 m depth (figure 5).

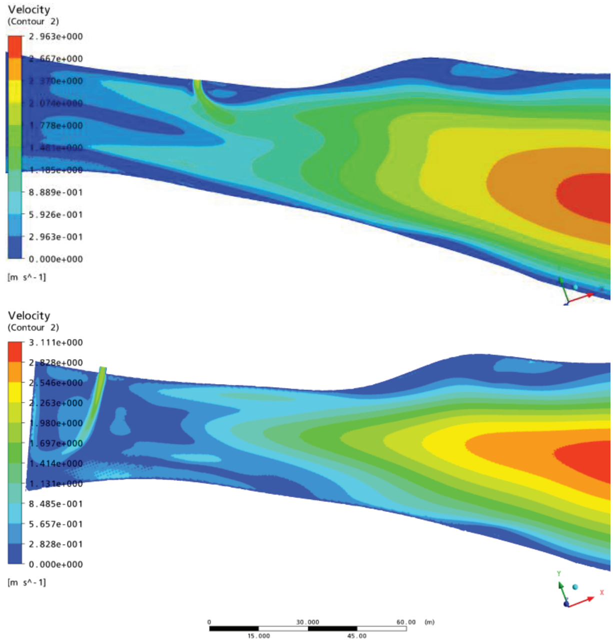

Figure 4. Hypothetical fishway outlet at two different positions in the tailrace channel, at 1 m depth and a discharge of 1000 m^3s^{-1}. If the fishway outlet is placed close to the tunnel exit, the attraction water will reach across the entire channel.

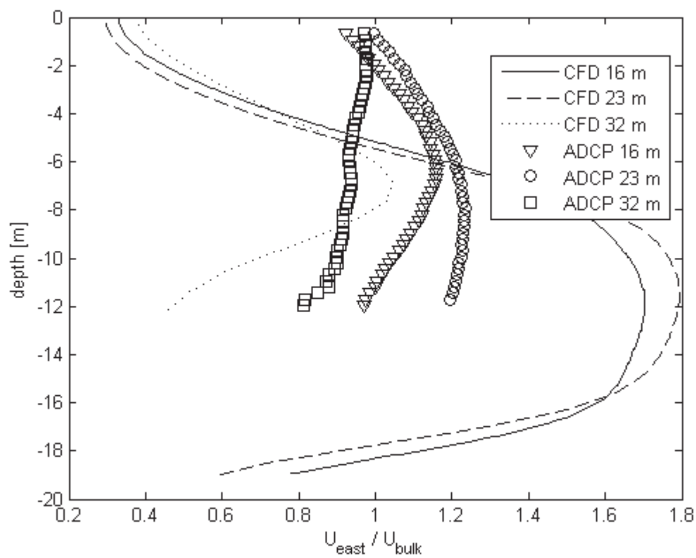

Figure 5. Comparison between ADCP measurements and CFD modelling. ADCP measurements showed less variation both vertically and with increasing distance from the tailrace tunnel exit.

4.2 Comparison between SIMRAD and Radio Telemetry

Looking at the first results from our hydroacoustic survey, there was some skepticism regarding the fish data. For example, what if one or a few fish circle in the area, getting detected over and over again, to what extent will this bias the data? Also, in the highly turbulent environment there were instances where it was difficult to, with certainty, tell the difference between an air bubble drifting through the water and an actual salmon echo. Even if we only selected tracks that were moving in the opposite direction as the main water flow, perhaps the turbulence could make an air bubble move that way too?

Some salmon were tagged with active radio tags in a different research project in River Umeälven. We took advantage of this and placed a series of underwater antennas in the same area as the hydroacoustic survey. By comparing frequency distribution in the area we could compare both technologies. Additionally, by comparing size distribution among hydroacoustic detections with that of the fishway where fish were manually handled, we could trust that we were not tracking lots of air bubbles with the sonar.

In other words, our result of comparing hydroacoustic positioning with radio telemetry detections was that these two technologies produce comparable results. That also means that anyone who is considering an investigation on where fish may be aggregating could choose any of these two technologies and get good results.

After establishing that the hydroacoustic data could be trusted, we were also able to confidently report a fish preference for a highly turbulent environment. To our knowledge, this was the first time such a preference was reported for actively migrating salmonids. However, there was also a possibility that this area was used during a resting period, between attempts to pursue main flow into the tailrace tunnel. Therefore, it was not entirely certain that the preference for turbulence was during active migration.

4.2.1 Paper II. Methods for locating the proper position of a planned fishway entrance near a hydropower tailrace

Hydroacoustic fish detections suggested that the salmon either maintain position or swim in circles near the surface in the inner most part of the tailrace channel; directly above the tailrace tunnel outflow. Most of the detections were recorded in the center of the channel around 1-2 m depth. Distribution of estimated size from detections corresponded well to weight distribution from fish migrating through the fishway, which indicated that we got a good sample from the population.

Fish tagged with radio tags confirmed that the area around 40-60 m from the tunnel roof was an aggregation zone for fish (figure 6). This coincided with the zone where the CFD modelling showed that attraction flow from a fishway could reach across the entire channel.

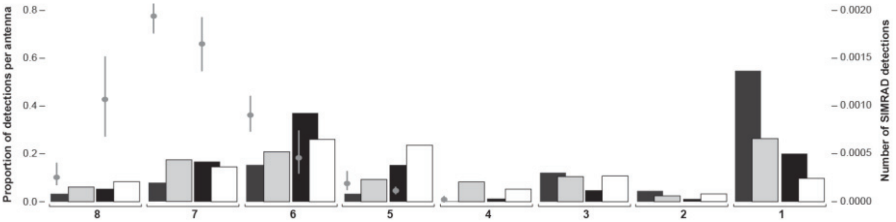

Figure 6. Proportion of radio tag detections close to the river bank (black/white bars) and further away (grey bars), compared with mean number of SIMRAD detections within 30 m from the river bank (grey circles) with min/max within 10 m wide bands.

While we were recording hydroacoustic data, we noticed by ocular observation that the salmon moved through turbulent areas with ease, and barely moving their tails to swim against the current. An overlay of fish detections and CFD modelling of turbulence intensity also showed a pattern that seemed to match well (figure 7).

