Introductory Research Essay

# Atlantic salmon (Salmo salar) migration behavior and preferences in smolts, spawners and kelts

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## Background

Baltic populations of Atlantic salmon (*Salmo salar* L.) have gone through dramatic changes over the past few centuries. In the mid-18th century, salmon runs were so bountiful that "the roar of their ascent could be heard along the river banks as they crowded and splashed through the surface waters", and "fishermen lost their nets because there were so many fish caught that the fish carried the net with them", translated from Gisler (1751). There is no estimate available over how many salmon were migrating upstream Baltic rivers at that time, but the descriptions by Gisler are similar to descriptions of the Pacific salmon runs where estimations have been for example 20 million salmon entering Amur River and up to 16 million salmon entering Columbia River (Cederholm et al. 1999). Today, most of the major salmon rivers in the northern Baltic have less than five thousand salmon migrate upstream yearly in each river (ICES 2010). These changes are reflected in the catch statistics from River Tornionjoki (figure 1) and from total Baltic catch statistics (figure 2) and the number of returning spawners (figure 2).

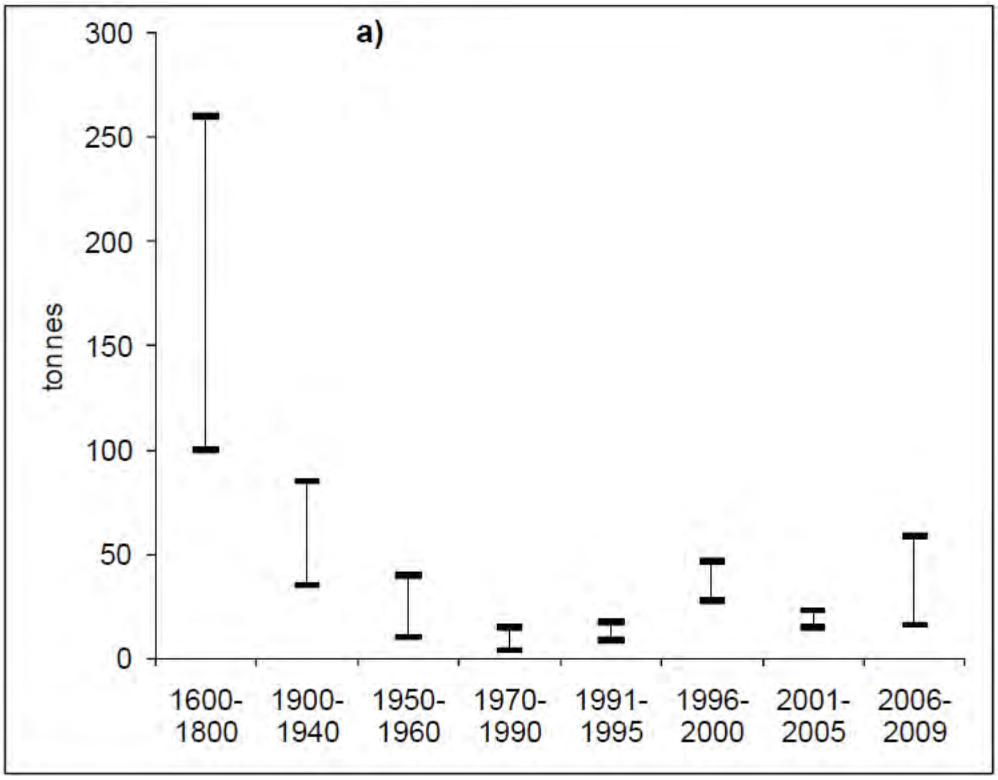

**Figure 1.** Total catches of Atlantic salmon in the River Tornionjoki from 1600 to present (range of annual catches), from ICES (2010).

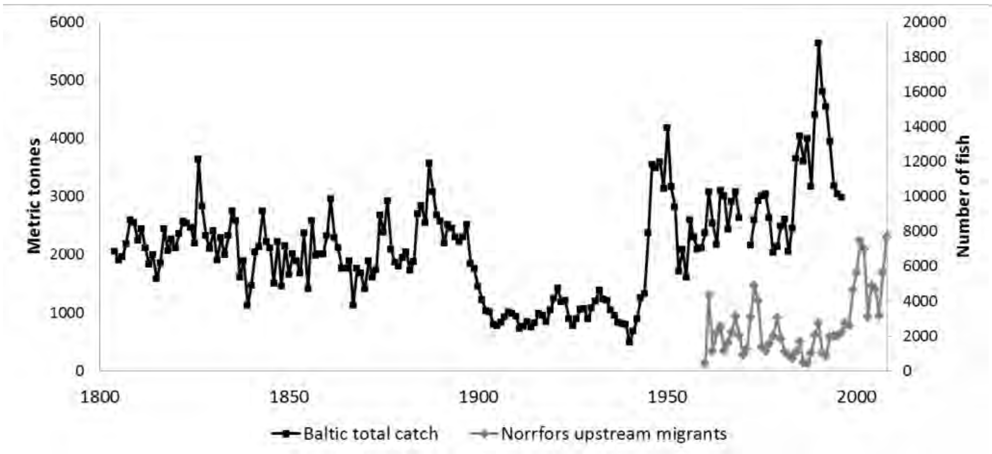

**Figure 2.** Total catch of salmon in the Baltic fisheries from 1800 to 2000 in metric tonnes (adopted from McKinnell 1998) and total number of returning spawners (wild + stocking) passing through the Norrfors fish ladder in River Umeälven from 1960 to present.

All anadromous salmonids have declined significantly in numbers during the past few centuries. For example, Cederholm et al. (1999) states that the Columbia River runs have declined from possibly 16 million fish down to about 2 million. Baltic salmon numbers are down to much lower levels than that. There are many factors that limit population size and regulate population dynamics. These factors will be covered in the following chapter. The two major impacts on anadromous salmon populations are when their migration route is cut off so that they cannot reach or leave their spawning area, and mortality rates by fisheries. My work will focus on migration aspects, which is covered with more detail in the third chapter.

# Salmon life history

## *The salmon life cycle*

According to Quinn (2005), there are about 160 species of fish that migrate between saltwater and freshwater habitats as part of their life cycle, a behavior termed diadromy. Some of these fish spawn at sea and migrate to freshwater for growth (for example *Anguilla sp.*), which is termed catadromy. Others spawn in freshwater and migrate to sea for growth, which is termed anadromy. Atlantic salmon is considered to be an anadromous fish, but there are also landlocked populations that spend their entire lives in freshwater. Semelparous species generally die after their first spawning, while iteroparous species (such as Atlantic salmon) may return to spawn several times over a lifetime. The age of anadromous spawners is generally counted by the number of years they have spent at sea (sea winters).

The life cycles and nomenclature of both Atlantic salmon and Pacific salmon have been outlined by for example Mills (1971) and Quinn (2005), which will be summarized in this paragraph (see also figure 3). Starting their lives as eggs embedded in gravel, the emerging alevins continue to hide in the gravel until their yolk sack is depleted. Atlantic salmon lay their eggs in October-November and hatch in February-March, depending on temperature. After the alevins have consumed the yolk sack, they are called fry. The fry disperse from the redd into suitable habitats where they feed on plankton. At the end of their first summer after hatching, the fry develop into a parr life stage. The parr are territorial and feed on drifting as well as benthic invertebrates. The parr smoltify, or some males become sexually mature, depending on food availability. When a parr reaches a length of > 10 cm at the end of a growth season, it will usually smoltify the next spring. Smoltification is metamorphosis during which the parr develop salt water tolerance and silvery scales which work better for predator avoidance in the sea. As the smolt leave the river mouth and enter the coastal area, they are referred to as post-smolts. They can spend a number of years feeding in the sea before returning as spawners. During their first year at sea, if they stay in the sea for feeding and growing they are called post-smolts, but if they return to the river for spawning already on the first autumn after smoltification they are called pre-grilse (SW 0; zero Sea Winters) or in the case of brown trout; finnock or whitling. Fish that return to the river after their first sea winter (SW 1; one Sea Winter) are called grilse. Older fish are referred to as MSW (Multi Sea Winter) spawners when they come back to their river of origin. After spawning, the surviving adults are referred to as kelts. Some kelts die because of old age (senescence) or weakness, but some may return to the sea and are once again labeled as MSW fish or return-spawners. The pacific salmonids, with the exception of Steelhead, are semelparous which means they usually die from senescence after their first spawning.

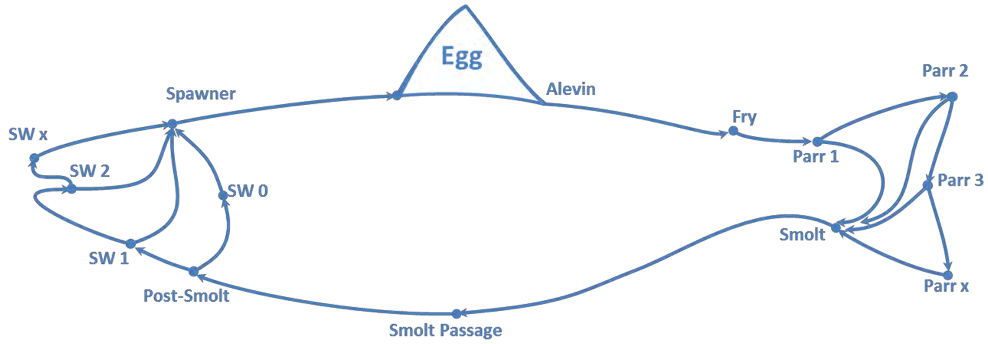

**Figure 3.** Generalized life-cycle model of anadromous salmonid fishes. SW = Sea Winters. Kelts and early mature parr are not included in the model.

## *Hatchery fish*

In the late 20th century, the Baltic salmon fishery was recovering, but the adult return spawners stayed at low numbers (figure 2). This recovery of the fisheries was probably due to extensive stocking programs (figure 4). Even though mortality rates of hatchery smolts is higher than for wild smolts (ICES 2010), the hatchery females have over 30 times higher smolt output than females spawning in the wild (Eriksson & Eriksson 1993). With a high return rate of hatchery smolts as spawners, the result may be a rapid decline of genetic variation in wild stocks, which can be a more serious threat to conservation than population decline (Hansen et al. 2009). However, some studies show very limited impact from supplemental stocking programs, probably due to a much higher mortality rate of hatchery fish in those specific rivers (Heggenes et al. 2002, Östergren 2006). It is important that breeding material is chosen from local and native wild fish so that at least some of the genetic variation is preserved (Vainikka et al. 2010). A similar problem, with equally serious effects, is the escapement of cultured fish into wild populations (Hindar et al. 1991), where some scenarios even predict the possible extinction of wild populations (McGinnity et al. 2003).

The stocking programs supply the coastal and offshore fishery with a large number of hatchery fish, which enables them to exert a higher pressure on the wild populations (Heggberget et al. 1993). At any life stage, subsequent to stocking efforts, the increased availability of prey can lead to an increased presence of predators, which may contribute to the adverse effects on wild populations (Armstrong et al. 2003). Thus, stocking may strengthen the density-dependence in wild populations since it increases density of fish (see figure 5 for a picture of some of the density dependent factors). Stocking accounted for over 90 % of the total smolt production in the Baltic for over a decade, at the end of the 20th century (Romakkaniemi et al. 2003). With commercial fisheries supported by the stocking effort, and indiscriminate yields from that mixed-stock fishery, the impact of human activities on the genetic composition of Baltic salmon may never be fully understood (McKinnell 1997).

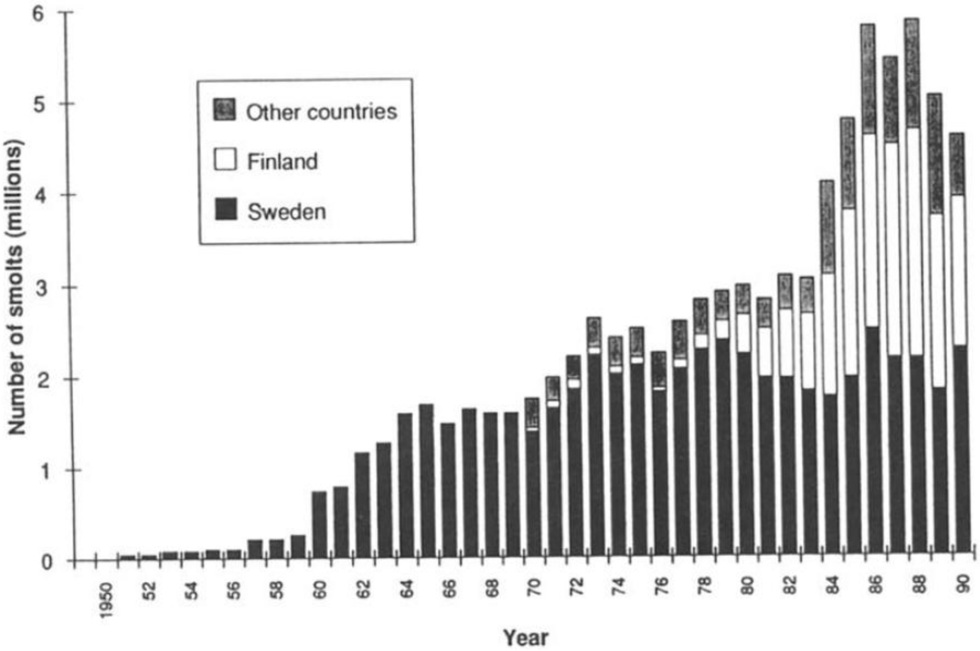

**Figure 4.** Number of hatchery smolts released in the Baltic from 1950 – 1990 (Eriksson & Eriksson 1993).

## *Spawners*

The bulk of the decrease in Baltic salmon populations seems to have occurred around the turn of the 20th century (figure 2). At this time, timber floating had a significant impact on spawning grounds in Swedish and Finnish rivers. Bulldozers were used to remove bottom substrate and turn rivers into smooth channels for timber transport (Törnlund & Östlund 2002). In addition, hydropower dams were constructed that cut off salmon from their spawning grounds and also destroyed a lot of spawning habitat. Loss of spawning substrate has a strong negative effect on salmonid recruitment (Palm et al. 2007) and cutting off access to spawning grounds with a dam or weir may completely wipe out entire populations.

