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THINKING LIKE A FISH: A KEY INGREDIENT FOR DEVELOPMENT OF EFFECTIVE FISH PASSAGE FACILITIES AT RIVER OBSTRUCTIONS

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ABSTRACT

Worldwide, obstructions on watercourses have interfered with migratory pathways of fish species, reducing life-cycle success and often eliminating diadromous fish species altogether from river basins. Over the last century, efforts to mitigate these effects were initially directed at developing fishways for upstream, high-value migrant adult salmon. In more recent years, efforts have turned to developing fishways for other species. Results of past research suggest that the development of effective fishways requires biological knowledge of fish behaviour when encountering variable flows, velocity and turbulence, combined with hydraulic and civil engineering knowledge and expertise to develop facilities that provide appropriate hydraulic conditions that fish will exploit. Further, it often requires substantial financial resources for biological and hydraulic testing as well as engineering design, particularly where prior knowledge of the behaviour of target fish species does not exist. Where biological or engineering knowledge (or both) is absent, development of effective passage facilities must take on a trial and error approach that will almost certainly require years to attain success. Evaluations of existing adult and juvenile fish passage facilities, where they have been carried out, suggest that migrant fish reject areas with hydraulic conditions they determine unsuitable. Even well designed fish ladders or nature-like bypass channels for upstream migrants, even those with good attraction flows, will fail if incorrectly sited. Although progress has been made, developing successful installations for downstream migrants remains much more difficult, probably because downstream fish move with the flow and have less time to assess cues at entrances to any bypasses that they encounter.

KEY WORDS: dams; fish passage; fish behaviour; fish bypass systems

INTRODUCTION

Worldwide, myriad anthropogenic obstructions on watercourses have had tremendous negative effects on the migratory pathways of diadromous and potamodromous fish. The consequent reduction in life-cycle success has often eliminated species, especially those that are diadromous, from river basins across the globe. Some obstructions in Europe had fishways installed to facilitate upstream passage as long ago as 300 years (Clay, 1995). For salmon, at least, it appears that the most successful early fishways were a series of small pool and weir configurations with a shallow slope that covered relatively short vertical rises (Francis, 1870). In contrast, fishways installed from the mid to late 1800s at dams on rivers of the east coast of the USA may have passed salmon (*Salmo salar*), but they were singularly unsuccessful in passing shad (*Alosa sapidissima*) (Stevenson, 1897). Construction costs for fishways have always been, and indeed remain, an issue for owners of weirs and dams; thus, the shorter and steeper the passage route, the less the cost to construct. However, historically, salmon did not successfully pass steep pool fishways (Francis, 1870), and this led to research and development of more effective types of passes. In the early 20th century, research began that would lead to a successful design of relatively narrow sloping fishways with various vanes (Denil, 1909a, 1938), and variants of these were later tested by McLeod and Nemenyi (1941) in the late 1930s. Although most early efforts were directed at salmon and alosids, the large number of fishway designs tested by McLeod and Nemenyi (1941) involved fish present in Iowa River, which included trout, catastomids, clupeids, cyprinids and percids. Species of fish from these groups showed different preferences for pool and weir configurations—with or without orifices, various vane configurations in Denil-type fishways and preferences for passage in light or dark. In the early 1980s, further variants

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on Denil fishways provided an ability to juxtapose wider and shallower types of bottom baffle units to create passes with considerably higher discharge (Larinier, 2002a). Some of the designs pass a wide range of species with varying swimming capabilities probably by virtue of the relatively heterogeneous conditions within them.