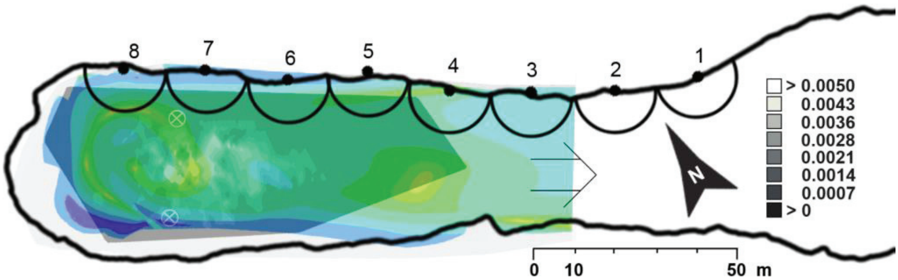

Figure 7. Combined plots of fish detections per hour (gray scale) overlaid by turbulence intensity (color, where blue is low and yellow is high). Green and yellow areas has a turbulence intensity > 1; that is, the fish cannot maintain positive rheotaxis there because there is no main direction of flow.

For the comparison of hydroacoustic and telemetry detections, only the area within 30 m of the north river bank was considered. We used this same subset of data to examine preference for turbulence intensity. As it turned out, most of the area had turbulence intensity between 0.5 and 1.0, and this was also the range that salmon showed a preference for. The only other turbulence intensity that had neutral or positive preference was no turbulence at all; both weak turbulence intensity and strong turbulence intensity was shunned by the fish (figure 8).

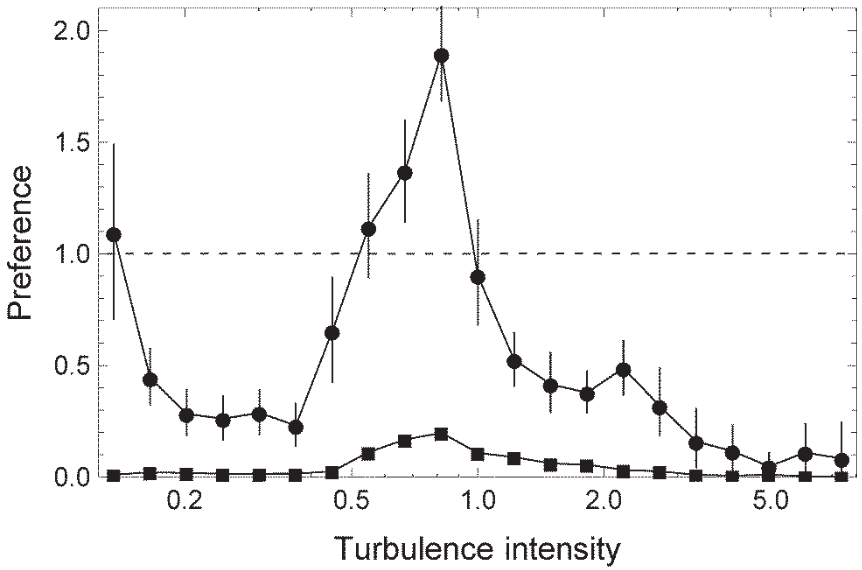

Figure 8. Preference for turbulence intensity among detected salmon in the tailrace channel (circles) and availability of each turbulence intensity estimate (squares). Bootstrapped 95 % confidence intervals are shown by error bars.

Those fish with radio tags which visited the tailrace channel spent on average 21 days between their first and last visit. Because of this long delay, we thought it was reasonable to conclude that the salmon try to enter the tailrace tunnel, but fall back regularly looking for alternative paths. The tailrace channel bathymetry is fairly smooth since it consists of blasted rock and bulldozed cobbles. There are no stones that can offer a refuge for rest (Gisler, 1751; Liao et al., 2003). Therefore, the preference for turbulence intensity just under 1.0 could be explained because it offers the most rest for the fish. In other words, if a fishway attraction jet would be installed, the fish may not want to aggregate there anymore.

4.3 Energy saving preferences

Paper I and II mainly worked with the traditional approach that salmon are attracted to high velocity jets. In Paper III we were able to show that the salmon actually prefer a lower water velocity if they are presented with a choice.

One aim with this study was to investigate if the energy saving potential of turbulent structures was being used by actively migrating salmon. However, the passages past the weirs in the fishway were so narrow that the scale of any remaining turbulent structures must have been too small for the fish to utilize. Smolt ($L_b \sim 0.15$ m) released in the fishway were captured on video to slowly drift through areas that should have had water velocity exceeding 2 ms^{-1}. So small fish were probably able to take advantage of turbulent structures to move through the fishway, but those smolt were not part of the study. In retrospect, including video surveillance for the adults in this study would have been a good idea. In fact, we discussed it but decided against due to budget restriction.

Without being able to utilize the energy from vortices, the high water velocity made each weir passage a migration obstacle for the salmon. We recorded several rushes past a couple of antennas with a burst swimming velocity of around 3 ms^{-1}, but all the fish had very low velocity over the length of the entire fishway (Figure 10). Thus, the fish must have been resting for extended periods in the pools between weirs. During those resting periods, it would be reasonable to assume that they utilized turbulent structures in the pools to save energy, since there would be larger scale structures in the pools than over the weirs, but we did not set up the experiment to capture that type of behavior.

Even though we were not able to show any preference for turbulence or turbulent structures, the preference for lower resistance can be seen as indirect evidence for preference of turbulent structures. For if the salmon prefer lower resistance, then why would we observe them near high velocity jets so often in the river? The answer to that question could be that the high velocity jets produce turbulent structures in their boundary layer which enable the salmon to save energy.

4.3.1 Paper III. Path Selection of Atlantic salmon (Salmo salar) migrating through a fishway

In the Norrfors fishway, there are only two available paths upstream. The bottom orifice is a small square opening of 0.4 m width and 0.4 m height. Mean velocity magnitude through the bottom orifice is about 2.2 ms^{-1}. The surface passage is 1.5 m wide and even though the water pillar is only 0.3 m, there is plenty of room upwards if the fish don't mind breaking the water surface. Mean velocity magnitude over the weir is 1.4 ms^{-1}.

Salmon migrating through the fishway showed a preference for the surface passage. The preference for surface passage got stronger towards the end of the fishway (Figure 9).