Similar patterns have also been evident at other locations. For example, Galway weir on the River Corrib in Ireland had a fishway installed in 1853 to give salmon access to spawning grounds that had been cut off because of the weir. Eleven years later the Atlantic salmon catch in that river had risen from 1600 per year to 20500 per year, where a further 20000 salmon were estimated to have passed upstream through the ladder to reach spawning grounds (US Bureau of Fisheries 1873 p. 608). However, extensive arterial drainage works were undertaken on the Corrib System in the 1950’s, which destroyed a lot of the spawning substrate for salmon. At the same time, the fishway was reconstructed. Between 2007 and 2010 the number of adult salmon passing upstream through the fishway at Galway weir varied between 6000 and 10000 individuals according to data from a recently installed automatic fish counter (WRFB 2008, Hartigan 2011).

In a review on habitat requirements, Armstrong et al (2003) found that Atlantic salmon and brown trout occupy different niches in habitats. Atlantic salmon prefer to dig out redds at a depth of 17-76 cm, with a water velocity of

0.2-0.8 $ms^{-1}$. Preferred substrate grain size depends on female size (max 10 % of body length), but should generally be between 20-100 mm with a low (< 8) percentage of fine material. Brown trout generally prefer more shallow water with lower velocities and more fine grained bottom substrate. In other words, brown trout spawn in smaller streams than Atlantic salmon.

Poor spawning substrate, i.e. with a high proportion of fine material, may have a negative effect on embryo survival. This is mainly due to lack of oxygenation and poor removal of metabolic waste, since the fine materials limit water flow through the substrate (Armstrong et al. 2003). Other causes of embryo mortality may be flow changes, low temperatures or predation, leaving an average total survival from egg to alevin of around 30-40 % (Bardonnet & Baglinière 2000, Milner et al. 2003). Pollution and acidification can also cause high mortality events of more or less temporary nature in some streams (Hendry et al. 2003).

The effect of size on fecundity differs between male and female salmon. Fecundity has a strong positive correlation with female size (Milner et al. 2003). Larger females carry fewer eggs relative to the mass of the female, but produce larger eggs with more stored nutrition for the alevins which increases survival and carries over into subsequent life stages (Fleming 1996). However, large males will not necessarily have an advantage for egg fertilization; in fact early male maturation is a common feature of many salmonid populations, where parr fertilize a large portion of the eggs (Quinn 2005).

As long as the salmon are, with regard to physical obstacles, able to reach the stream where they once hatched there is a high probability that they will go there. Around 95-99 % of salmon that survive to adulthood will find their way to their natal river for spawning (Quinn 2005). Those fish which for some reason can't find or access their natal river will often enter another nearby river or tributary where they will spawn (Foerster 1929). Such strayers facilitate gene flow between populations and will strengthen biodiversity traits within the species (Hansen et al. 2009).

## *Egg – Alevin – Fry*

Skoglund et al. (2010) concluded that early hatching fry survive better than late hatchers. They say that the reason would be a strong density dependent regulation of juvenile salmon, so early hatched fry would be better able to defend their territory. However, natural hatching occurs later than what would be considered optimal for survival, which means that other factors are more important for evolutionary fitness than fry survivability. One explanation for the difference in emergence timing could be that late spawning females have a reduced risk of getting their nests destroyed by other spawners, and a delayed spawning generally means delayed hatching.

Palm et al. (2009) found that predation on salmon eggs and fry is mainly attributed to European sculpin (*Cottus gobio*) and juvenile salmon densities can be as much as 10 times lower where sculpin is present.

In the beginning of the 1990's up to 90 % mortality was observed in salmon fry in most Baltic rivers due to thiamine deficiency – a disease labeled M74 (Romakkaniemi et al. 2003). In 2010 the fry mortality caused by M74 was down to an average of 20 % (Börjeson 2011). Restrictions on both coastal and offshore fishery in the late 1990's enabled a net population increase of Baltic salmon despite the high mortality rates of fry due to M74 (Hansson et al. 2001, Romakkaniemi et al. 2003). The cause of M74 is still unknown. One hypothesis is concerning food web changes, where a combination of extensive fishery and a change of salinity and surface temperatures in the Baltic has altered the abundance of European sprat (*Sprattus sprattus*) and other species that form the diet of multi sea winter fish in the sea, as well as some species of plankton that may be important for post-smolts (Hansson et al. 2001, Vuori & Nikinmaa

2007). Another sign that the problem originates in the food chain is that several species of birds who feed in the Baltic Sea express a high rate of mortality caused by thiamine deficiency (Balk et al. 2009).

## *Parr*

Habitat availability is an important consideration in determining the carrying capacity of a stream for salmon parr. Armstrong et al. (2003) listed 31 different abiotic factors and 32 biotic factors that affect salmon parr site selection. Habitat limitations for growth and survival are density dependent, but may only be a population size bottleneck for part of the year. As long as water temperature permits (Breau et al. 2011), parr prefer to be stationary and as close as possible to rapid waters where food availability is high. In addition, during the cold seasons, parr prefer slower flowing water since their swimming ability is impaired by the low temperatures. Armstrong et al. (2003) thus concluded that the availability of winter habitat would be the most limiting factor in some streams, where parr unable to establish their own territory in the stream would probably die from fatigue in the rapid waters.

Increased heterogeneity of bottom substrate allows for higher density of fish, since dominant and territorial behavior is only displayed towards competitors that can be seen (Armstrong et al. 2003). Heterogeneity of streams also results in higher production of benthic invertebrates which will increase food availability for parr and increase growth and/or densities. Stream restorations in Ireland resulted in up to 6-fold increases of trout juveniles (Hendry et al. 2003). Headwater streams heavily influence food availability and habitat for both fry and parr, but headwater quality is constantly under pressure from forestry, road construction, etc (Freeman et al. 2007).

Parr are the prey of avian, terrestrial and aquatic predators, including cannibalism from older conspecifics (Milner et al. 2003).

## *Smolts*

Age at maturation and smoltification is considered to be related to growth (Metcalfe 1998, Larsen et al. 2006), which in turn is depending not only on food availability but also from how dominant the parr is, which can be evident as early as the fry stage (Metcalfe et al. 1992). Other factors that influence smoltification are photoperiod, temperature (Greenstreet 1992) and physiology (for example early maturation). Precocious male parr sacrifice body growth for gonadal growth, which means they are less likely to smoltify the next year (McCormick et al. 1998).

## *Post-smolts*

Baltic salmon post-smolts migrate from the estuary of their natal river to main feeding grounds in the south of the Baltic Sea (Alanärä 1988) while brown trout generally stay close to the coastal areas. Young post-smolts may feed on zooplankton, but juvenile herring and sprat are the most important food sources (Vuori & Nikinmaa 2007 with references).

Post-smolt survival in the coastal areas and Bothnian Bay was analyzed by ICES in 2008 against 100 different environmental variables. The factors with highest correlation to the post-smolt mortality were grey seal abundance, herring recruitment and trawling effort. It was unclear if the correlation to grey seal abundance is due to predation or other factors (ICES 2010). Food availability, from plankton or herring fry, is likely to be the most important factor for post-smolt survival. Food availability at sea is not considered to be a density-dependent factor, but rather depending on sea surface temperatures and densities of other species which influence the growth rates of prey (Kallio-Nyberg et al. 2006, Friedland et al. 2009).

## *Sub-adult*

Coastal fishery as well as offshore fishery exploits sub-adult salmon in the Baltic Sea. During 1995 – 2000 the offshore fishery was responsible for 66 % of the total salmon catch, with 26 % going to the coastal fishery and only 8 % in river fishery (Romakkaniemi et al. 2003).

There is no evidence for density-dependent growth in the Baltic sub-adult populations, even though Pacific salmon are subject to density-dependent growth (Hansen & Quinn 1998). Growth rate and age of maturation is influenced by food abundance, which in turn is influenced by sea surface temperature (MacKenzie et al. 2011 with references). However, fishery industries may be considered as density-dependent mortality, since the total allowable catch (TAC) is updated annually with aims to maximize a sustainable harvest level. In the case of Baltic salmon, the TAC is determined by politicians and set at a level where the fishery is actually regulating the population size. Predation on salmonids in the open ocean is mainly due to seal, whales and shark (Hansen & Quinn 1998). For Baltic salmon it would be exceedingly rare to be predated on by shark (Zidowitz et al. 2008). Porpoises are nearing extinction in the Baltic which means the main predation in the Baltic is due to seals.

## *Spawning migration*

Salmon are capable of accurately finding their way back to the stream which they left as smolt. The sea migration is most likely navigated through means of sensing the earth's magnetic field, but as the fish come close to the river mouth they instead go by olfactory cues (smell) (Nordeng 1971, Leggett 1977). If a smolt is transported to the sea in a tank, instead of following the river flow and imprinting on the scent of the water, it will not find its way back to spawn but it will move towards the general area of the river (Hansen & Quinn 1998). Some straying to other rivers occurs; usually between 1-5 % of spawners stray to other rivers, which enables gene flow which may strengthen salmon populations (Quinn 2005). The homing of salmon is so accurate that if stocking is used to strengthen local populations it is important to release fish in the exact site where they are expected to come back for spawning, not just do stocking in a random segment of the river (Gorsky et al. 2009).

Introducing a migration obstacle in a stream may wipe out an entire genetic strain, especially for Atlantic salmon and sea run brown trout. It can also pronounce genetic differentiation in resident brown trout populations. Restoring connectivity facilitates gene flow, which may be more important for conservation than increasing population numbers (Hansen et al. 2009; Östergren 2006). Some populations of Atlantic salmon have been extirpated from the US coastline, and 314 native stocks of Pacific salmon have been or are at the risk of extinction or extirpation – mainly due to dam construction without adequate fishways (Pringle et al. 2000). The Baltic salmon used to spawn in 60-70 rivers, but damming and pollution has reduced this to a total of about two dozen rivers where smolt production is only 20-25 % of the potential production (Karlsson & Karlström 1994).

When a population of anadromous fish is wiped out or significantly reduced, that also cuts of a path of nourishment that is brought back from the sea to the area around the river. In a study on 50 watersheds in British Columbia, Hocking & Reynolds (2011) showed a strong correlation between salmon abundance and plant diversity, plant productivity and nitrogen levels within 35 meters of each stream.

## *Summary*

Looking at the different factors influencing the Baltic salmon populations, a complicated picture emerges. The potentially most influential sources of mortality and fecundity are shown in figure 5, where density dependent (black, fig 5) factors are separated from density independent (white, fig 5) and factors which limit population size in each life stage (triangles, fig 5) are separated from factors which limit population growth rate (balloons, fig 5). The sum of all these factors (and especially bottlenecks) is important to consider in the management of salmonids, even if other factors not included in this simplified model may interact (i.e. precocious male parr). For instance, genotype will influence fitness and growth at several different life stages, which makes biodiversity an important density-independent variable to consider for long-term management (Youngson et al. 2003). There are also difficult challenges facing managers who want the full picture of population dynamics. For example, large fluctuations of flow may alter the amount of available habitat for riverine life stages, which makes the habitat factor difficult to assess in some streams (Heggenes et al. 1996, Jonsson & Jonsson 2009).

There are three major factors with potential of regulating the size of the salmon population (figure 5). First of all, access to riverine habitat, i.e. migration obstacles that can cut off a population from their spawning grounds (partially, i.e. only those who are able to jump 10 feet are able to continue past, or completely). Secondly, the size and quality of the riverine habitats, i.e. if substrate heterogeneity has been destroyed by log floating measures. And last but not least, the fisheries. Food availability is of course important too, but the food resources that can be altered from a management perspective are closely connected with size and structure of riverine habitats. Abiotic factors have a major influence on food availability, and these factors are often very difficult for managers to address. For modeling, the recursive effects add even more complexity. If more adult spawners return, there is a higher influx of nutrients (Hocking & Reynolds 2011), which increases food availability for parr, which decreases their territoriality, which increases available habitat, which if the larger amount of smolts is supported at sea would lead to more returning adult spawners, and so on.