Although some migrating fish might have successfully passed upstream over low-head obstructions with rudimentary fishways in the early last century, Calderwood (1928) lamented that hydropower dams nearly always blocked salmon runs completely and that, essentially, no fishways in either Europe or the USA successfully and effectively passed salmon above them. Because of the importance of salmon and steelhead (*Oncorhynchus* sp.) runs in the Columbia River, USA, great concern existed about the ability to construct effective fishways for Bonneville Dam when it was designed in the 1930s (Holmes and Morton, 1939). The fear of possibly destroying runs on the largest Chinook (*Oncorhynchus tshawytscha*) salmon bearing river in the world (Griffin, 1935) led to designs for a complex passage system that consisted of three fish ladders—one for the powerhouse and one on each side of the spillway and three pairs of fish locks—one pair located adjacent to each ladder entrance (one lock was always open for fish passage whereas the other was filled with water to lock fish to the forebay). The fish lifts were mostly used experimentally, but it appeared that salmon more readily used the ladders than the locks, thus, the lifts were essentially abandoned after several years. Improvements to pool and weir ladders and entrance conditions did not occur until after considerable research during the 1950s and 1960s at the fisheries engineering research laboratory constructed at Bonneville Dam (Collins and Elling, 1960; Collins *et al*., 1963; Connor *et al*., 1964; Monk *et al*., 1989). Although pool and weir ladders worked at Columbia River dams, they were not feasible in the Fraser River, British Columbia, Canada, where a rock slide at Hell's Gate in 1913 substantially narrowed the river, increased velocities and decreased upstream passage of sockeye salmon (*Oncorhynchus nerka*). Little mitigation occurred for decades, but by the 1930s, concerted efforts began to develop a new type of fishway that could pass fish upstream through the area. The result of the research was the design of vertical-slot fishways (Clay, 1995). Vertical-slot fishways were finally installed in 1945/46 and upstream passage of sockeye salmon increased tremendously under the flow levels for which the fishways were designed (Talbot, 1950). The estimated 32+ million adult sockeye return to the Fraser River in 2010 was the largest since prior to the blockage in 1913.

The development and refinement of pool and weir, vertical slot and steep slope fishways continued into the latter half of the 20th century and were primarily targeted at salmon and shad (*Alosa* spp.) in North America and Europe although as early as the 1930s, variants of pool and weir and steep slope fishways were found to successfully pass a range of other fish species (McLeod and Nemenyi, 1941). In the last 20 years, more efforts have been expended toward adapting these types of passes to a wider range of fish such as lamprey (Keefer *et al*., 2010) and potamodromous species (e.g., see Katopodis *et al*., 1991; Silva *et al*., 2009; Silva *et al*., 2010). Because these latter species often have lesser swimming capabilities than salmon and shad, the efforts have been directed toward quantifying the rather complex fishway hydraulics beyond mean velocities and depths and developing configurations with lower velocities, slopes, head drops and power dissipation, breaking up eddies or using roughness in the bottom of the passes (Katopodis, 1992, 2005). More recent research has also focused on the development of fishways with greater amounts of hydraulic heterogeneity to provide conditions that allow both more species and much greater range in sizes of fish that can pass through them (Katopodis *et al*., 1991; Mallen-Cooper, 1999; Katopodis, 2005; Mallen-Cooper and Brand, 2007; Mallen-Cooper and Stuart, 2007; Tarrade *et al*., 2008; Baumgartner *et al*., 2010).

In some cases, despite a lack of knowledge about a local species ability to utilize fishways, regulators may have required that dams have fish passage facilities installed. In South America, for example, numerous hydropower dams were constructed with fish passes and subsequent evaluations of some of these facilities have indicated that only small percentages of fish pass them (Oldani and Baigún, 2002; Agostinho *et al*., 2007b; Pompeu and Martinez, 2007). In other cases, adults have appeared to successfully pass upstream (Agostinho *et al*., 2007a; Pelicice and Agostinho, 2008), but it was not clear if juveniles could make it downstream. Although considerable efforts over decades led to effective fish passes for salmon, the same configurations installed in areas where other species migrate will not necessarily work. To develop good passage systems, it requires knowledge of swimming capabilities and hydraulic preferences of fish. In Brazil, work has started to develop this important information for some species of concern (Santos *et al*., 2007, 2008).

When taken in combination, the early research to develop upstream passage facilities indicated that carefully controlled studies in laboratories, using naturally migrating fish, could lead to fishway designs that upstream migrant fish could effectively ascend. Nonetheless, Francis (1870) had already recognized that the best designed fishway would not work unless fish could readily find the entrance; whereas Denil (1909b) and McLeod and Nemenyi (1941) concluded further that fishway entrances needed to attract fish and have a quantity and characteristic of flow that would enable them to easily enter. For upstream migrants, outside of laboratory settings, little information existed about how fish found ladder entrances or the effectiveness of location and attraction flows for fish.