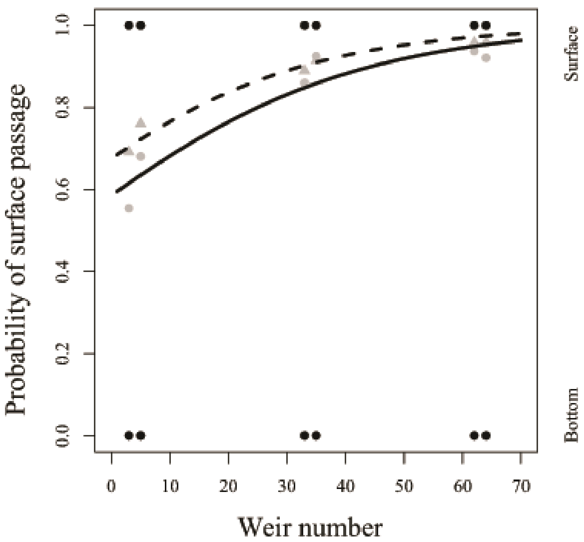

Figure 9. Regression of male (triangles and dashed line) and female (circles and solid line) path selection through the Norrfors fishway. What appears to be a difference between sexes is more likely to be a size dependence (smaller fish were more likely to select surface passage). Black dots show where a choice between bottom/surface was recorded.

We constructed a model with the aim of predicting path selection through the fishway. One prediction was that preference for water velocity is size dependent, so that smaller fish should choose the surface path with lower velocity. It did seem like there was a size dependence in preference for the surface path, but since almost all the fish (95-97 %) selected the surface path at the end of the fishway, it was impossible to make any distinction as to where any size dependence would begin or end. Another model prediction was that larger fish should move faster through the fishway since they prefer higher water velocity, but we found out that the opposite was true; the largest fish were also the slowest (figure 10).

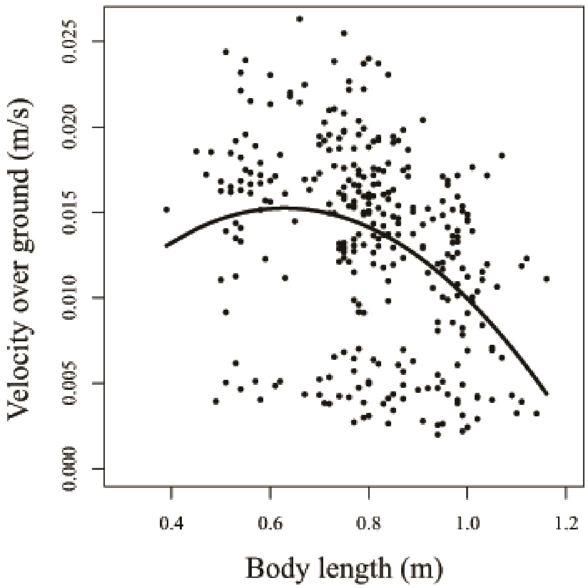

Figure 10. Velocity over ground through the length of the fishway pools (180 meters in total). Larger fish spent longer time to swim through the fishway.

Even though the model prediction was not accurate, there were some things which imply that the model was still correct. Most importantly, the model predicted that both surface and bottom passages had too high velocity; so that the salmon would only stand still if it was trying to find a path that is optimal in terms of conserving energy. And in fact, the salmon were all moving very slowly through the fishway overall; only doing small bursts of fast swimming to pass a few weirs at a time.

For the largest fish, it is possible that the small dimensions of passages could have deterred them from passage. This could be an explanation for why larger fish had a lower swimming velocity, as opposed to our model prediction.

4.4 The instrumental failure

Measuring water velocity with the ADCP appears to be functioning fairly well. At least, over a river-wide scale the total discharge reported by the ADCP matches fairly well with the discharge reported by Vattenfall Vattenkraft AB hydropower turbines. But for measuring turbulent properties, the ADCP did not produce measurements that were useful for determining fish preferences.

Turbulence forms in boundary layers close to protruding objects, or around velocity gradients. The expectation was therefore to record high turbulence close to the bottom and in some central areas of the river near velocity gradients. Increasing discharge provides increased kinetic energy, which should produce a higher amount of turbulence. However, ADCP measurements reported the lowest turbulence close to the bottom and barely any difference with increasing discharge (Figure 13).

The failure to record turbulence was likely due to the large cell size of the ADCP. Our instrument has a minimum bin size of 0.1 m, but to ensure good quality data without information loss we had to increase bin size to 0.25 m. Each bin is calculated from four different sonar heads, angled out from one another. So while the vertical bin size is fixed at 0.25 m, the horizontal size is increasing with increasing distance from the transducer. Since each transducer is angled 20 degrees, the measurement points at 10 m depth will be 8.39 m apart (c.f. Figure 3). So if there is a vortex and it passes by the upstream sonar, then the vortex has to remain unchanged and travel parallel with the ADCP orientation to be measured by the downstream sonar. Even in this rather unlikely scenario, that vortex was never detected by either of the side lobes. In fact, it would not be unlikely over this distance if a different vortex was recorded at either side lobe that gave completely opposite information about velocity and direction of flow. Thus, the ADCP bins close to the bottom could be seen as averages over a 0.25 m deep circle with a diameter close to 8 m. That could explain the poor results from turbulence measurements. It does not necessarily mean that the measurements were wrong; it could be that the measurements are correct for the scale of 1 m to 8 m large cells. In other words; if we would be interested in very large eddies we might get accurate results, but for finding a pattern of vortices with the scale of ~30% of fish body length the ADCP was unable to record anything on that scale. Therefore, the results were contrary to my expectations, but not necessarily incorrect.

Of course, I was aware of this technical limitation of large cell sizes when I did the field measurements. My hope was that given enough data, the variation in flow would shine through and give some measurement of turbulence, and while I did expect some inaccuracy I did not expect a total failure to detect smaller structures. After all, some previous laboratory experiments showed that there might be a possibility to use this method (Nystrom et al., 2007). But I was wrong and the study only served to show that salmon are indeed often positioned near high velocity water, despite the Paper III results showing a preference to conserve energy.

An interesting observation from this study was that almost all of the salmon started diving towards the bottom as soon as they entered the detection area. My interpretation of this behavior was that they were fleeing from an unpleasant sensation caused by the 300 W acoustic ping. Similar flight responses have been seen in other studies (e.g. Knudsen et al., 1997). Salmon hearing (otolith) does not span over the frequency used by the sonar, so I would assume any unpleasant experience is felt in their lateral line. Since so many first detections were near the surface, the fish were most likely not affected before they entered the detection area, but the flight response does beg the question if acoustic survey methods are completely unbiased.

4.4.1 Paper IV. Path selection of migrating Atlantic salmon (Salmo salar) is near the highest available water velocity

ADCP measurements identified a clearly discernible high velocity jet in high discharge measurements (figure 11). At lower discharges, the jet was much less pronounced, but there were areas with higher velocity. When we were at the river taking those measurements, it was clear to the naked eye that turbulence also increased at the same rate as velocity increased, because of surface upwelling and vortices. But the ADCP measurements did not show any increase of turbulent kinetic energy.