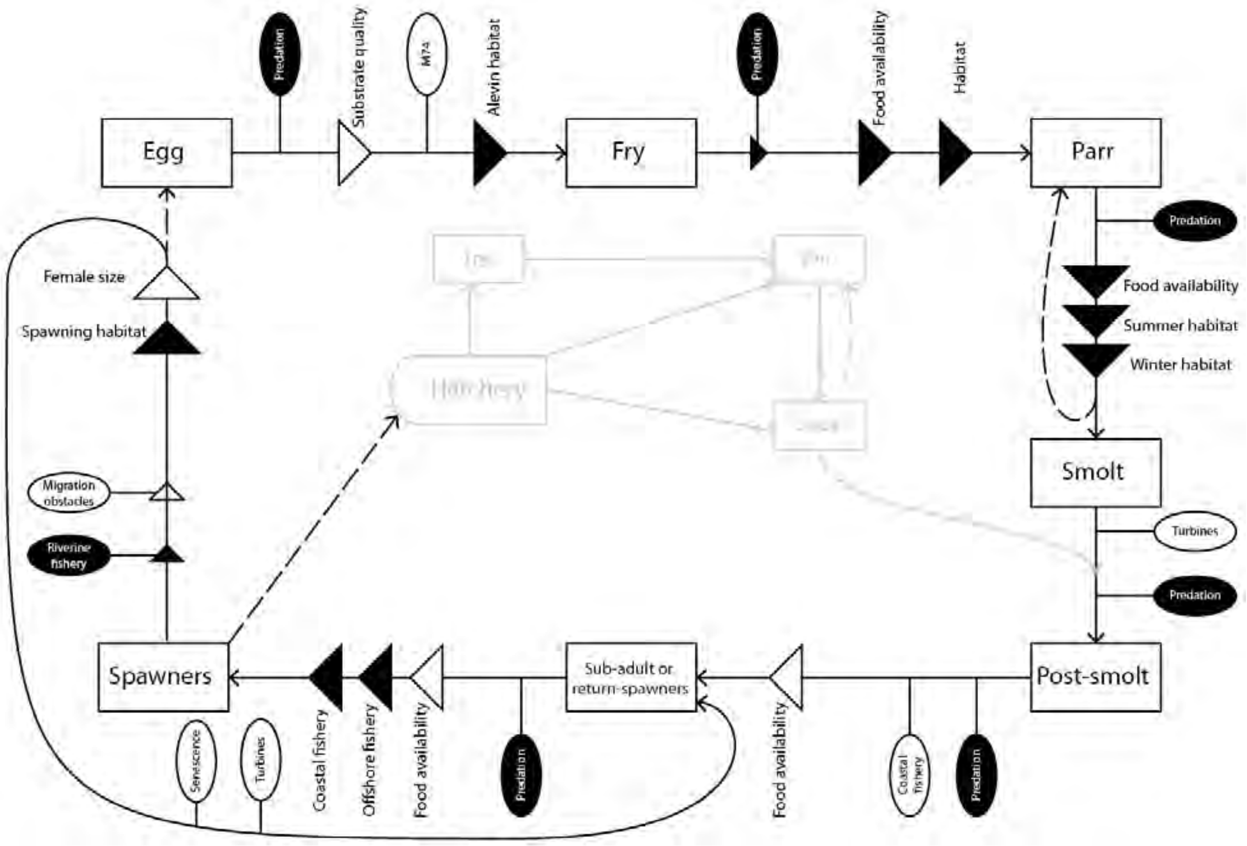

**Figure 5.** Simplified life history model for Baltic salmon. Density dependent (black background) and density independent (white background) factors influencing population growth rate (balloons) or population size (triangles). Some factors are most often only influencing growth rate, but can be a population size limit (i.e. partial or complete migration obstacle). Dashed lines represent special transitions (i.e. multi-year parr). The full impact of stocking is not represented in this figure.

# Salmonid migration

Since migration between spawning grounds and feeding grounds is important for the survival of anadromous fish like Atlantic salmon and sea run brown trout, migration will be the focus from now on in this paper. In the following sections, I will highlight fish behavior associated with migration, fish preference during migratory phases of the life cycle, and measures managers can incorporate to mitigate migration obstacles and ensure high passage efficiency both to and from spawning grounds.

## *Fish locomotion*

All animal locomotion is energy optimized from the relationship between body mass ($M_b$) and friction ($F$), where the most energy conserving speed is equal to an output of force of $F=2gM_b$, where $g$ is gravitational acceleration and $M_b$ is body mass (Bejan & Marden 2006). This means that when any animal is outputting a force using their muscles and we know the energy loss to friction (for fish friction equals drag, which is roughly equal to the density of the displaced body of water: $D_b$), we get the optimal speed for minimizing work per distance traveled ($V_{opt} = g^{1/2} * D_b^{-1/6} * M_b^{1/6}$). This is the same speed as that of a surface wave with the height $L_b$ and the length $2L_b$ (where $L_b$ = body length). Thus, the optimal speed in terms of energy conservation for fish is defined primarily by the physical characteristics of water and to a lesser degree by morphology. In contrast, maximum speed is defined by morphology – especially size and shape of fins which are the main propulsory organs.

Sfakiotakis et al. (1999) discuss the major contributors of fins to swimming ability. They find that the most important factor for speed is the span (height) and area of the caudal fin, curvature of the caudal fin leading edge, fin stiffness and oscillatory motions (which depend more on muscular function). According to Sfakiotakis et al., a fish that is morphologically adapted to high maximum swimming speeds will have a high caudal fin with small area and pronounced curvature of the leading edge while all the fins will have a high stiffness. By combining the works of Bejan & Marden (2006) and Sfakiotakis et al. (1999), it is inferred that fish like tuna are adapted for high maximum speed swimming, while salmonids are adapted for having a high optimal speed with minimal work.

Salmon are able to swim against the currents of streaming water with seemingly little effort, and they also have resting periods where they take refuge from fast flowing water by standing behind rocks and other extruding surfaces (see for example Gisler 1751, Mather 1887). In fact, the first countercurrent fishways were constructed to effortlessly transport both boats and fish upstream using vortices (Mather 1887). Fish use their lateral line to sense water movements that are favorable (Bobinger 1938, Faucher et al. 2010). But it was only recently that we developed the technology to show exactly how salmonids use vortex exploitation to decrease their cost of locomotion when swimming in schools (Weihs 1973) and solitary use of the Karman vortex street (series of vortices) formed behind objects (Liao et al. 2003). So while muscular capacity and morphology does play a role in deciding the maximum swimming capacity (or rather, force output) of fish, we must also take into account that the fish are able to exploit their surroundings in a way that enables them to traverse water with less effort. Karman gaiting behind stationary objects in a stream reduces drag and may even produce thrust (Mather 1887, Liao 2007), while school formations may increase fish endurance by two to six times (Weihs 1973). Salmon use both of these hydrodynamic phenomena when migrating upstream (see for example Gisler 1751).

The sensory system of fish can gather detailed information about depth, acceleration, turbulence, vorticity, turbidity, smell, earth magnetic fields and much more (see for example Moore et al. 1990, Walker et al. 1997, Montgomery et al. 2000, Quinn 2005, Liao 2006, Faucher et al. 2010). All of these senses form the basis of the decisions each fish will take when they migrate, and if we want to understand the principles of salmon path selection it is important to know the preferences of the fish in various environmental conditions.

Optimal temperature for swimming salmon is 16-17°C (Salinger & Anderson 2006). High water temperature (22+ °C) may result in difficulties for Atlantic salmon to pass rapid river sections, and they will seek out thermal refuges if possible (Holbrook et al. 2009). High water temperature (24+ °C) also means that parr will build up high levels of lactate in their muscles due to lack of oxygenation, which may even be fatal if the fish are not able to find a thermal refuge (Breau et al. 2011). This means that the thermal niche for Atlantic salmon may be moving northward due to global warming, which means some of the southernmost populations may become extinct (Jonsson & Jonsson 2009).

## *Preference of water properties*

Discharge is a migration cue that the salmon seem to follow; it has been shown both for Pacific (Osborne 1961) and Atlantic salmon (Karppinen et al. 2002, Thorstad et al. 2004a). In contrast, Thorstad & Heggberget (1998) found no clear relationship between discharge and migration activity. A response to discharge may cause problems at hydroelectric power plants if the bypass entrance isn't placed properly. In such cases the salmon will ignore (or are unable to find) the bypass since the discharge from the turbine tailrace is generally much greater (i.e. Leonardsson et al. 2005, Lundqvist et al. 2008). Keefer et al. (2006) found that the salmon are following the strongest discharge and olfactory cues of their natal river or tributary and staying close to that shore where they can sense these cues.

Previous studies on energy use of migrating spawners (i.e. Osborne 1961, Hinch and Rand 1998, Standen et al. 2004), show that salmon are not swimming according to the theoretical optimum for energy conservation or energy accumulation. The fish choose to swim in higher velocity water at higher speeds than what would be optimal in terms of energy expenditure. For fishway designers it is known that there is a critical velocity requirement for the fish; if the velocity drops beyond a certain point the fish will exit from a fishway instead of being attracted to continue upstream (i.e. Castro-Santos & Haro 2009). Prince (1902) states that *"salmon and trout naturally make for swift water"*. Other species of fish have other hydrodynamical preferences. For example, McLeod and Nemenyi (1941) compared various fishway designs and found that weak swimmers prefer countercurrent fishways where they are helped upstream by vortices while strong swimmers, such as Atlantic salmon, prefer pool and weir fishways where they can burst swim through an orifice or overfall.

The most common study of fish preferences may be the evaluation of fishway functionality. Unfortunately, in the cases where the fishway isn't functioning, this may often be studies of what the fish don't prefer. Roscoe and Hinch (2010) concluded in their review of fish passage efficiency that it is very difficult to compare results from different facilities due to the diversity of facility designs and other site-specific environmental factors. Once we have a better understanding of how fish experience their environment and what environmental factors they prefer, we may also be better able to compare studies between various facilities. Castro-Santos and Haro (2009) conclude that most modern fishway designs are based on studies of swimming performance, but even if the fish should be able to ascend the fishways they often choose not to ascend.

Looking at fish preference rather than ability is therefore needed to optimize passage efficiency. This becomes clear in a historical review of fishway development (see Appendix A for a more detailed description on the history of fishway development). Technical designs of the first fishways from the 19th century were based only on ocular observation of fish behavior, in the natural environment of rivers. These first technical fishways incorporated all four of the basic success factors for fishway design as outlined by Roscoe & Hinch (2010) and saw many thousand fish migrate through each year (Francis 1870). These four key issues for fishway efficiency depends on 1) guidance to the fishway entrance, 2) entry into the fishway, 3) passage through the fishway and 4) post-passage effects (Roscoe & Hinch 2010). Fishway design in the 20th century, on the other hand, was centered on studying abilities of fish, such as maximum sustainable swimming speed.

## *Migratory behavior – upstream spawning migration*

Most of the Baltic sub-adult salmon start their spawning migration in the southern parts of the Baltic sea where the main feeding grounds are located. Age of first sexual maturation is influenced by growth rate at sea, where a higher growth rate means earlier return to spawn (Jonsson & Jonsson 2007). Fish reach river estuaries early summer (May-June). At this time the morphological transformation for a fresh water existence is already developed and preparation for gonadal maturation starts. Most of the natural challenges for migrants start at the estuary. For example, predation by seals is more common as the fish get closer to the coast, and as they migrate in the rivers they may encounter more or less difficult passages.

Higher difficulty of upstream passage due to rapids means that the mean age of first spawners increases, because larger fish are more able to transcend passages with fast flowing water. However, commercial fishing generally target large and fast growing fish, which means they also decrease mean age and number of MSW spawners (Schaffer & Elson 1975), in effect decreasing or removing potential spawners for watersheds with a high passage difficulty. Because of the high cost associated with ascending a difficult river, Atlantic salmon from such rivers also wait a longer time before they are ready to repeat spawning (Schaffer & Elson 1975). In contrast, arrival date within season may not necessarily depend on size and energetics.

## Does energetics determine onset of spawning migration?

Spawning occurs during a limited time frame, in October-November, which means the fish are responding to environmental cues to determine onset of migration so they will reach the spawning area in time. Arrival at spawning grounds is determined by time of departure, distance travelled and swimming speed. It is generally assumed that migrating fish will optimize their energy budget when swimming, which can be modeled by 1) minimizing energy expenditure during the migration, 2) minimizing work per distance travelled or 3) maximizing energy gain before departure. In this section I review the literature on energy expenditure by fish to check if there is evidence in support of the three hypotheses on optimal swimming speed. I also construct three simple swimming cost models to compare the three hypotheses. In the river, hydraulic conditions differ from that in the sea or lakes since there are velocity gradients and vorticity gradients. Thus optimal swimming speed and swim path in running water should differ compared to still waters (Liao et al. 2003, Standen et al. 2004). Since there are no explicit optimality hypotheses on swimming speed and path selection in turbulent water, I focus on the hypotheses related to swimming in non-turbulent water.

One model of optimal swim speed is to minimize total energy cost during movements from one place to another (see for example Jonsson et al. 1997, Smith et al. 2009). A second definition of optimal swim speed will minimize work in relation to distance travelled over ground (see for example Osborne 1961, Hinch & Rand 2000, Standen et al. 2004). This type of optimal swim speed differs from the first by disregarding resting periods where the fish aren't actually moving but still consuming energy. The energy that remains when the fish reach their spawning grounds can within certain limits be spent on gonadal production, defending a spawning territory or improving chances of survival after spawning which will enable the fish to return as respawners (Jonsson et al. 1997). Therefore, an alternative third hypothesis would be that there is a fitness trade-off between maximizing total energy intake and minimizing total migration cost, resulting in a longer stay at a feeding area to maximize energy gain and then swimming faster than minimum work in relation to distance travelled because that combination yields a higher total energy remaining at the spawning site.

Jonsson et al. (1997) show a model of energy expenditure during migration for a Norwegian population of Atlantic salmon, which is related to length. Fish length increases during feeding, which means that this model can be used together with growth rates to predict an energetically optimal onset of migration. Growth rate in the sea is similar for Baltic salmon (Larsson 1984) and Atlantic salmon from Norwegian populations (Gunnes & Gjedrem 1978). When this growth data is fit to a polynomial linear model of the second degree, the growth rate of both subspecies will roughly equate to $Wt = \alpha-0.00043x+0.000007x^2$, where $\alpha$ is weight in kg on day one in the sea and x is total number of days of growth and Wt is total weight. This means that a post-smolt that weighs 0.1 kg upon entering the sea will weigh about 1.2 kg after one year (grilse) and about 4.1 kg after two years in the sea (2SW).

According to Jonsson et al. (1997), energy content (E; kJ) in each individual fish is relative to bodylength (L; cm) before spawning; $E = 1085.72e^{0.044L}$ and after spawning four months later; $E = 671.826e^{0.035L}$ (adapted from Jonsson et al. 1997). This means that a 4 kg salmon will lose 21000 kJ from migration and spawning combined (figure 5). As long as the fish stay in the sea and feed they will continue to grow. At the onset of return migration they stop feeding and will hence have attained their maximum energy content, which correlates with length. In contrast to small fish, larger fish have more energy to spend on eggs, as well as on swimming because of their greater mass, despite that they also spend more energy in total.