Finally, technical fish passes are not the only possible solution to passage at river obstructions. In Canada since the 1970s (Katopodis, 2005) and particularly in Europe somewhat later (Parasiewicz *et al*., 1998), nature-like fish passes have been constructed at many obstructions including even large dams. They look essentially like a small stream. Nonetheless, for these alternative passage systems to work effectively, just as with technical fish passes, they need to have entrances that fish readily find, hydraulics that attract fish to enter and hydraulics within the nature-like systems that fish will readily pass to the upper end where the exit is (Schmutz *et al*., 1998; Aarestrup *et al*., 2003; Calles and Greenberg, 2005; Katopodis, 2005; Calles and Greenberg, 2007).

In contrast to the considerable efforts that had gone into the development of upstream passage facilities, much less effort had been expended to develop facilities for downstream migrants, particularly for salmon. This resulted for a number of reasons. Most downstream-migrating salmon are juvenile fish and the magnitudes of fish passing dams were 'out of sight, out of mind'; concern about loss of fish passing one dam often did not exist, and fish hatcheries were considered a solution (Ebel, 1985). Nonetheless, mortality to downstream migrants had long been recognized. In Europe, during the early 20th century, Denil (1909b) identified damage inflicted by turbines as well as bottom or surface bypasses on silver eels (*Anguilla anguilla*) in Germany. Later on, Otterstrøm (1936, 1942) identified mortality to salmon, trout and eels passing turbines. In the USA, after the completion of Bonneville Dam, Harlan Holmes released fin-clipped juvenile Chinook salmon through turbines and spillways at the dam. Based on adult returns, he determined (unpublished US Fish and Wildlife Service internal report) that fish passing through turbines had about a 10% increase in mortality compared to those passing through spillways. Systematic mortality estimates of juvenile salmon passing through Kaplan turbines at Columbia River dams was quantified in the 1950s (Schoeneman *et al*., 1961). In the 1950s, Von Raben (1955) established the first model-relating damage of fish passing turbines to turbine characteristics. Taken together, decreased survival of fish passing through turbines led to directed efforts to develop strategies that would actively (screen fish away) or passively (alter migration behaviour or allocation of water to a non-turbine route) increase survival for downstream migrants.

Tremendous efforts in the last 50+ years have gone into developing effective screening systems to divert downstream juvenile salmon migrants from turbines at Columbia River dams (Williams, 2008). Efforts to develop screening systems in other river systems for downstream anadromous fish have been less successful (Haro *et al*., 1998). As an alternative to expensive screening systems, most research in the last 20 years has focused on the development of surface bypass routes for fish (Johnson and Dauble, 2006; Travade and Larinier, 2006). Further, these efforts have generally focused on salmonids and shad; little is known about behaviour nor has much research been directed at developing solutions for generally catadromous, potamodromous and non-salmonid fish (Coutant and Whitney, 2000).

The greatest improvements in fish passage facilities have resulted from research identifying how fish react to varying and well-defined hydraulic conditions—conditions they avoid and ones they seek. This research has led to configurations that upstream migrants can successfully negotiate. Information on the ability of upstream-migrating fish to effectively find and move into fishways has mostly come from field observations and directed studies with radio or acoustically tagged fish. With the exception of some hydraulic models to understand how systems designed to guide or deflect downstream migrants affect hydraulic flow characteristics encountered by downstream migrant fish, nearly all information on the effectiveness of systems to pass downstream migrants at dams has come from field observations of installed prototypes. In recent years with the technology to downsize tags, some radio and acoustic tags inserted in juvenile salmonids (Williams, 2008) and adult eels (Travade *et al*., 2010) have provided some behavioural information on how these fish approach dams and bypass systems.

Successful fishways have hydraulic conditions that fish choose or do not actively seek to avoid. Although most installed fishways have targeted anadromous fish, the general approach to the development of effective fishways of identifying fish behaviour and developing good hydraulic conditions will likely directly apply to catadromous and potamodromous fish. Here, we provide some additional details.