All of the fish detections at high discharge (800 m^3s^{-1}) were at an area with higher velocity than the mean velocity for that river section (figure 12). At lower discharge, the fish detections were not significantly different from the mean velocity, but most of the fish were still detected in the high velocity area about 40 m from shore.

One might be tempted to explain the salmon behavior by saying that they mostly swim close to the surface and the highest velocities are at the surface (figure 13a). However, there were no fish detections closer than 20 m from the river bank. If the fish were not looking for high velocity water, then they should be swimming close to the river bank where velocity is lower (figure 12).

What further speaks for the interpretation that salmon are looking for high velocity water is that most of the fish were detected at high discharge. Additionally, those fish that were detected at low discharge were usually detected when discharge was increasing (figure 14). Many of the fish that were detected at 400 m^3s^{-1} had experienced discharge around 100 m^3s^{-1} within six hours before detection. That means even fish detected at low discharge were actually detected at the highest discharge available for the past few hours.

Everything I looked at pointed to salmon aiming to find a higher water velocity, which should mean a higher resistance. Yet, it would be reasonable to assume that the fish want to conserve energy by selecting lower resistance and this has also been shown in previous research (e.g. Paper III). In a comparison with encountered mean velocity magnitude of the water versus the optimal swimming velocity of the fish, all of the fish were swimming faster than the optimal velocity (Figure 15). Additionally, most of the smaller fish were swimming faster than their maximum sustainable swimming velocity. If they were swimming at this velocity for a longer period of time, it would be proof that the fish utilize energy from turbulent structures, because there is no other way they could keep up that high swimming velocity. Unfortunately, my setup did not monitor the fish for more than a few meters in a transect of the river, so I could not say if they maintained this velocity for an extended period of time. I could, however, point out that many even smaller fish were recorded as holding position for minutes at a time in these fast flowing sections of the river. Although, those fish were obviously not salmon so they were removed from the survey results.

In the end, there is no clear evidence from this study that Atlantic salmon utilize turbulent structures during their active migration. There are some indications or circumstantial evidence that they should be utilizing turbulent structures, for how would the fish be able to swim at those velocities otherwise? But the ADCP measurements did not get a sufficiently detailed picture of turbulence, so there was nothing to connect the fish behavior with. To get stronger evidence of utilization of turbulent structures, it is necessary to use instruments capable of measuring hydrodynamics with higher resolution.

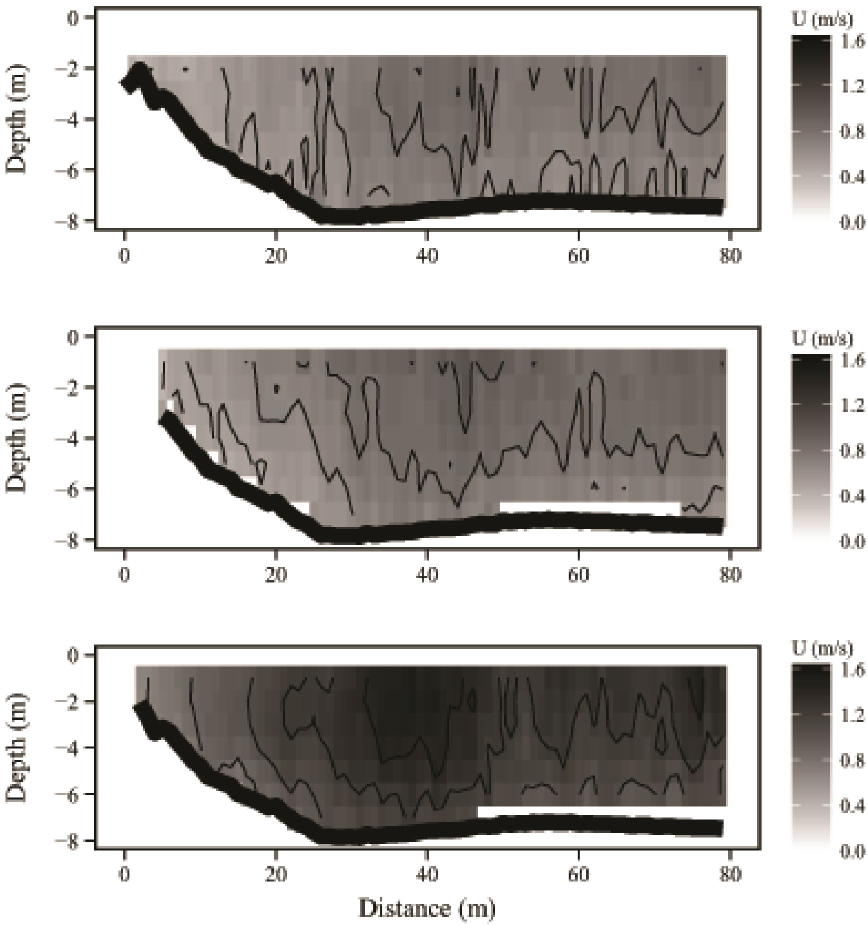

Figure 11. At 800 m^3s^{-1} (bottom) there was a pronounced high velocity jet, but at lower discharge (400 m^3s^{-1} top and 600 m^3s^{-1} middle) this jet was not as obvious.

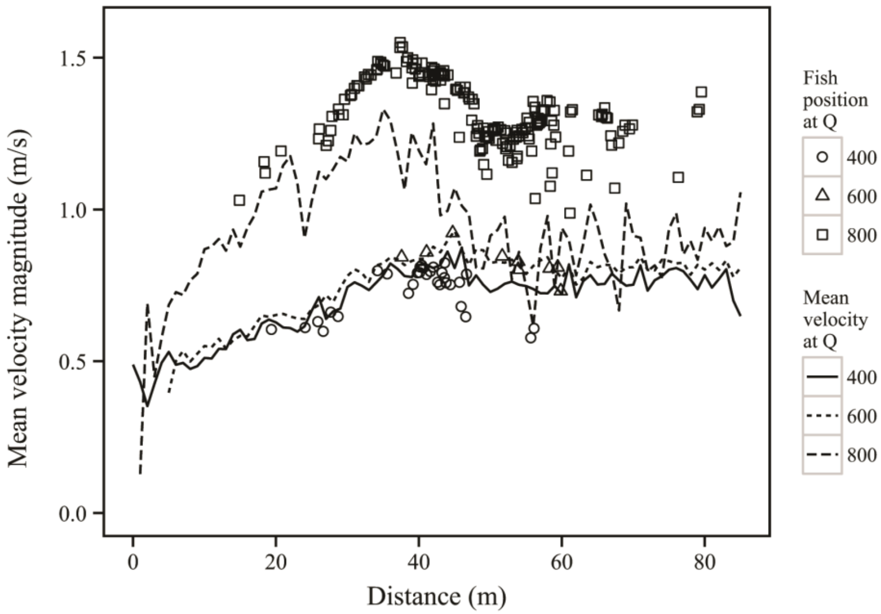

Figure 12. Mean velocity magnitude (ms^{-1}) around each point where a fish was first detected (symbols) and mean velocity magnitude for the water column surface to bottom (lines).