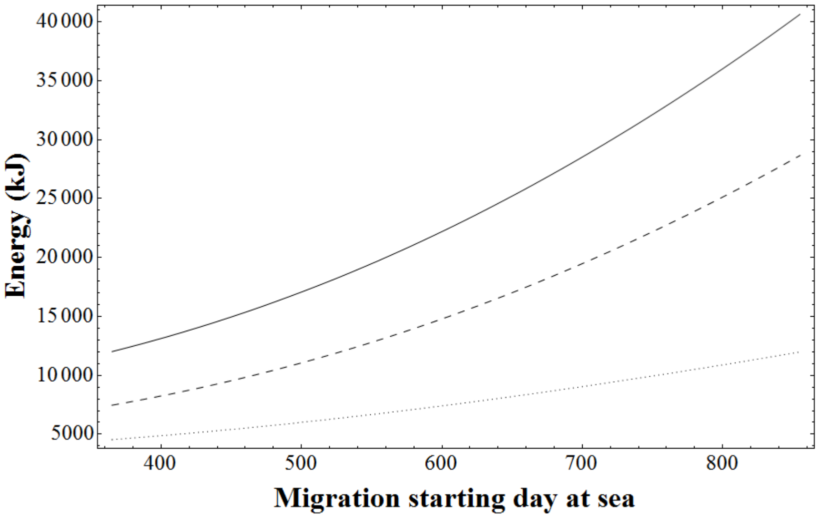

**Figure 5.** Energy content of fish before migration start (solid line) and after spawning (dashed line) according to Jonsson et al. (1997). Energy consumed by migration and spawning (the difference between the two top lines) is shown by the dotted line.

The energetically optimal swimming speed increases with body mass (Bejan & Marden 2006), which correlates with length (unpublished data from Norrfors fishway, River Umeälven, Sweden was used in these calculations). If we use the available energy from figure 5 in combination with optimal swimming speed from Bejan & Marden (2006) and then assume a migration distance of 2000 km and a constant swimming speed 24 hours per day, the grilse and the 2SW salmon would start their journey from the sea at 21 and 18 days prior to spawning, respectively (figure 6). When Hinch and Rand (1998) were looking at sockeye migration they found that smaller fish swam faster than larger fish and spent more energy on migration, which therefore seems to disprove the first hypothesis that salmon optimize swimming speed on minimum energy expenditure.

If, according to hypothesis three, the optimum solution is to have as much energy as possible available for spawning, it is more beneficial for the fish to stay at sea and grow a few more days. Using an equation from Smith et al. (2009) we can get the energy expenditure from swimming at a certain speed. By combining available energy during growth (figure 5) minus the increased energy expenditure from the increased swimming speed needed to compensate for a longer stay at sea (combining figure 6 with the equation from Smith et al. 2009), we get the optimal energy accumulation (peaks in figure 7). Large fish accumulate energy faster and should optimally stay at sea longer. The most energy accumulating of all strategies would mean that grilse leave the sea 19 days prior to spawning and that 2SW fish stay at sea six days longer (again under the assumption of a 2000 km migration distance and 24 hour swimming). By extension, this should mean that larger and MSW salmon would be expected to return even closer to the spawning date.

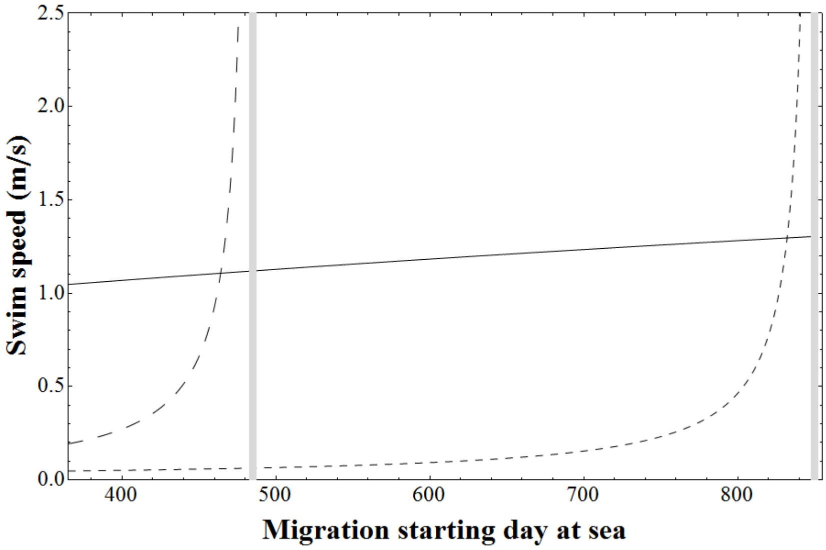

**Figure 6**. Number of days at sea (x-axis) will determine size, which in turn determines optimal swimming speed (solid line, adapted from Bejan & Marden 2006). We assume that the salmon have to be at the spawning grounds mid-October (gray vertical lines) and they have 2000 km to travel from feeding grounds in the sea. The dotted lines show necessary average speed to reach the spawning grounds in time depending on if they choose to migrate after their first or second year at sea. The point where the dotted lines meet the solid line is the optimal swimming speed to minimize energy expenditure (21 days prior to spawning for grilse and 18 days prior to spawning for 2-sea-winter fish).

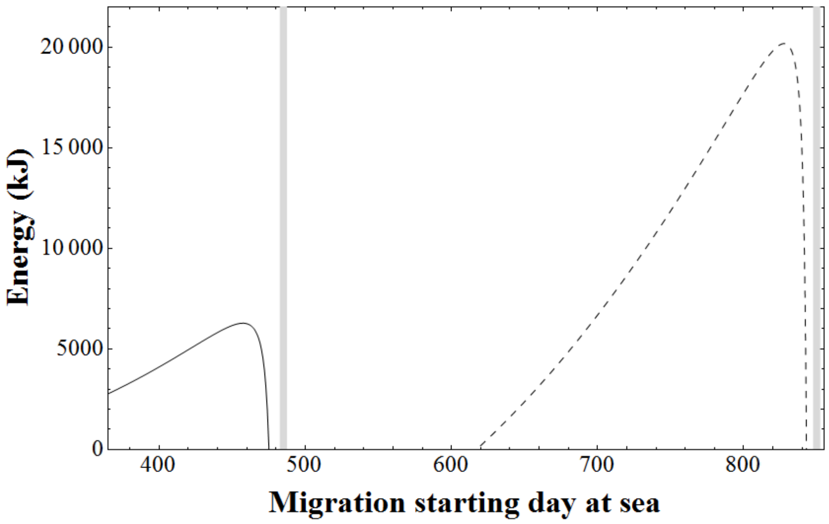

**Figure 7**. Available energy for spawning and migration (adapted from Jonsson et al. 1997 as shown in figure 5) minus energy needed to swim at the necessary speed to reach spawning area in time (dashed lines in figure 6 converted to kJ from Smith et al. 2009). Energy peaks at 19 days prior to spawning for grilse (solid black line) and 13 days prior to spawning for 2-sea-winter fish (dashed line), which equates to a swimming speed of 1.2 m/s and 1.8 m/s respectively (significantly higher than optimal swim speed from figure 6).

There are no data available to compare with the model predictions about the onset of return migration for Atlantic salmon. But since all three hypotheses show that it would be optimal for small fish to start migrating early and larger fish have a late onset of migration, this should be evident in arrival data. Data on arrival dates of different size classes are available from the Norrfors fishway in River Umeälven (unpublished data, figure 8). According to these observations, the largest and oldest fish seem to arrive first, then 2SW fish followed by grilse. However, this pattern is for the first arrivals. During the remainder of the season there is an overlap in arrival dates of all the size classes. Thus, there is only a minor fraction that displays behavior according to figure 5 and 6 with the theoretical optimum energy saving or energy accumulating strategies were grilse should arrive first and larger fish later. From this it seems like Baltic salmon are not optimizing swimming speed in relation to any of the optimality criteria defined above.

So what determines the start of the spawning migration for sub-adult or respawning salmon at sea? Dahl et al. (2004) showed that there is a strong correlation with sea surface temperatures (SST) and arrival of spawners in the River Dalälven. Gisler (1751) also reports a correlation between time of ice melting (presumably at sea) and arrival of spawners to river estuaries, so it seems that this link between temperature and behavior is consistent over time. The reason for this correlation may be related to spring floods in the rivers, where some migration obstacles are easier to pass if there is a higher total discharge. However, Lilja & Romakkaniemi (2003) has shown that the salmon will migrate up through their natal river as soon as they arrive; they will not wait for a high discharge event.

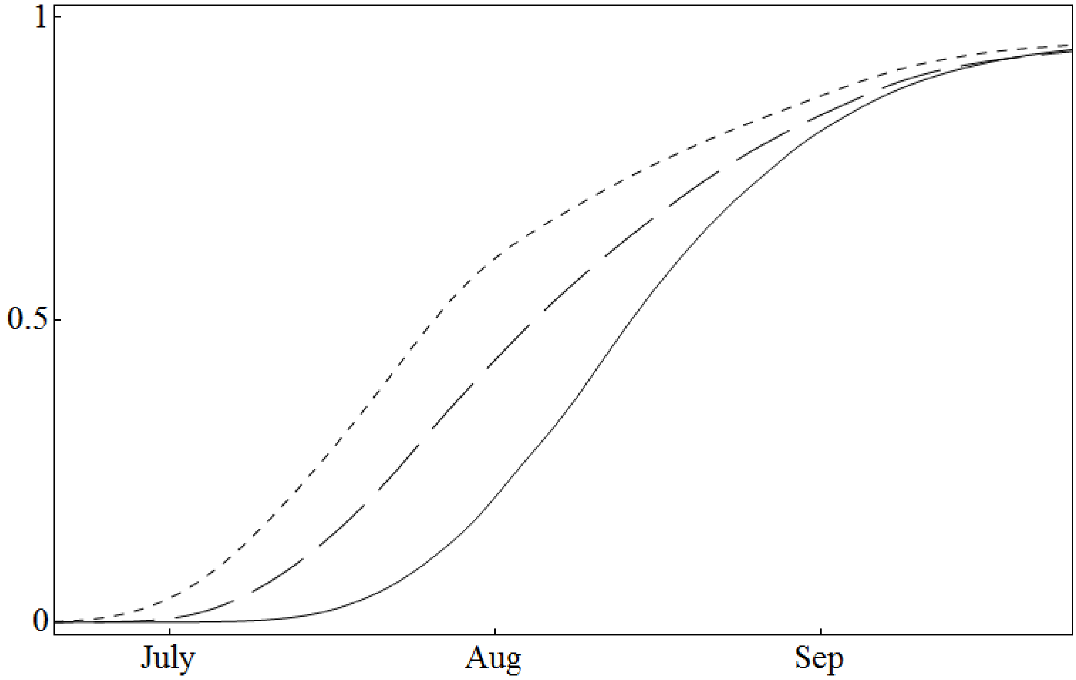

**Figure 8**. Cumulative distribution functions of three different size classes of salmon at the Norrfors fishway, River Umeälven (unpublished data pooled from 1974 to 2009 from totally 95000 fish). Weight classes (kg): 0-2.8 solid line, 2.8-7.3 long dashed line, 7.3+ short dashed line.

## What constitutes a migration obstacle for spawners?

Atlantic salmon have been observed to pass a 5 m high, almost vertical, waterfall at Carratunk Falls on the Kennebee River, Maine, USA. The fish would jump 3-4 meters high and then swim through the remaining part of the waterfall (US Bureau of Fisheries 1873 p. 593). Yet, Ovidio and Philippart (2002) describe a waterfall only 58 cm high in the River Meuse, Belgium as a migration obstacle where no brown trout or grayling were able to pass. The difference between these two sites is that at Carratunk Falls there is a pool below the waterfall that is "so deep it will swallow a whole tree trunk without it hitting bottom" (US Bureau of Fisheries 1873 p. 593), while the pool at the River Meuse obstacle has a maximum depth less than 20 cm. The pool below the migration obstacle can be used by the fish to gain enough speed to create high jumps. So the classification of a migration obstacle for upstream migrants is not just the height of the weir, but a combination of how much speed the fish can attain for a jump plus the height and slope of the waterfall.

## *Migratory behavior – downstream migration of kelts*

After spawning, the kelt may start migrating to the sea directly or stay and spend the winter in the river. Kelt survival varies between rivers, from 0.5 % to 80 %, but building pools for overwintering habitat can increase survival (Bardonnet & Baglinière 2000). In the river, kelts will usually migrate rather slowly downstream (10 km per day). They also tend to swim within 1 meter of the surface. Migration can be interrupted by short periods of residence or upstream swimming (Hubley et al. 2008).

When the kelts reach the estuary, they will stay for several weeks (presumably for feeding) after which they will swim actively towards the sea; even maintaining a net seaward movement against a flood tide (Hedger et al. 2009). At sea, the kelt mostly swim close to the surface at a mean movement rate of 15-30 km per day, unless they stay in the estuary to feed (Hubley et al. 2008, Halttunen et al. 2009), which is the same migration speed as post-smolt (Davidsen et al. 2009). At least for chum salmon, it seems that this movement of around 30 km per day is typical for the entire sea foraging life stage as well (Tanaka et al. 2005).

## *Migratory behavior – downstream migration of smolts*

Path selection of downstream migrating smolts seems to be active, swimming near the surface with a preference for deep waters in the middle of the stream (Svendsen et al. 2007). After the smolts have selected their position in the stream, the transportation downstream is almost passive (Rivinoja et al. 2004). Most of the time, smolts swim head first in the same direction as the main current (negative rheotaxis) towards the sea, but when they encounter a steep velocity gradient (accelerating flow), they change to positive rheotaxis and try to escape (Enders et al. 2009). If they cannot escape or if they after avoidance of the velocity gradient find that there is no other way to continue downstream, they switch back to negative rheotaxis (going head first downstream) and continue migration (Haro et al. 1998).