THINKING LIKE A FISH

If we understood what goes through a migrating fish's mind…if anything at all… or at least understood its innate behavioural preferences when it encounters varying hydraulic conditions; ones it chooses to accept or avoid, we could more easily develop hydraulic conditions that lead toward successful migrations. Humans harvesting fish in rivers have known for aeons that correct placement of fishing gear leads to higher catches of fish because migrating fish in rivers are not randomly distributed. Becker (1938) used the term of 'thinking like a fish' over 70 years ago in an effort to persuade boys to try to understand where to find and catch the biggest fish in a body of water, thus, the idea of understanding fish behaviour in flowing water is not new. Although we do not have a clear understanding of fish reactions to macro-hydraulic and micro-hydraulic conditions, based on decades of observations on upstream migrant fish, considerable knowledge exists on what locations of fishways and attraction flows generally lead to the most successful rates of passage. As early as the 19th century, Francis (1870) observed installed salmon ladders at weirs and based on location or attraction flows suggested why most did not pass fish effectively. For salmon and shad (possibly also Pacific lamprey—*Lampetra tridentata*), biologists and hydraulic engineers with considerable experience with site placement of upstream fishways could probably have a ready answer to the question, 'What would fish do when they migrate into the area?' (see Clay, 1995; Larinier, 2002c; Armstrong *et al*., 2004; NMFS, 2004). For upstream migrants, the answer to the question while not 'thinking like a fish' does rely on some common behaviours related mostly to changes in water velocities (acceleration) and volume of flow near a fishway site (or potential site) compared to total discharge at a dam (although we recognize that fish also likely consider turbulence, noise, smell, temperature and oxygenation).

On the other hand, although downstream migrants also appear to rely to a large degree on changes in hydraulic conditions, the ability of engineers/biologists to look at a site and determine a location and means to bypass fish is generally lacking for large obstructions. Despite decades of efforts directed at juvenile downstream migrant salmonids; early research that considered behavioural systems—electrical guidance (Pugh *et al*., 1970), louvres (Bates and Vinsonhaler, 1957), louvres and electrodes combined (Monan, 1967), lights (Fields, 1957), additional work with incandescent and strobe lights in the 1980s (Gessel *et al*., 1991) and more recent ideas such as creating turbulent flows that fish will follow (Coutant, 2001b) and additional work with lights and infrasound (see Coutant, 2001a for additional behavioural papers), no clear behavioural solutions exist that one can apply to new locations. Physical systems, particularly fish screens, have been more effective for water intakes, irrigation canals and a few small-scale hydroelectric projects (Gessel *et al*., 1991; Congress of the United States/Office of Technology Assessment, 1995; Katopodis, 2005; Katopodis *et al*., 2005). It appears that external stimuli will not sufficiently influence passage success of the majority of fish that actively migrate downstream through fishways; success depends on fish finding hydraulic conditions they consider acceptable.

Based on success and failures of passage systems for upstream and downstream migrants, it clearly appears to us that migrant fish have a directed, not random migration. They seek conditions that indicate that their migratory pathway will keep them within the main flow of a river, for if not; they might continually end up in unfavourable areas and miss the optimum window for migration or else find themselves in sub-optimal habitats, such as minor tributaries. In either case, evolutionary selection likely weeds out the majority of fish that do not maintain an optimum migration. Upstream migrants tend to seek areas with higher velocity gradients, whereas downstream migrants tend to avoid them. In areas of a river with low velocity, fish may distribute across the width of the river, but as velocity increases, as it does at man-made obstructions, the upstream migrants tend to migrate on the edges of the main body of water—conditions generally found either more toward the shoreline or nearer the bottom—where water velocity gradients exist. In contrast, downstream migrants tend to move toward the area with the highest flow volume as this generally has the highest water velocity but the lowest velocity gradient.

Changes in hydraulic conditions, as reflected in water velocity, turbulence characteristics and momentum, provide the major cue fish use to seek a migration pathway in rivers when confronted with variable hydraulic conditions (near-field behaviour). Below we expand on how migrants respond to hydraulic conditions and why this knowledge is critical to the development of effective fish passage facilities.