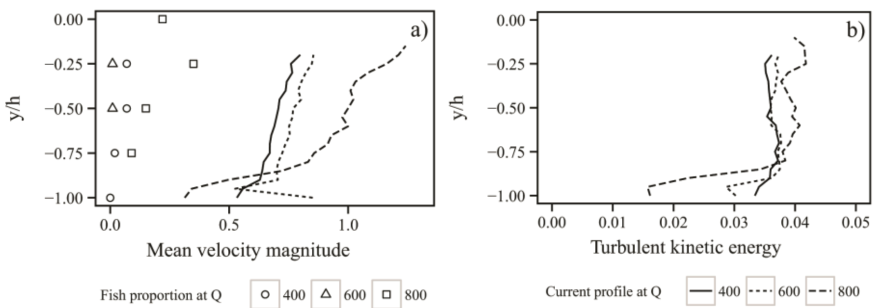

Figure 13. Mean velocity magnitude (left) and turbulent kinetic energy (right) profiles grouped at total discharge 400, 600, or 800 m^3s^{-1}. Y-axis shows relative depth (measurement depth divided by total depth). Most fish were detected at 800 m^3s^{-1} and 25 % distance from the surface (left).

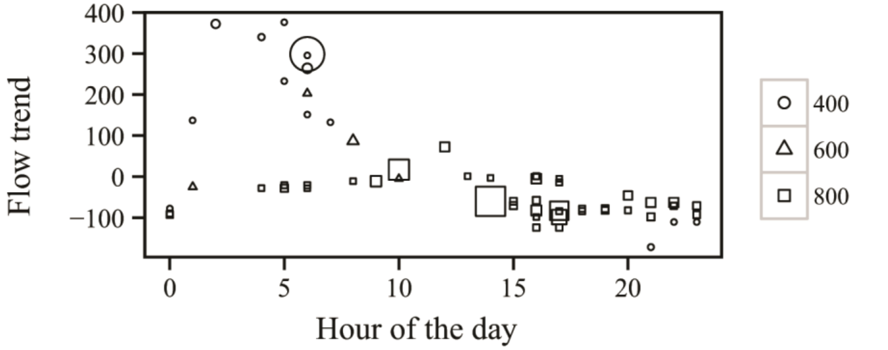

Figure 14. Flow change trend (ΔQ, m^3s^{-1}) for the six previous hours each time a fish was detected (x-axis is fish detection time). Symbols denote total discharge at the time of detection (Q, m^3s^{-1}) and symbol size denote number of fish detected that particular hour.

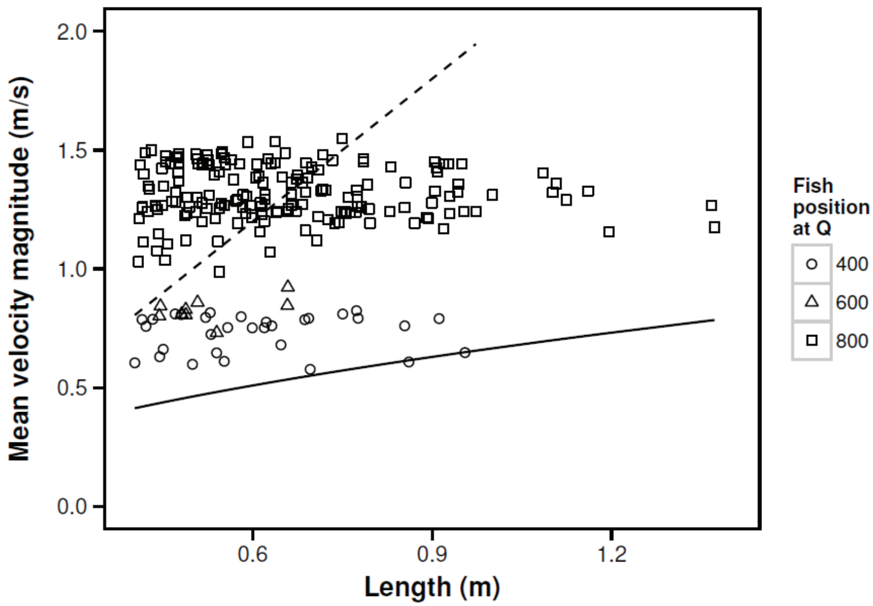

Figure 15. Mean velocity magnitude (U) around each point where a fish was first detected (points) and predicted optimal swimming velocity with zero effect from turbulent structures (u_{opt}, solid line) and approximate maximum sustainable swimming velocity (u_{ms}, dashed line). X-axes denotes fish body length reported by the Sonar5-Pro software.

5 Conclusions

A man finds he has been wrong at every preceding stage of his career, only to deduce the astonishing conclusion that he is at last entirely right.

Robert Louis Stevenson, 1881

Atlantic salmon are traditionally attracted with a high velocity jet. I can identify three possible reasons for why a high velocity jet will act as an attractor:

First of all, it may be the case that the salmon are attracted to the high velocity. If this is the case, then the salmon are willing to pay a higher cost energetically in exchange for some other advantage that is more important. Perhaps the high velocity water enables their olfactory organs to pick up more molecules over a shorter time so that they can be more sure of finding their natal stream for spawning (Keefer et al., 2006). Or maybe their memory imprint from the smolt migration took them downstream in the high velocity water, so they follow exactly the same path back upstream.

Secondly, it may be the case that a high water velocity fools the salmon into thinking that it is caused by high discharge, and they follow the highest discharge to find their natal stream for spawning. It would be dangerous for the salmon to follow low discharge, because they may become stranded and in low discharge it is possible for predators like otters to catch them more easily (Carss et al., 1990). This can be seen in small streams, like in the UK where salmon move upstream much later in the season than in Sweden and other countries with large rivers that do not run the risk of drying out (Banks, 1969; Dahl et al., 2004; Tetzlaff et al., 2008).