Preferred velocity for downstream migrating smolts is not uniform, but depends on total discharge. If the total discharge is high, smolts will seek out lower water velocities (Holm et al. 2001). In a Canadian study, it was shown that preferred water velocities was less than 0.5 m/s, and that the smolts were able to swim indefinitely at speeds up to 1.2 m/s (Peake & McKinley 1998) so it seems unlikely that the preference for slower velocities is a result of seeking refuge from water currents.

Water temperature is likely a trigger for smolt migration (Whalen et al. 1999), which means that global warming can have a detrimental effect on populations of Atlantic salmon. Since the temperature of rivers has steadily increased, the smolts migrate out to sea earlier in the season now than what they used to do (Kennedy & Crozier 2010). The earlier migration causes a problem if it isn't matched by an equally warmer sea surface temperature (SST) since SST determines food availability in the sea (Kallio-Nyberg et al. 2006).

## *Post-smolt and sub-adult migration at sea*

Baltic salmon post-smolts prefer to stay within areas where the sea surface temperature (SST) is between 9 and 11 degrees Celsius, which may influence their behavior and timing of emergence from the estuary (Holm et al. 2000, Jutila et al. 2009). Atlantic salmon post-smolts which are affected by tidal currents are more swiftly swept to sea than their Baltic counterparts (Thorstad et al. 2004b, Davidsen et al. 2008, 2009), but tidal currents account for less than one third of migration speed; the post-smolts are actively migrating out through the estuary (Martin et al. 2009). Alanärä (1988) showed that Baltic salmon post-smolt long term migration patterns are highly correlated to water currents in the Gulf of Bothnia. The same correlation with surface currents has been recorded in the Atlantic (Holm et al. 2000). So it seems that a large part of the sea migration of post-smolts is passive transportation through sea and/or tidal currents, but since the Baltic currents are weaker than those in the Atlantic, the behavior of Baltic salmon post-smolts may be slightly different from their Atlantic conspecifics.

If food abundance is high near the estuary, there is a higher probability that the post-smolts will stay closer to their natal river, but there is also a genetic effect on tendency to migrate longer distances (Kallio-Nyberg et al. 1999). From post-smolt (Alanärä 1988, Karlsson & Karlström 1994, Dadswell et al. 2010) to sub-adult (figure 9 & 9) it seems like Atlantic salmon are drifting with the surface currents. Since there is a circulatory current in the Baltic going south along the Swedish coast and north along the eastern coast (figure 10 left), this means that salmon of Swedish origin migrate south as sub-adults to the southern main basin, while salmon and trout of for example Polish origin migrate north as sub-adults towards the Bothnian Bay and Gulf of Finland areas (Bartel 2001, Bartel et al. 2010). If the fish were attracted to main densities of prey, it would be strange to see sub-adults migrating long distances like this to opposite ends of the Baltic Sea, but if the migration is mainly due to the circulatory sea surface currents the distribution seems reasonable. However, the sea surface currents in the Baltic Sea are mainly wind-driven, which make them variable over time (Jedrasik et al. 2008). Jedrasik et al (2008) modeled a 44 year hindcast of sea surface currents in the Baltic Sea and found that the average velocity has been steadily increasing. It is not clear how, or if, this change affects the Baltic salmon migration at sea. A connection between wind direction and salmon migration in the Baltic has been noted as far back as the 18th century (Gisler 1751).

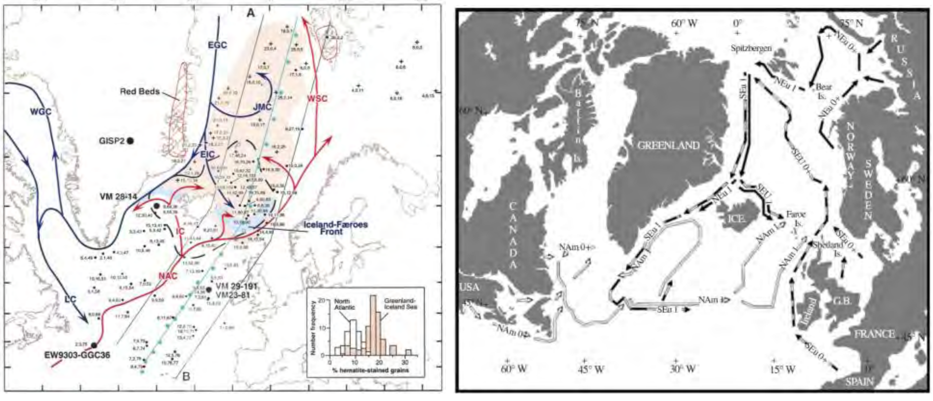

**Figure 9.** Surface currents in the North Atlantic to the left (Bond et al. 1997) and probable migratory routes of post-smolts and sub-adult Atlantic salmon to the right (Dadswell et al. 2010) which seem to have a rather high correspondence.

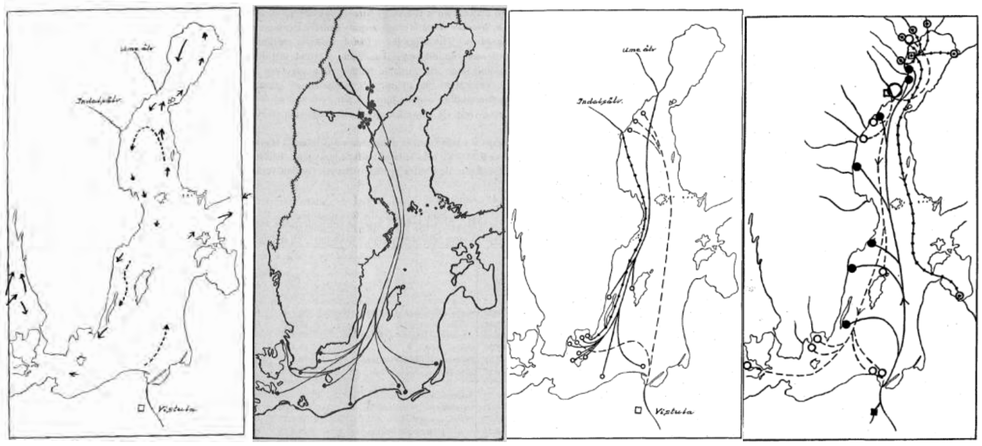

**Figure 10.** Average annual surface currents in the Baltic Sea (adapted from Lehmann and Hinrichsen 2000) to the left, and recaptures of tagged sub-adult Baltic salmon (middle left; Alm 1931, middle right; Alm 1938, right; Alm 1941).

When the sub-adults decide to head towards their river of origin for spawning, they most likely navigate through means of sensing the earth's magnetic field through magnetic particles in either their olfactory system (Walker et al. 1997) or in their lateral line (Moore et al. 1990), or a combination of both. As the fish come close to the river mouth they instead go by olfactory cues (smell). If a smolt is transported to the sea in a tank, unable to imprint on the scent of the water, it will not find its way back to spawn but it will migrate in the sea towards the general area of the river (Hansen & Quinn 1998). But even if the fish actively navigate towards their natal river, a passive transport with the ocean currents seems to be common (Tanaka et al. 2005, Dadswell et al. 2010).

## Discussion

To enable migration, equal regard needs to be taken to preference and ability of the fish. Modern migration studies have had a large focus on fish ability (see Appendix A). Only recently, scientists have started to focus their attention on the role of fish preference in behavior.

Studies on juvenile brown trout have shown that preference in the early life stages can be formed from both genetic effects and environmental effects (Adriaenssens 2010). There is a preference for migrating in groups (social behavior) that is not only due to energy gains from schooling (Weihs 1973) or predator avoidance (Humphries & Driver 1970) although those two factors are certainly also part of an explanation for fish behavior. For example, Olsén et al. (2004) show that smolts will group up more often with siblings they have never encountered before than with unrelated fish. When looking at fish behavior, it is important to choose the right tool to record this behavior. For example, with some technologies (for example sonar) we do not know if fish are related or if they belong to a stock with high juvenile densities, which may have contributed to a certain behavior as adults. Maybe this complicated web of cause/effect and the difficulties in determining the stem of a preference is the reason to why most modern studies of fishway design are based on fish ability rather than fish preference. But even if we recognize some difficulties in making conclusions about individual fish preference, we should be able to find behavioral patterns caused by general preferences. Such general preferences could be used in applications such as fishway design or stream restoration. The next step would then be to connect these behavioral patterns with factors such as genetic, social and environmental variables. Establishing the cause of preference could give us a better understanding of evolutionary successful strategies in fish.

Studies on upstream migration by spawners are most often focused on problematic areas, such as a migration obstacle. But to understand the best way of mitigating such problematic areas, we need to study migrational behavior in different types of habitat and get a full understanding of fish preference of hydrodynamics (Roscoe & Hinch 2010). To fully understand fish preference a very large facility would be required where PIV (particle image velocimetry) and similar technologies could be set up to describe every detail of hydrodynamics. To my knowledge, such a facility doesn't exist yet, and building one would take a long time. Therefore, it would be beneficial to set up study sites both in natural river sections as well as regulated parts where flow can be measured and/or controlled and then in technical constructions such as fishways to get comparative results of a population. By combining such study sites in areas with varying hydrodynamics and where it is possible to describe fish preference in relation to hydrodynamics, we could start putting together some pieces of the puzzle.

My studies will focus on two major areas within the River Umeälven in the North of Sweden. One study area is from the tailrace of a major power plant and the confluence area where the fish bypass channel joins the tailrace. In this area, flow is regulated and constantly varying, but it is a large body of water where sonar can be used to detect fish (split beam sonar) and measure hydrology (advanced Doppler current profiler). The other study area is a large fishway (300 meters long) at the end of the bypass just mentioned, where flow is constant but very turbulent with high vorticity. The small volume of water in the fishway allows for studies using video technology and short range detection of fish tagged with passive integrated transponders (PIT-tags). In addition to these sites where the fish can be studied in a semi-natural environment without being handled, we will also set up some experiments within the circular pools at the fish hatchery in Norrfors. These pools have a diameter of 11 meters and we plan to build walls and add other structures to manipulate the circular flow and create conditions that enable us to describe fish preference. The hatchery pools will only be used to study smolt behavior, because the pools are too small to do a study on adult spawners. With these three study sites, I hope to be able to cover a wide enough span of environments to see differences in fish preference during various conditions.

## *Future research*

In a recent literature review, Roscoe & Hinch (2010) concluded that European studies of passage efficiency neglect to look at hydraulic parameters and fish behavior that affect passage through fishways. They especially note that studies of biological aspects of passage are applicable to other passage facilities, which may be a greater scientific contribution than a report that is specific to one site. They further conclude that basic research on migration cues and swimming behavior in complex flows would be of great benefit for fishway science. Optimally, fish behavior based on preference should be studied in a natural environment with as little human influence as possible. However, to explain fish behavior in relation to flow, a detailed description of site hydraulics is necessary. To describe hydraulics, one can use instruments such as Particle Image Velocimetry (PIV), where a laser sheet is used to highlight one slice of water at a time and a high speed camera with computer software is used to analyze currents. PIV is laboratory equipment and will be difficult or impossible to set up in the field, so such a study could probably not be done in a natural environment. In the laboratory, a flume could be set up where juvenile fish can swim (as was done by Liao et al. 2003) and some hydrodynamics resembling a natural stream could be set up. To my knowledge there is no flume in Sweden which is big enough to house adult spawners in semi-natural conditions while at the same time being suitable to use PIV equipment. Another way to describe hydraulics is to use Advanced Doppler Current Profiler

(ADCP), which uses hydro acoustics to measure current speeds and directions. The ADCP is transported along a river transect from shore to shore and gives the current profile with total discharge and other hydraulic measurements. This means that we need a large body of water where we can do such measurements. There are also other types of ADCP equipment where measurement cell size is only a few centimeters, but they only measure a single cell at a time so using that to describe natural flow conditions will be complicated since total discharge may vary between measuring points. However, that type of ADCP would be suitable for fishway or flume measurements. One problem with hydro acoustic devices is that they are highly influenced by air bubbles. If there are too many bubbles in the water body, their function will diminish partly or completely. Bursting bubbles and surface splashing also creates noise that interferes with the ADCP sonars, which makes such equipment unusable in or near rapids. It is possible to design an experiment in a calm river section using the ADCP to describe flow and then track fish movements within the current profile, but it would be very difficult to do so in a rapid river section. Standen et al. (2004) used video cameras to follow debris in the river and thereby establishing currents where the recorded fish were swimming. Video analysis is an adequate tool where water visibility is high and if only the immediate area around the fish is of interest, but it would require a vast array of cameras and a massive amount of work to establish transects across a river, especially if there is high turbidity and low visibility. Computational Fluid Design (CFD) can be used to model theoretical averages of flow, but it will not give the exact cues that individual fish are responding to. In conclusion, finding a technology that describes hydrology where it is also possible to connect results with individual fish behavior is a challenging task. Therefore, new engineering research in this area would be beneficial, especially in rapid waters with high content of air bubbles.

Looking at studies of fish passage through fishways, there is a knowledge gap on long term effects of passage (Roscoe & Hinch 2010). Opening up passage past a migration barrier may be detrimental to some fish populations, due to increased predation, competition for habitat, etc (see figure 5). Roscoe & Hinch (2010) also mention that little is known about the long term effects on individual fish of passage through various fishways, such as fatigue and effect on reproduction efficiency, or in the case of downstream migrants fatigue and losses to predation.

All of the fishways that are mentioned in Appendix A (15 different designs) have had Atlantic salmon swim through them. There are also numerous slight modifications and variants of these designs where Atlantic salmon have been able to make their way through the fishway. But since Atlantic salmon are such agile swimmers, their ability to transcend various fishways is hardly surprising. To satisfy one aspect of preference, it seems that for Atlantic salmon it is important to have a good attraction flow so the fish are able to find the fishway entrance. But other species of fish are not as strong swimmers, even though they may still wish to migrate through the river. Therefore, new studies should determine if it is possible to design a fishway that is efficient in attracting Atlantic salmon to its entrance, while still accommodating the hydrodynamic preferences of weaker swimmers.