UPSTREAM PASSAGE

Upstream migrants swim into flow that provides the ability to assess conditions that they encounter for essentially as long as they choose. Thus, they can slowly move upstream and assess possible passage routes carefully. They can reject areas with velocity gradients too low and accept ones where they detect velocity gradients they find acceptable. Likewise, they can choose routes close to the bottom with lower velocities or swim higher in the water column to seek higher water velocities. Knowledge of hydraulic conditions favoured by salmon led to the design of successful fishways for these species. Yet, these fishways do not always pass other species of fish effectively (Moser *et al*., 2002; Knaepkens *et al*., 2006; Mallen-Cooper and Brand, 2007). Concern about passing a broader range of species has led to research to obtain information on conditions more favourable for passage for non-salmonids (for example, see Katopodis *et al*., 1991; Mallen-Cooper, 1999; Moser *et al*., 2000; Larinier, 2002b; Haro *et al*., 2004; Katopodis, 2005; Santos *et al*., 2007; Santos *et al*., 2008; Silva *et al*., 2009; Roscoe and Hinch, 2010; Silva *et al*., 2010).

Whether with large or small fish or those with good or poor swimming capabilities, the ability to develop a successful fishway starts by laboratory testing of a potential passage configuration to see if fish move past it, then determining what hydraulic conditions fish prefer or avoid. Repeat testing with modifications to, for example, weir heights, slot openings, vane arrangements and slopes to alter water velocity and turbulence will lead to a configuration that a species will pass. A successful fishway just links a series of passage configurations, with the recognition that some fish species might need resting or holding areas if they must pass a large number of passage chambers to transit a high vertical distance. For salmonids initially, but subsequently tested for many other fish species, research to determine acceptable velocities, slopes, resting areas, etc. within pool and weir, vertical slot or Denil configurations has led to successful fishways through which many species of fish readily and successfully pass (Katopodis *et al*., 1991; Larinier, 2002b; Armstrong *et al*., 2004; NMFS, 2004).

Although seemingly easy to determine passage conditions that upstream migrant fish will choose and successfully pass, research, for the most part, has only occurred for economically important species such as salmon and shad. It takes considerable resources including both financial and time and a laboratory to conduct the research. Further, it requires engineers and biologists working together to determine the hydraulic conditions through which fish most readily pass and then translate this into a successful design for a fishway. This is particularly important because studies in laboratories seldom have the scale of a fishway installed at a passage barrier.

Clearly, the most effective fishway would take the whole flow of the river. Because of this, probably one of the most complicating factors about fishway design relates to the 'requirement' to actually use as little water as possible in the fishway. This results generally from two factors: (i) the more volume of water in a fishway, the higher the cost to construct; and (ii) desire of dam operators to divert as little water as possible to fishways because the more water diverted, the less they have available to produce power or for other purposes. Thus, even the largest fishways at Columbia River dams where hundreds of thousands of adult fish may pass a year utilize only about $5\,m^3\,s^{-1}$ flow. This fact leads to the most critical part of fishway design for upstream migrants. Although fishways themselves may successfully pass fish upstream once fish enter them, they will not work if the entrance is located in an area unattractive to fish. Migrants tend to move as far upstream as possible when they encounter the high velocity water discharged at dams and avoid low velocity areas (for example, see Arnekleiv and Kraabol, 1996; Karppinen *et al*., 2002; Lundqvist *et al*., 2008). Because fishways nearly always have miniscule flow compared to flows passing a dam, locating the fishway entrance becomes crucial for success. As a result, most successful fishways have entrances located as close to a dam as possible, the entrances are oriented such that fish can move in the current as directly as possible into them (entrances perpendicular to river flow attract fish poorly), and generally, additional attraction water at the entrance is required to provide a large enough flow volume, velocity and favourable turbulence characteristics to attract fish to the fishway entrance. Generating attractive conditions and providing additional flow are often not trivial, yet fishway effectiveness rests on efforts to provide such attraction. Attraction flows used at fishways in the USA, France and the UK typically range from 5 to 10% of the total discharge at a dam. In the Columbia River, this equates to 100 s of $m^3\,s^{-1}$ flow. In our experience, modern fishways often fail not because they have unsuitable hydraulic conditions but because fish fail to find and enter them. Possibly, prior migration experiences also influence the rate of passage (Thorstad *et al*., 2008). When fishway entrances are placed too far downstream, fish often fail to find them because the entrances have insufficient attraction to compete with the hydraulic conditions in the river that draw fish upstream to the impassable area. Likewise, fishways placed in the middle of a dam also do not attract fish very effectively because they do not have sufficient velocity gradients and because fish tend to approach a dam via the shorelines.