Third, and last but not least, it is possible that it is not the velocity that the salmon are attracted to, but that they are attracted by the turbulent structures that are created in the boundary layer of a high velocity jet. Such turbulent structures can be used by the salmon to save energy, and it is possible they are trying to minimize energy expenditure by finding those turbulent structures which provide the highest amount of kinetic energy. If this is the case, then it could be an important finding for meeting human preferences. Human preferences usually include minimizing discharge of spill water, so that a maximum amount of energy can be utilized from the water. If the fish preference is to utilize a specific turbulence then this could be created without a high velocity jet, and a lot of water discharge could be saved for energy purposes.

5.1 Does the traditional method work?

In Paper I and II we used the traditional method of creating a high velocity jet that could compete with the main flow and reach across the width of the river. Then we confirmed that the fish were aggregating in that area, and that a high velocity jet would indeed be encountered by the fish so that the possibility of attraction was there.

After those studies, the hydropower company did some prospecting and concluded that the bedrock is of poor quality in this area. Their conclusion was that any construction could lead to rock falling into the tailrace channel and thus a reduction of energy production. The costs of producing a new fishway here in a safe way, and the risk assessment of production losses from the hydropower plant, led to the decision that they refuse to build a fishway at this location. So we were not able to evaluate the efficiency of our method, and we do not know how well a fishway at this location would have functioned.

If we look at other sites where a similar method has been used, there is little doubt that a fishway at the location we suggested would have been functional and well used by the fish. The traditional method of finding where the fish gather and then placing a high velocity jet there is well proven, even from when the first fishways were built (Francis, 1870; US Bureau of Fisheries, 1873; von Bayer, 1908).

5.2 Are Atlantic salmon attracted by turbulent structures?

In Paper II we found a preference for high turbulence intensity. But this preference may have been during the resting state, between active periods, where it has already been shown in the laboratory that the fish prefer to save energy by utilizing turbulence (Liao et al., 2003).

In Paper III we failed to find any preference for turbulence parameters. But we did observe behavior which indicated some preference to save energy.

Paper IV identified a clear preference for high velocity water. This preference is contrary to the observations in Paper III; that the salmon prefer to save energy. Thus, it is near at hand to draw the conclusion that the salmon seek out turbulent areas near high velocity water to save energy, and not that they actually prefer high velocity water. However, limitations in the measurement technology prevented any clear results.

5.3 Usefulness of used methods

During my studies, I have come across a variety of tools to monitor fish behavior and measure hydrodynamic qualities. I have also seen that there are many limitations about the methods used in these behavioral studies, and that some researchers seem to be blind to these limitations. Therefore, I would like to take a moment to go through my experiences with some of these technologies.

In general, my conclusion is that the currently available technology to measure hydrodynamics is unsatisfactory. There is some research being done on an artificial lateral line, which I think could be a very interesting development. Not only because it might be more accurate than our current methods, but also because it is entirely unobtrusive to the fish since it is passive detection.

An artificial lateral line (or an array of them) might also be used to detect fish movements. If that would be possible, that would also be entirely preferable to the fish monitoring tools that are available today. All of the tools we have available to study fish behavior are actually modifying the behavior of the fish as they are being studied. But that is not all; there are also many other sources of error, like air bubbles misinterpreted as fish in hydroacoustics or noise/interference causing misdetections in radio telemetry. Therefore, all behavioral studies will be full of bias. Video surveillance is the exception, but that requires a river with good visibility which is rarely the case in Swedish waters.

5.3.1 ADV

ADV measurements appear to be very accurate. This accuracy is probably due to the small sampling volume. Because of the ADV accuracy, it is often used as comparison for alternative methods (e.g. Nystrom et al., 2007).

While the small sampling volume is a benefit for accuracy, it is also strongly negative in other aspects. How many ADV's with 1 cm^3 sampling volume do you need to monitor a river that is 300 m wide and 9 m deep? How many ADV's can you deploy in a river before they noticeably change water flow? Shortly put; the ADV is entirely impractical to use in a river setting.

5.3.2 ADCP

Building a current profile over a river is as easy as pulling a small boat from bank to bank. The ADCP is amazingly fast in measuring water velocities from surface to bottom and using them to calculate river discharge.

It is clear that the discharge calculation from the ADCP is accurate. However, the velocity measurements seem to be mislabeled. I would like to say that the "velocity measurements" are actually time averaged and also area averaged so that what you are really presented with is closer to a mean velocity magnitude calculation rather than an actual velocity measurement. Thus, the current profile from an ADCP might be useful for looking at where most of the water flows through, but it should not be used to look at turbulence or flow complexity that could be of importance for fish. If you want to calculate turbulence with some accuracy, you need instantaneous and actual measurements of velocity, not calculations or estimates.

5.3.3 CFD

When I first saw a plot from CFD modelling in an area where I had spent a lot of time and I was well familiarized with the water flow, I said "this is completely wrong". But as it turned out, it was my first impression that was completely wrong. It takes a bit of training to interpret the results from CFD modelling, but once you understand how to read the results, you also realize that it is surprisingly accurate.

What makes interpretation of CFD results so difficult is that they are the mean from a long time period. If the flow is undulating or oscillating within that time period, then you are not presented with any oscillations, you just get the mean values. If you stand by a river and observe oscillation and undulation and other variations, then it is really quite difficult to translate it into mean values in your head. Nevertheless, those CFD modelling mean values are just as accurate as if you would have been there to manually take measurements over a long time.

Unfortunately, since CFD modelling produces mean values over a long time, it will never tell us exactly what the fish are experiencing. So while I have come to be convinced of its accuracy, I am not convinced that it is the best tool to understand fish behavior. I believe CFD modelling is best used in engineering, to look at sediment transport and similar things.

The only place I see for CFD modelling in studies of fish behavior is over large areas where it is impractical to do any measurements of water velocity. Because in those cases, there are no other alternatives available at this time.

5.3.4 SIMRAD

Hydroacoustics is a great technology for studying how objects move in water. But there are many limitations imposed with this technology, and I have come across many studies where the experimenters do not understand the limitations.

First of all, the high energy ping produced by active sonar will create a flight response in many aquatic organisms. So by using this technology to study animal behavior, you need to be aware that you are causing a change in behavior. I believe that the first ping is still useful, but anything after that is a study of how the fish react to the sonar and it is not natural behavior.

Transponder frequency is very important. For low frequencies, the fish can hear the ping, and you get a reaction to the sound. For higher frequencies (i.e. 120 kHz used in my studies), the ping is not audible but the fish may sense it as a pressure wave through their lateral line. It is possible that the reaction to the ping will be different depending on what frequency is used, but I have not found any studies on this.