One area of research where a lot of knowledge gaps exist is about the marine life stage of salmonids. There are a few hypotheses out there about how the fish follow surface currents (for example Dadswell et al. 2010) and use their ability to sense earth magnetic fields to find their way back. But very few tagged salmon have ever been reported as caught in the sea with a reliable position, so it is difficult to confirm these hypotheses. Long range communication from telemetry tags is needed to study details of sea migration, but the salt water impedes any radio signals making this possible. A Japanese study using archival loggers on chum salmon only managed to retrieve data from one single fish (Tanaka et al. 2005). Recently, studies of stable isotopes hope to shed new light on the general areas which the fish feed in, and it looks like this data supports the hypothesis that the fish move with surface currents (K. Mackenzie, personal communication). On the US west coast a massive array of loggers has been set up to gather data from fish tagged with acoustic tags, which do work in saline waters but only within a range of a few hundred meters. European funding agencies have so far rejected applications to set up similar systems in the Baltic Sea, probably because of the high cost involved to get a high density grid with reliable data (S. Larsson, personal communication). Environmental conditions at sea that are influenced by global warming may change sea migrational behavior (Kallio-Nyberg et al. 2006). Therefore, sea migration during both the post-smolt and sub-adult life stages is in need of more research. Post-smolt survival has decreased significantly over the past few decades and the reason is still unclear (ICES 2010). We know very little about what is the deciding factor behind timing of smolt migration, although a lot of research has shown how light and temperature can be used in hatcheries to change smoltification timing. One hypothesis is that the smolt needs to reach the sea when there is plenty of prey of the right sizes, which means the smolt migration timing is probably correlated to herring and sprat hatching. If the timing of hatching for these species has changed (for example as a result of global warming and increased sea surface temperatures) while smolt migration timing remains the same, which could be part of the explanation for the lower post-smolt survival.

## *My own research*

In light of the aforementioned knowledge gaps and problems for migrating fish that needs to be solved, my studies will focus on the following areas:

- **Main hypothesis**: Migrating salmon spawners respond to environmental variables such as water velocity, discharge and light, which will affect their behavior in rivers.
  **Research hypothesis:** Telemetry data of fish movements in River Umeälven (spawning migration) will correlate to measured data on water velocity, discharge, time of day or weather data.
  **Method:** Existing data from previous surveys will be used with statistical software.
- **Main hypothesis**: Migrating salmon spawners have a preferred water velocity span, and will select their path upstream within this velocity span – regardless of discharge.
  **Research hypothesis:** Measured current profiles in a river section where there is a velocity gradient will show a correlation between average water velocity and fish positioning acquired with split beam sonar.
  **Method:** Water velocity for each fish will be estimated from current profiles measured at a few different discharges with interpolation to the discharge at the time of fish passage.

- **Main hypothesis:** Migrating salmon spawners use vortices to swim upstream, even in turbulent environments such as a fishway.
  **Research hypothesis:** The vortices in a fishway has a certain size range, thus fish of a certain size range who use vortices to swim upstream will be able to swim upstream faster and/or with less effort.
  **Method:** Salmon spawners will be tagged with Passive Integrated Transponders (PIT-tags) and released downstream of a type "Half Ice Harbor" fishway. An array of interrogation points within the fishway will be used to determine migration speed within the fishway. Tagged fish will be sexed and sized to determine if such factors are influencing migration speed. Current velocities and direction will be measured within the fishway. Using video cameras to monitor both tagged and untagged spawners we will try to identify key behaviors that can explain any differences in overall migration speed and/or effort (i.e. tail beat frequency).
- **Main hypothesis:** Downstream migrating salmon stay close to the surface and near the middle of the river, but they will not dive under obstacles.
  **Research hypothesis:** A surface guidance device with maximum depth 2 meters that extends to the middle of River Umeälven will guide a majority of downstream migrating salmon smolts and kelts into a fishway even though flow through the fishway is less than 8 % of total river discharge.
  **Method:** Fish will be tagged with Passive Integrated Transponder tags (PIT-tags) where they can be detected in the fishway to see how many were guided into that structure. Sonar will also be used to monitor the surroundings of the fish guidance device and try to detect fish that escape past the guide. In addition, ADCP transects will describe the hydraulics of the area.

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# Appendix A

## – History of fishway development

*Dan-Erik Lindberg*

Umeå 2011

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# Introduction

The term fishway is generally referring to a man-made structure facilitating upstream passage of fish. The word fishway is more commonly used in America, while the European common term is fish pass. This distinction may be because the first fish passes in Europe were merely gaps in dam dykes or weirs, which would enable both upstream and downstream passage for fish and were not technical constructions aimed at directing the water in a special way. Technical fishways were mostly developed in North America, where the main focus was to allow fish to pass problematic passages in order to reach spawning areas. From now on I will use the term fishway for all constructions aimed to ameliorate upstream passage of fish.

I have not been able to find any historical records that determine when the first fishway ever was constructed. The romans had the know-how to construct aqueducts to lead water to their cities over 2000 years ago, so it would be reasonable to assume that if they had a reason they should have been able to build fishways. Mills (1971) says that the first fishways were constructed in China in the 15th century, but he isn't giving a source for this claim so I consider it very uncertain. There are several sources claiming that the first fishways were constructed in France in the 16th century by putting bundles of branches in a channel to break current velocity, but no one is providing a source for this claim either so I consider that too very uncertain. Closely related to the fishway are the contraptions designed to catch fish in rivers, where the fish would be guided into closed or gated pools. Such contraptions have likely been around for centuries, but I have not been able to find a source that can be used to determine earliest use. Therefore, the origin of the fishway remains an open question. But there are quite a few patents and other documents describing new fishway designs that have been invented from the 19th century and onwards, so those will be the focus of this paper.

Downstream migrants have not received the same focus of engineering efforts. Newly developed physical screens as well as using light, sound or air bubbles have recently been used to direct fish into downstream passage routes with varying success. These designs are usually referred to as fish guidance devices, rather than using the term fishway or fish pass. But sometimes the fish guidance device is used to steer fish into a fishway. In other words, a structure that was originally intended for upstream passage is used to offer fish a less hazardous route downstream. The fish guidance device is needed to help the fish find their way into the safe path, especially in association with hydropower where the main river flow passes through turbines which may kill a significant amount of fish. The rest of this appendix will focus on the use of fishways for upstream passage.

# Purposes for building fishways

The first legislation for dam owners to allow fish to pass was a legal act passed in Scotland in the 12th century (Mills 1971). This act only prescribed for a gap to be open so that fish were able to pass, they didn't have anything resembling a technical fishway. The reason given to protect the fish migration path was that it was for the profit of the realm, in other words the fishery was an important economical resource.

The US state of Massachusetts passed a law in 1741 that required a fishway to be built through or around all dams on rivers used by migratory fish (Massachusetts 1874 pp. 1087-1088). The purpose of the law was to lessen the conflict between dam owners and the natives or settlers who had an economical interest in fishing. But there were conflicts with dam owners going on for over a hundred years after this law was established before some dams were opened for fish passage.

Among the first technical fishways to be installed were those of Galway, Ireland (1853) and Ballisodare, Ireland (1856). At Galway there was a weir which hindered upstream migration, and at Ballisodare there was a waterfall constituting an impassable migration obstacle (Francis 1870). The construction of these fishways was ordered because the fishery was economically important in the area. Both of these fishways were very successful and only a few years after the fishways were installed, thousands of fish passed upstream for spawning, while thousands more were caught by the fisheries. Interestingly, while there were at least 40'000 salmon passing the Galway weir fishway at the end of the 19th century, only 10'000 salmon passed upstream in the beginning of the 21st century. The reason for this substantial decline is probably that in the 1950's arterial drainage was conducted, to improve agricultural economy, which destroyed a lot of spawning grounds (WRFB 2008, Hartigan 2011).

Similar works as the arterial drainage were performed in other parts of the world. For example, during the period 1800-1950, a large portion of rivers in Sweden were prepared for timber floating, which meant vast areas of spawning grounds and juvenile habitats were lost or reduced in quality (Törnlund and Östlund 2002). Recently, a lot of effort has been put to restoring some parts of these rivers to their original state and building fishways to allow fish to reach their new and improved spawning grounds. This stems from an increased awareness of the importance of biological diversity and other values than economical being considered in politics (or biology receiving an economical value in Cost-Benefit analyses, for example Håkansson 2007).

# Types of fishways

*"The underlying principle in the construction of fishways is the retardation of the current velocity of a waterfall so as to enable fish to surmount it"* (von Bayer 1908).

There are two major types of fishways; the technical fishway, which is usually a concrete or wood structure meant to break water velocity over a very short distance, and the natural fishway, which is more or less a man-made river that is constructed to reduce water velocity by distributing the water fall over a longer distance and thus reducing inclination. A third, but so far minor, category includes the semi-natural fishways, which is a combination of technical constructions and a natural fishway.

## Technical fishways

There are five major types of technical fishways, which are sometimes combined within the same fishway (such as the Cail fishway in figure 10);

1) the most simple type where the water is only forced to travel a greater distance (figure 1).
2) the overfall fishway where the water velocity is retarded in pools separated by walls, where each wall has an overfall of water to the next pool (figures 2, 10 and 11).
3) the vertical slot fishway where the speed of a water jet is broken by hitting a wall or corner (figures 3-8).
4) the submerged orifice fishway where water passes through a small hole in a weir which limits total discharge through the fishway (figures 9-11).
5) the countercurrent fishway which is using the momentum of water currents to break water speed (figures 12-15).

Fish have been shown to migrate through all of these different types of fishways, as long as their point of entry is properly located and there is sufficient attraction flow (US Bureau of Fisheries 1873). However, some fish species prefer certain types of fishways when given a choice (McLeod and Nemenyi 1941, Roscoe and Hinch 2010).

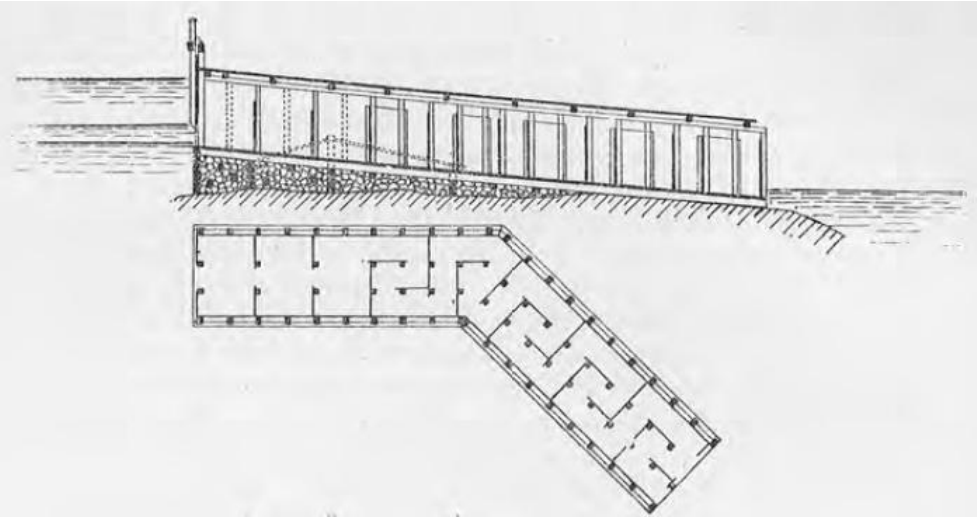

**Figure 1**. The first fishway in Sweden, constructed 1892 in the river Dalälven at Domnarvet ironworks, was a Brackett's type fishway, which essentially only aims to prolong the water route as far as possible over a short distance (Lundberg 1893).

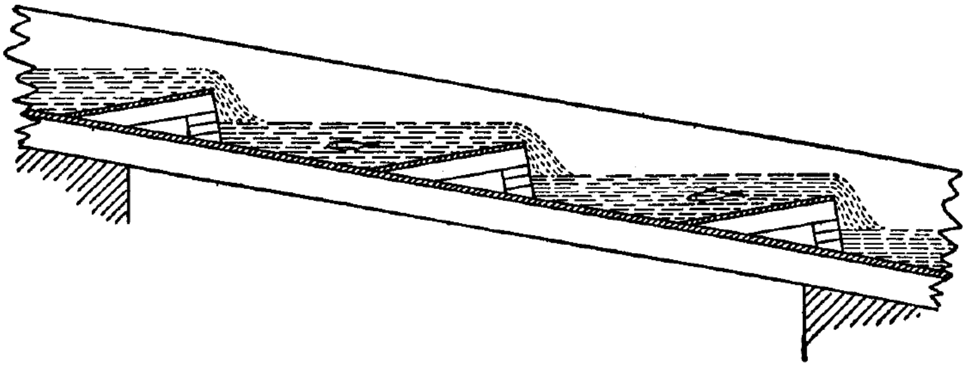

**Figure 2.** This simple fishway creates shallow pools by having inclined steps, just like a fish staircase (von Bayer 1908).

### *Vertical slot fishways*

The vertical slot fishway was invented by James Smith of Deanstone, Scotland, in 1827 (Landmark 1884, Lundberg 1893). A model of the Smith fishway is shown in figure 3.