Another aspect of transponder frequency is that it determines detectability of specific object sizes. Lower frequency is optimal for large objects, and higher frequency is optimal for small objects. When I was first presented with our SIMRAD equipment, I was told that “it is great, because you can even see plankton”. Well, I am not studying plankton. As it turns out, there is plenty of debris in Swedish rivers, and the high frequency of our transponder (120 kHz) meant that all of those small leaves and sand etc were detected as moving objects by the sonar. To find fish detections I had to go through an encumbering manual process to filter out all the non-fish detections. If we had a transponder with lower frequency, then only large objects like fish would have been detected, and my job would have been that much easier. By reducing workload you also reduce another source of bias from the human factor where a tired operator might mistakenly include an object as a fish or discard a fish as an object.

Finally, different frequencies can be used to identify fish species. This requires that two different frequencies are used at the same time. When two transponders of different frequencies detect the same object, the difference in response can be used to identify the size and shape of the swim bladder and thereby get a species identification. Since I only had access to one frequency, I had to assume that all fish were salmon. That assumption was most likely true, but I would have preferred to use the capabilities of this technology.

5.3.5 Radio Tags

Using active radio tags has become common practice in animal behavior studies. What I found out from analyzing radio tag detections was that interference and/or noise would often randomly appear with the same configuration as a tag ID. If you only look at individual detections, the same tag can be detected at many locations at the same time, hundreds of kilometers apart. So it is necessary to filter out individual detections and only keep those detections that have been recorded many times in a row at the same site. It appears that some loggers do this automatically, but the loggers we used were custom built by NOAA and did not have that functionality.

Signal strength dissipates rather fast even when travelling through the air. A radio signal that has to travel through water dissipates so fast that it is only reasonable to expect detections when a fish is swimming close to the surface. That means you miss out on any behavior from fish travelling closer to the bottom. Fortunately, most salmon swim close to the surface during active migration. But the combination of signal loss from filtering (because of noise/interference bias) and signal loss from weak signals adds a lot of uncertainty and room for interpretation during the analysis.

Despite many shortcomings, radio tags offer a fairly inexpensive way of following the movements of individual fish. But because of the shortcomings of the technology, I believe it is most sensible to look at mean values over time rather than individual detections, which means the analysis is closer to CFD modelling in that it only gives a rough estimate without any details of individual behavior.

5.3.6 RFID

PIT-tags are very inexpensive, currently priced at less than 1 € a piece, compared to 150 € a piece for active radio tags. This means that hundreds or thousands of fish can be tagged, which gives you much higher statistical significance of any study, and the possibility of capturing differences in behavior from sub-groups.

On the downside of using PIT-tags is that the antennas have a very short range. Full duplex tags will rarely be detected beyond 1 m from the antenna. Half duplex tags can be detected at slightly further distance, but if you want to detect tags in a small area (such as a fishway, which is usually the case), then the half duplex tags can cause signal echoes in the system so that a fish appears to be detected at several places simultaneously.

To make a short summary of PIT-tag abilities and shortcomings, it could be said that the full duplex tag is optimal for detection in a fishway, while the half duplex tag is optimal for detection in small and shallow streams, but no PIT-tags are suitable for detection in large rivers due to depth and range problems.

Setting up an RFID system can be very complicated and expensive, as opposed to the tags themselves. The readers are very sensitive to Electromagnetic Interference (EMI) and this will often cause a lot of problems. EMI can come from any electrical engine or generator, but also from transformers and other electrical equipment. This type of equipment is very common in the vicinity of fishways, especially if the fishway is located at a hydropower dam. Additionally, there is EMI coming from space radiation, radio traffic, and many other sources. Therefore, it is essential to have an electrical engineer go over the grounding scheme at the location where a reader is going to be installed. The power source needs to be quiet in terms of noise. All of the equipment should be put in a well shielded Faraday cage with proper grounding for everything.

An RFID reader is usually set up to only store the tag with the strongest signal. It is easy to design a system that can read several PIT-tags at once (Dawei Shen et al., 2009), but for some reason manufacturers have not pursued any products with this functionality. What this means is that if a fish swims close to the antenna, then no other fish will be detected. We once saw a smolt make an antenna its new home, swimming only a decimeter away from the coil continually for several weeks, even returning several times after the fishway was emptied of water (routinely done weekly to clean from debris). Such unexpected fish behavior can in effect disable the functionality of an antenna even after you spend millions on EMI proofing and similar measures. So you need monitoring and routines to handle such occurrences.

Once you have an RFID system up and running, it will be very reliable and you can tag a lot of fish at a low cost per tag. But before you get it up and running, there are many hurdles to pass.

References

Balk, H., Lindem, T., 2004. Sonar4 and Sonar5-Pro. Post processing system. *Operator manual v5.9.4*.

Banks, J.W., 1969. A Review of the Literature on the Upstream Migration of Adult Salmonids. *J. Fish Biol.* 1, 85–136. doi:10.1111/j.1095-8649.1969.tb03847.x

Brewer, J.D., 1872. Improvement in Chutes and Fishways. *US Patent 126257*, Muncy, Pennsylvania, USA.

Carss, D.N., Kruuk, H., Conroy, J.W.H., 1990. Predation on adult Atlantic salmon, Salmo salar L., by otters, Lutra lutra (L.), within the River Dee system, Aberdeenshire, Scotland. *J. Fish Biol.* 37, 935–944. doi:10.1111/j.1095-8649.1990.tb03597.x

Dahl, J., Dannewitz, J., Karlsson, L., Petersson, E., Lof, A., Ragnarsson, B., 2004. The timing of spawning migration: implications of environmental variation, life history, and sex. *Can. J. Zool.-Rev. Can. Zool.* 82, 1864–1870.

Dawei Shen, Woo, G., Reed, D.P., Lippman, A.B., Junyu Wang, 2009. Separation of multiple passive RFID signals using Software Defined Radio. *IEEE*, pp. 139–146. doi:10.1109/RFID.2009.4911203

Denil, G., 1909. La genèse d'une échelle a poissons nouvelle. Bull. Pop. Piscic. 2, 155–183.

Fan, Z., Chen, J., Zou, J., Bullen, D., Liu, C., Delcomyn, F., 2002. Design and fabrication of artificial lateral line flow sensors. *J. Micromechanics Microengineering* 12, 655–661. doi:10.1088/0960-1317/12/5/322

Francis, F., 1870. Reports on salmon ladders. Horace Cox, London.

Gisler, N., 1751. Ron om Laxens natur och fiskande i de Norrlandska Alfvarna. *Kongliga Vetenskapliga Academiens Handlingar*.