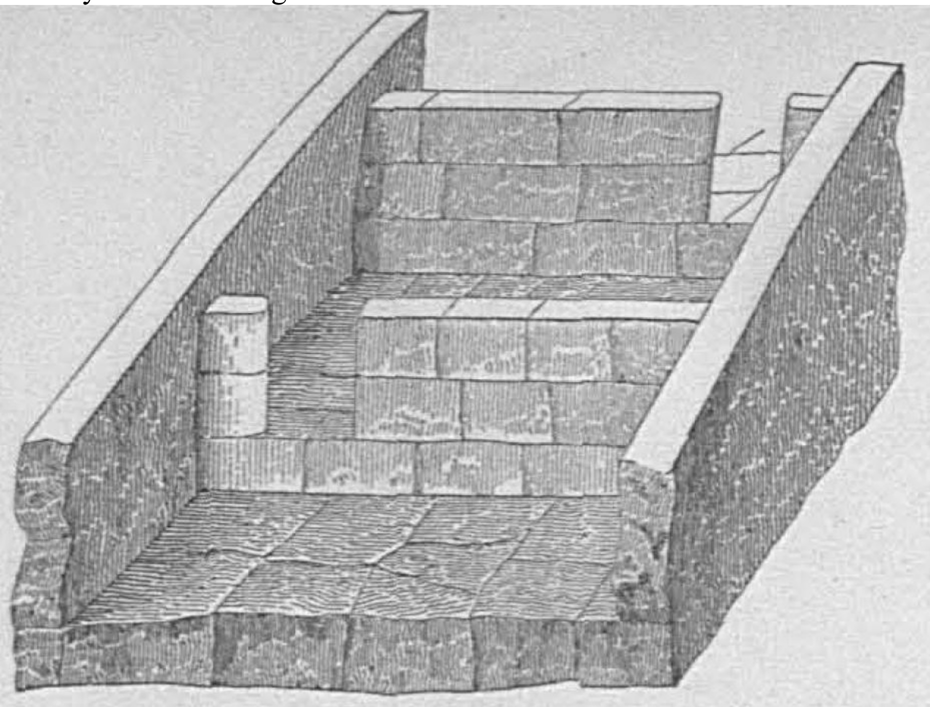

**Figure 3**. Smith's fishway, invented in 1827 but here shown as an improved model from 1840, was probably the first vertical slot fishway (US Bureau of Fisheries 1873).

The Ballisodare fishways in Ireland, constructed by Edward Cooper in 1856, was widely discussed during the 19th century. Ballisodare River had no salmon because of three natural waterfalls obstructing the way to spawning areas, but after constructing the vertical slot fishways past those obstacles and then stocking with Atlantic salmon, close to 10'000 fish were caught in one year with an average weight of 3 kg (Francis 1870). These fishways were the first really successful fishways, which put them in focus when mill owners tried to argue that there was no such thing as a functional fishway and that constructing fishways was a waste of money. The Ballisodare fishways had only about 40 cm deep pools and a slope of 1:13.

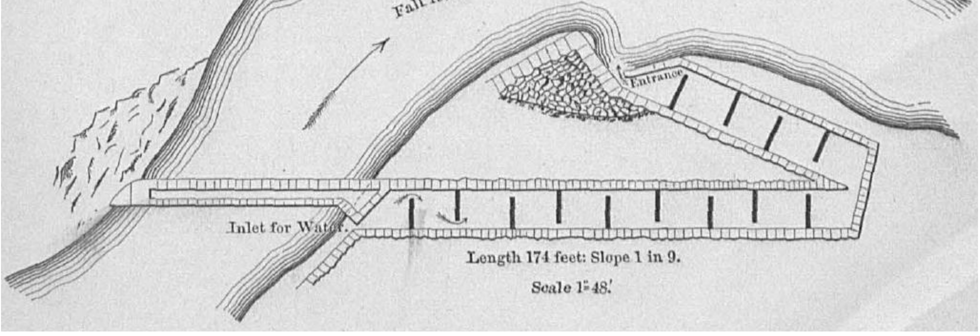

**Figure 4.** The Smith's fishway as implemented at Ballisodare, Ireland, in 1856 (US Bureau of Fisheries 1873).

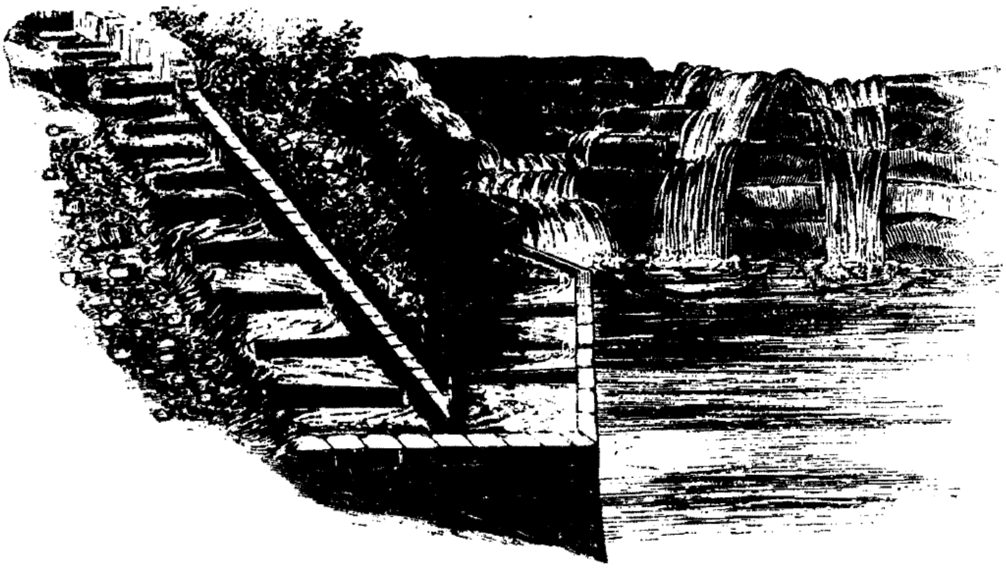

**Figure 5.** Perspective view of the Ballisodare fishway (Francis 1870).

Prince (1902) states that one of the most common fishways in North America at the turn of the 19th century was the Rogers fishway (figure 6). According to him, it required a lot of maintenance to keep it free of debris and to repair damage caused by ice, but it was functioning well when the entrance was placed very close to the main flow of the river. In Scandinavia, where ice and debris is common due to cold winters and large spring floods, the Landmark fishway was most common at this time (figure 7).

One of the most popular vertical slot designs used in 20th century fishways is the Hell's Gate fishway, which has dual vertical slots (figure 8). This fishway was designed to accommodate the massive spawning runs of sockeye salmon going up the Fraser River in British Columbia. For sites with smaller numbers of fish migrating through, it has also proven effective when cut in half to a single vertical slot fishway.

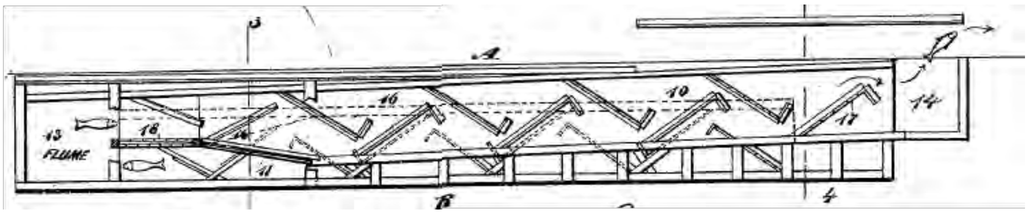

**Figure 6.** A commonly implemented design of a vertical slot fishway patented by William Rogers in 1892. He also claims to have an older patent for a similar fishway dated 1880 (Rogers 1892).

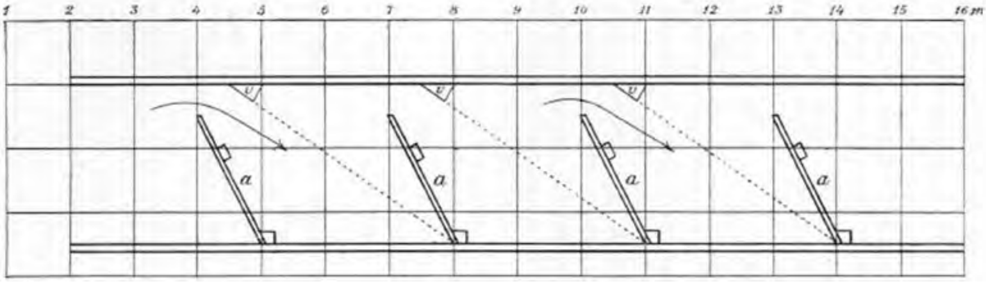

**Figure 7.** Landmark fishway, which was installed on several sites in Norway and Sweden around the turn of the 19th century. This simple modification of the vertical slot fishway dissipates more energy from the water (Landmark 1904). Each grid in the picture is 1 x 1 meters.

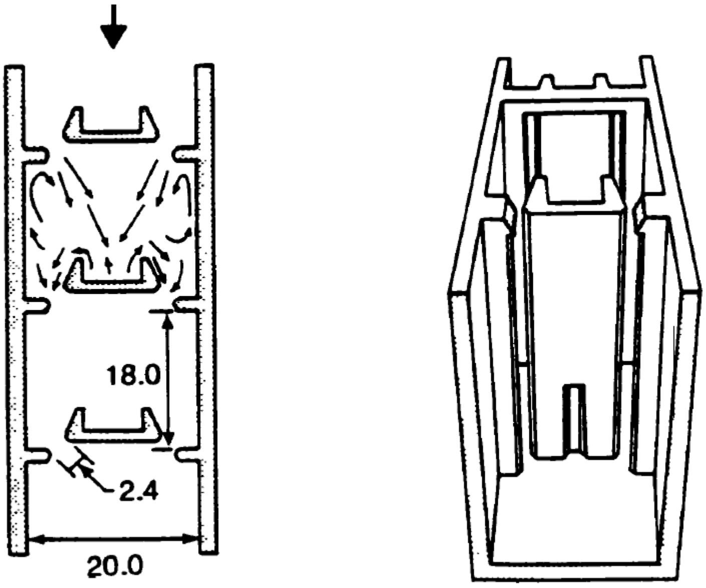

**Figure 8**. Hell’s Gate vertical slot fishway (Powers et al. 1985). Numbers indicate distance in feet.

### *Submerged orifice fishways*

One of the oldest public documents of a submerged orifice fishway is a patent owned by Alonzo Livermore (Livermore 1866), where he describes a tank or pipe of any dimension where the water velocity is reduced by installing weirs and where the orifices also have extruding walls for the same purpose (figure 9). Livermore claims that this will decrease total discharge by at least 40 % and that the water velocity in each pool will be only one quarter of that of the orifice jet (from his example; 1 foot per second from a 10 foot elevation over 164 feet length and a width of 4 feet). He also argued that each pool should be of equal size, so that flow characteristics are uniform throughout the fishway. Submerged orifice fishways which also has an overflow over the weirs is a common form of fishway in modern constructions at large dams. This was originally called a Cail’s fishway, after the Brittish inventor Richard Cail (US Bureau of Fisheries 1873 pp. 608-609). Modern fishways of this type are often slightly modified from the original design, and those changes are often site specific. Therefore, these fishways are now named after the site where they were developed, for example “Ice Harbor fishway” (figure 11).

Submerged orifice fishways are favored by dam owners, such as hydropower companies, because the water discharge is relatively low. The low discharge through the fishway means that more water is available for power production.

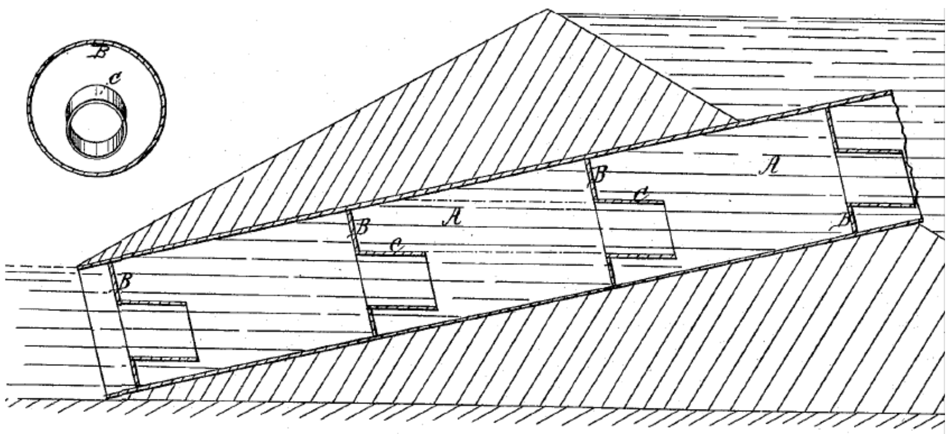

**Figure 9.** Submerged tubular pool and weir fishway, patented by Alonzo Livermore in 1866. The patent also states that the fishway can be constructed as a tank rather than a pipe (Livermore 1866).

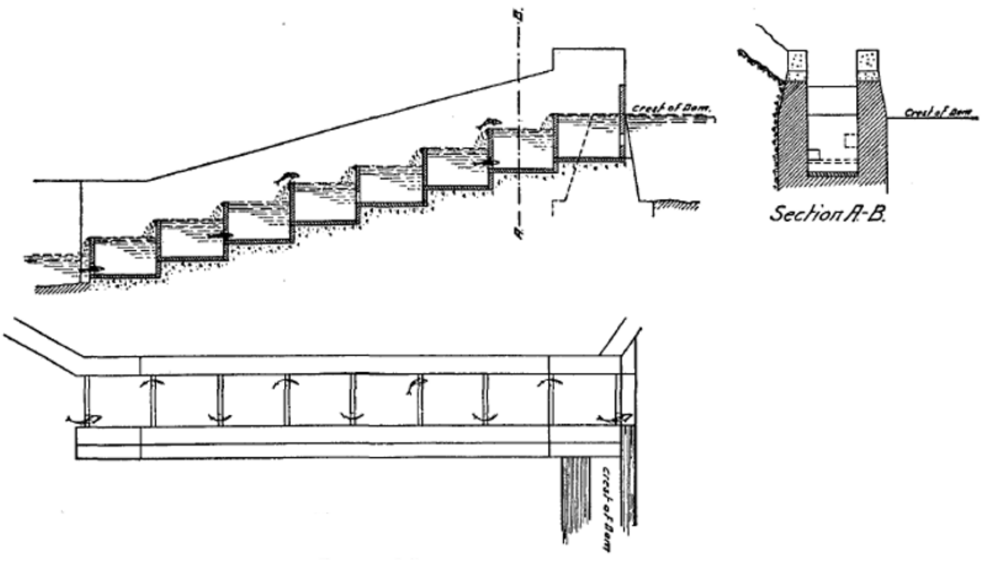

**Figure 10.** *Cail fishway* (von Bayer 1908).

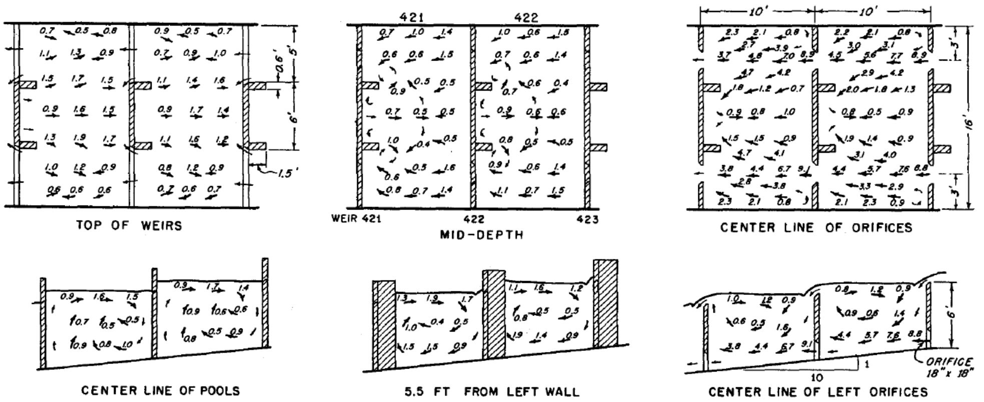

**Figure 11.** Top view and side view of the Ice Harbor fishway at three different intersections. Water is flowing both through submerged orifices and over part of the weir (Perkins 1974).

### *Countercurrent fishways*

Denil is commonly associated with fishways where the water velocity is reduced through the means of angular obtrusions which forces the water to change course, so more people may be familiar with the term "Denil fishway" than the term countercurrent. I am using the term "countercurrent" because it is the original term for these fishways and it also describes the function of the fishway. The actual energy dissipater of these fishways is not the baffles or extruding objects, but the momentum transfer from secondary currents (McLeod and Nemenyi 1941 p. 15). These countercurrents, or vortices, have a circular motion which means a fish (or other object) can position themselves in a street of water that is actually moving against the current. The theory of how objects cause vortex streets has been detailed by Rosenhead (1929) and observations on how fish use vortex streets to gain thrust has been published by Liao et al. (2003).

One such fishway was patented in the US in 1872 where only the bottom structure of the fishway has been modified to allow passage of both fish and boats (figure 12). The other part of what is now known as a Denil fishway was patented in the USA in 1879, where half the fishway had baffles fastened to the wall and sloping in the upstream direction, with the other half having baffles sloping in the downstream direction (figure 13). McDonald stated that this type of fishway is mostly suited for small streams (McDonald 1879), which has also been said about modern Denil fishways. The McDonald fishway was installed in both Columbia and in Scotland, but neither shad nor salmon would pass over these dams (Prince 1902 p. 6). Colonel James Worrall also installed a fishway with this concept in the Susquehanna River in 1873, a fishway of his own design and 40 feet wide where boats easily passed through, proving that it is possible to use these principles in larger rivers as well (US Bureau of Fisheries 1873).

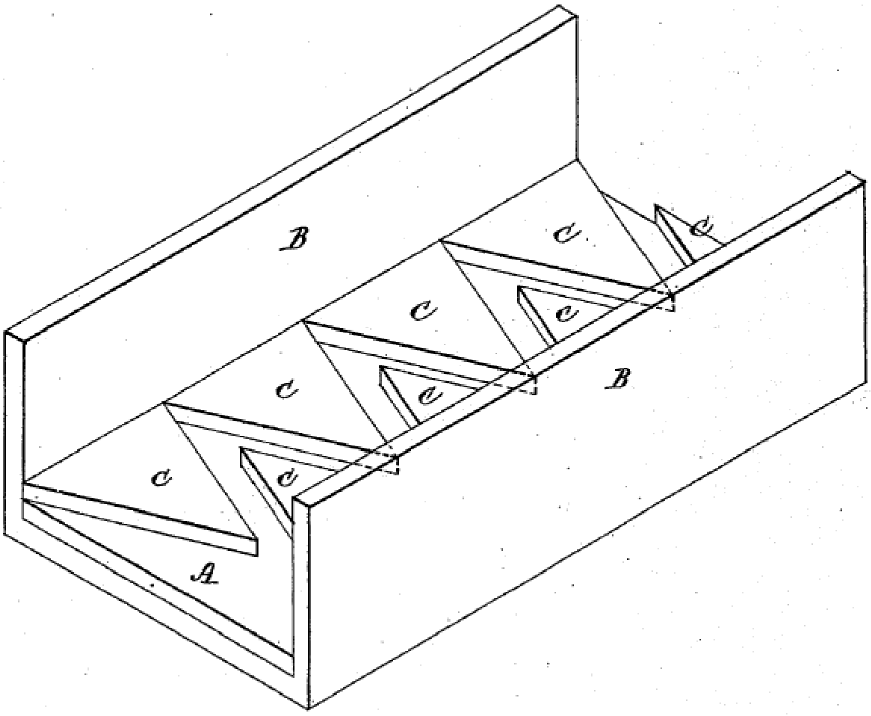

**Figure 12.** *Countercurrent fishway as described by James Brewer in his patent from 1872. The bottom of the fishway is cut (or extruding triangles added) to form a zigzag channel which forces the water up against the channel walls* (Brewer 1872).

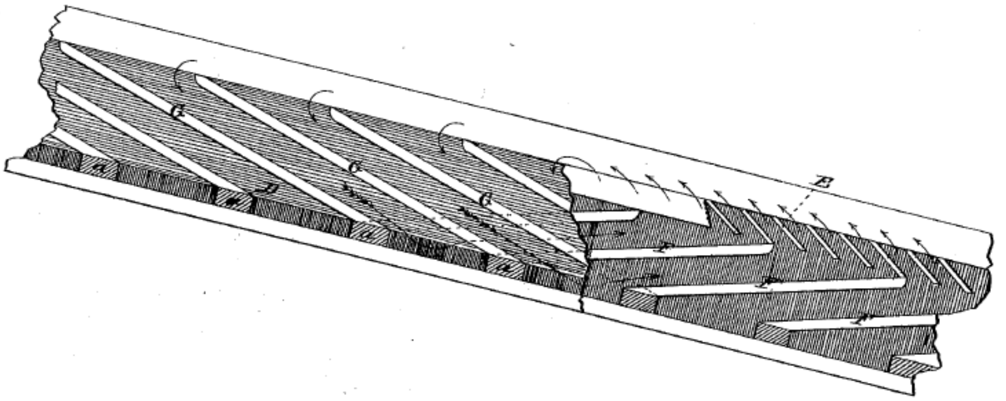

**Figure 13.** Marshall McDonald’s fishway where half the width had baffles sloping upstream and the other half sloping downstream with additional smaller baffles on top to reduce water velocity (McDonald 1879).

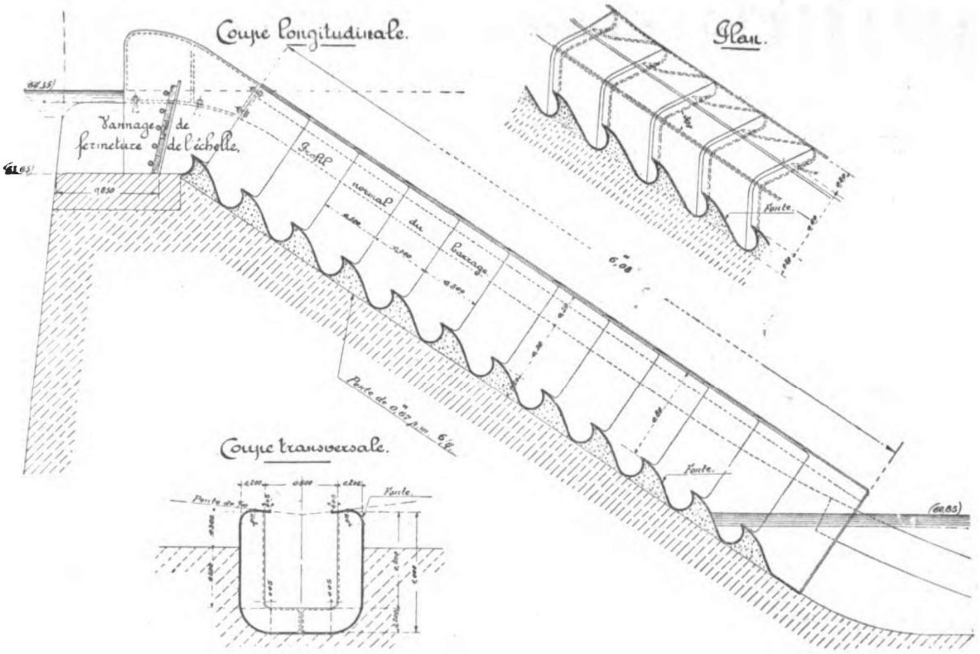

**Figure 14.** An early design of the Denil counter current fishway (Denil 1909).

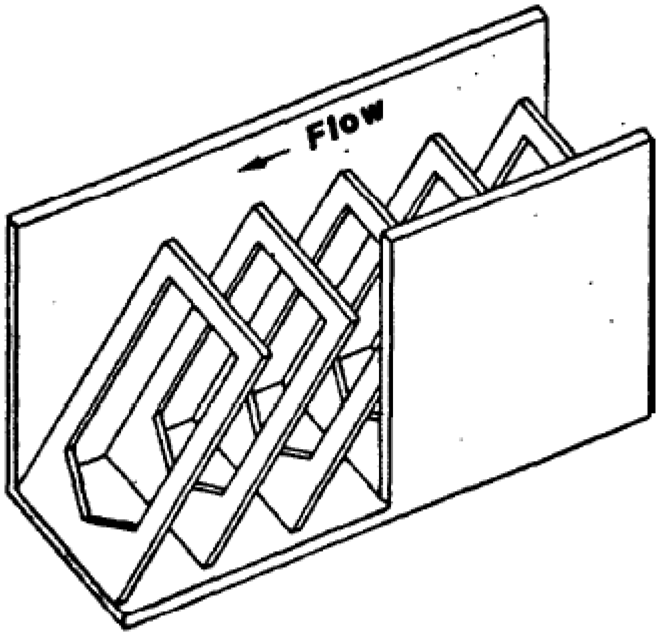

**Figure 15**. A modern version of the Denil fishway (Aaserude and Orsborn 1985).

## Semi-natural fishways

Many of the first fishways in Norway were semi-natural fishways, where no technical structures were put in the fishway, like the one in figure 16 (Landmark 1904). Instead, a series of resting pools were blasted out of the rock face, and then joined through narrow canals of about 3 meters length.

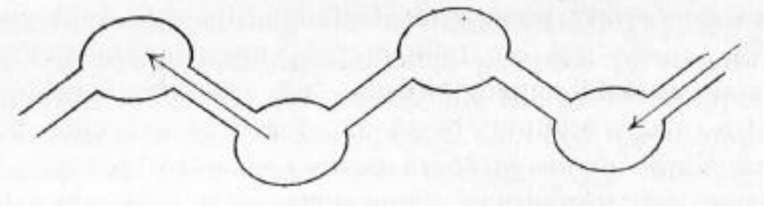

**Figure 16.** Semi-natural fishway, where circular pools with adjoining channels have been blasted out of a rock face (Landmark 1904).

### Natural fishways

One of the first records of a natural fishway being built is that of Damariscotta Falls, Maine, USA. This waterfall is about 15 meters high and a natural obstacle too great for any fish to pass. In 1806 a trench was dug out next to the fall, consisting of 20-30 pools where the fish could rest, and alewives from the neighboring Pemaquid River soon populated their new spawning grounds. In 1870 over a million alewives were caught in the Damariscotta River, and that was still said to be a considerable decline from previous years (US Bureau of Fisheries 1873 p. 605).

The Conference of Dominion Fishery Inspectors of Canada concluded in 1891 that "wherever a natural pass in a river can be maintained, either by building a wing dam or by making a channel, such is to be preferred to any artificial pass" (Prince 1902). However, they are making this statement because of the utter failure of numerous efforts at creating a technical fishway, not because their research has shown the natural fishway to provide ultimate hydrological conditions for fish (Prince 1902).

## Evaluation of fishways

One common way of determining whether or not a fishway should be constructed is cost-benefit analysis (i.e. Håkansson et al. 2004). This means that fishways are generally constructed for economically important fish, such as salmonids or eels, where it can be shown that society has an economical benefit from the fishway. To determine if there is a need for a fishway, government agencies usually consult experts in the field or follow general guidelines. One example of such general guidelines is the "Environment Agency Fish Pass Manual" published by the British Environment Agency (Armstrong et al. 2010). This manual is meant to help staff in the Environment Agency on how to determine if a fishway is needed, which type of fishway should be constructed, where it should be constructed and how to evaluate the success. Evaluation of fishway functionality is also required in other countries, such as France where passage efficiency is required to be higher than 80 % with a migration delay of no more than two weeks (Armstrong et al. 2010).

In comparison to some 30 years ago, modern tools now make us much more able to measure the hydrodynamics of fishways in detail which will facilitate our understanding of why some fishways have high passage efficiency while others have low (Williams et al. 2011). This can be done either in theory with computational fluid dynamics modeling (CFD) (i.e. Nestler et al. 2008, Heimerl et al. 2008) or measuring with particle image velocimetry (PIV) (i.e. Tarrade et al. 2008) or acoustic doppler current profiler (ADCP) (i.e. Andersson 2010), and with today's computers the large amount of data generated by these tools can easily be compiled and interpreted. With a detailed description of the environment the fish are experiencing, behavior studies based on for example telemetry or sonar can answer not only the question what the fish are doing but potentially also why they are doing it.

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