Håkansson, C., Kriström, B., Johansson, P.O., Leonardsson, K., Lundqvist, H., 2004. Salmon and hydropower: dynamic cost-benefit analysis, *Fifth International Symposium on Ecohydraulics, Congress Proceedings*.

Hocking, M.D., Reynolds, J.D., 2011. Impacts of Salmon on Riparian Plant Diversity. *Science* 331, 1609 –1612. doi:10.1126/science.1201079

Karppinen, P., M\äkinen, T.S., Erkinaro, J., Kostin, V.V., Sadkovskij, R.V., Lupandin, A.I., Kaukoranta, M., 2002. Migratory and route-seeking behaviour of ascending Atlantic salmon in the regulated River Tuloma. *Hydrobiologia* 483, 23–30.

Keefer, M.L., Caudill, C.C., Peery, C.A., Bjornn, T.C., 2006. Route selection in a large river during the homing migration of Chinook salmon (Oncorhynchus tshawytscha). *Can. J. Fish. Aquat. Sci.* 63, 1752–1762. doi:10.1139/F06-068

Knudsen, F.R., Schreck, C.B., Knapp, S.M., Enger, P.S., Sand, O., 1997. Infrasound produces flight and avoidance responses in Pacific juvenile salmonids. *J. Fish Biol.* 51, 824–829.

Lacey, R.W.J., Neary, V.S., Liao, J.C., Enders, E.C., Tritico, H.M., 2012. The IPOS Framework: Linking Fish Swimming Performance in Altereed Flows From Laboratory Experiments to Rivers. *River Res. Appl.* 28, 429–443. doi:10.1002/rra.1584

Landmark, A., 1884. Om laxetrapper. *Nor. Tek. Tidskr.*

Larinier, M., 2002. Fishways: biological basis, design criteria and monitoring. *Bull Fr Pêche Piscic* 83–101. doi:http://dx.doi.org/10.1051/kmae/2002109
Leonardsson, K., Belyaev, Y., Rivinoja, P., Lundqvist, H., 2005. Modelling upstream migration of Atlantic salmon as a function of environmental variables. *SLU Report.*
Liao, J.C., Beal, D.N., Lauder, G.V., Triantafyllou, M.S., 2003. Fish Exploiting Vortices Decrease Muscle Activity. *Science* 302, 1566–1569.
Livermore, A., 1866. Improved Fishway. *US Patent 57159*.
Ljungdahl, K.-G., 1935. Den nya laxtrappan i Norrforsdammen. *Sven. Fisk.* 44, 237–240.
Ljungdahl, K.-G., 1934. Laxräkningen vid Norrfors. *Sven. Fisk.* 43, 133–138.
Lundqvist, H., Rivinoja, P., Leonardsson, K., McKinnell, S., 2008. Upstream passage problems for wild Atlantic salmon (Salmo salar L.) in a regulated river and its effect on the population. *Hydrobiologia* 602, 111–127. doi:10.1007/s10750-008-9282-7
Mather, F., 1887. Report upon the results of salmon planting in the Hudson River. *Fish. Bull., Bulletin of the United States Fish Commission* 7, 409–424. doi:10.1577/1548-8659(1889)19[39:SITHR]2.0.CO;2
McDonald, M., 1879. Improvement in Fishways. *US Patent 218299*.
McElroy, B., DeLonay, A., Jacobson, R., 2012. Optimum swimming pathways of fish spawning migrations in rivers. *Ecology* 93, 29–34. doi:10.1890/11-1082.1
McLeod, A.M., Nemenyi, P., 1941. An Investigation of Fishways, *Bulletin No. 24, University of Iowa Studies in Engineering. State University of Iowa.*
Nystrom, E.A., Rehmann, C.R., Oberg, K.A., 2007. Evaluation of mean velocity and turbulence measurements with ADCPs. *J. Hydraul. Eng.* 133, 1310–1318.
Perkins, L.Z., 1974. Fish ladders for Ice Harbor dam, Snake River, Washington, *Technical report No. 92-1, Division Hydraulic Laboratory, U.S. Army Engineer Division North Pacific, Walla Walla District, Bonneville, Oregon.*
PostgreSQL, 2009. PostgreSQL. *The PostgreSQL Global Development Group*.
Prince, E.E., 1914. A Perfect Fish Pass. *Trans. Am. Fish. Soc.* 43, 47–56. doi:10.1577/1548-8659(1913)43[47:APFP]2.0.CO;2
Prince, E.E., 1902. The Fish-Way Problem, *No. 35, Fisheries. Department of Marine and Fisheries, Canada.*
Python Software Foundation, 2011. *Python Language Reference*.
R Core Team, 2013. R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing, Vienna, Austria.*
Rivinoja, P., Leonardsson, K., Lundqvist, H., 2006. Migration success and migration time of gastrically radio-tagged v. PIT-tagged adult Atlantic salmon. *J. Fish Biol.* 69, 304–311.
Rivinoja, P., McKinnell, S., Lundqvist, H., 2001. Hindrances to upstream migration of atlantic salmon (Salmo salar) in a northern Swedish river caused by a hydroelectric power-station. *Regul. Rivers Res. Manag.* 17, 101–115. doi:10.1002/rrr.607
Standen, E.M., Hinch, S.G., Rand, P.S., 2004. Influence of river speed on path selection by migrating adult sockeye salmon (Oncorhynchus nerka). *Can. J. Fish. Aquat. Sci.* 61, 905–912.
Stuart, T.A., 1962. The leaping behavior of salmon and trout, *No. 28, Freshwater and salmon fisheries research. H.M. Stationery Off., Edinburgh.*
Tetzlaff, D., Gibbins, C., Bacon, P.J., Youngson, A.F., Soulsby, C., 2008. Influence of hydrological regimes on the pre-spawning entry of Atlantic salmon (Salmo salar L.) into an upland river. *River Res. Appl.* 24, 528–542. doi:10.1002/rra.1144
US Bureau of Fisheries, 1873. Report of the Commissioner - United States Commission of Fish and Fisheries. *Washington, DC: U.S. Government Printing Office.*
Von Bayer, H.C.E., 1908. Fishways. *United States Bureau of Fisheries, Washington, USA.*
Williams, J.G., Armstrong, G., Katopodis, C., Larinier, M., Travade, F., 2012. Thinking like a fish: A key ingredient for development of effective fish passage facilities at river obstructions. *River Res. Appl.* 28, 407–417. doi:10.1002/rra.1551
Wolfram, S., 2011. Wolfram Mathematica. *Wolfram Research Inc.*

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