Even with well designed fishways, not all fish will pass equally well (Caudill *et al*., 2007). Fish vary in their physical capabilities and behaviours just as humans do. Research to determine the configurations that will work effectively for a species needs to assure that test animals represent a broad range of individuals. Fish populations have not survived for millions of years by all individuals within them having the same abilities or strategies.

In sum, for upstream migrants, we believe that fish seek specific cues from flow and water velocity gradients and successful fishways must account for these. Further, for upstream migrants, a fishway must not only attract fish, it must also have hydraulics that allows a fish to physically ascend it. Research and experience suggest that with sufficient laboratory testing, it is possible to determine hydraulic conditions that fish will actively use as a conduit and develop a fishway that will effectively pass most upstream migrants of any species over a dam of just about any height. Nonetheless, economic considerations might limit the ability to construct an effective fishway for fish without good swimming abilities at dams of considerable height. However, in some cases, this might not lead to recovery of stocks once abundant as very often appropriate habitat has been drowned out, and once fish no longer migrate above dams, activities are permitted that alter water quality, raise temperatures, remove water or change formerly habitable areas for fish into now inhabitable ones. Furthermore, although an individual upstream passage system may cause little harm in itself or only delay migration by hours to a few days while fish seek to find the entrance to the fishway and pass through it, the cumulative effect from a series of dams and fishways may alter timing sufficiently so as to decrease viability of upstream migrants (Caudill *et al*., 2007; Roscoe and Hinch, 2010). Consequently, passes usually need to be highly efficient and effective at passing fish upstream quickly and without delay. It takes biologists and engineers working together in tandem to develop an effective system, but given the widely different objectives between developers and regulators, this does not happen readily without specific directed efforts to have all parties working together. A facility that will effectively pass fish requires a fundamentally sound ecological approach and sympathetic engineering at the inception of the developmental design, not a retrofit after a project becomes completed—particularly one where a 'simple solution' was built with thoughts that an engineer could always modify it if it does not work. And finally, just as not all humans can run a 100-m dash, not all fish have the same physical capabilities. Although designs may not provide conditions to pass all fish of a species, they need to pass the large majority of them.

Clearly, catching fish upstream successfully past obstructions is not sufficient in itself to maintain a viable diadromous run. What goes up must come down. Yet, still less knowledge exists about effective ways to catch fish safely downstream past dams (Larinier and Travade, 2002; Katopodis, 2005). In the following section, we discuss some of the major issues involved in developing fishways for downstream migrants.

DOWNSTREAM PASSAGE

Probably the greatest factor that challenges development of fishway design for downstream migrants relates to how fish encounter obstructions. Unlike upstream migrants that swim into the flow and have time to 'check out' their environment, downstream migrants move with the flow, thus, they have much less time to assess conditions they encounter. Further, whereas both behavioural and swimming capabilities play a role in the success of upstream migrants passing through a fishway, because downstream migrants tend to move with the flow, they need relatively less swimming ability and rely more on behavioural adaptations. Developing strategies to keep fish from migrating through a deleterious route is often exacerbated for juvenile fish, particularly salmonids, because their behaviour may change with size or physiological state (Iwata, 1995), and also their vertical position in the water column may change with diel variation in ambient light (Smith, 1974). For instance, small subyearling Chinook salmon smolts tend to migrate closer to the shoreline, whereas yearling Chinook salmon smolts mostly migrate in the middle of the thalweg in areas with the highest flow. Thus, for the latter run type at least, the natural pathway for them generally follows the main flow, which usually takes them through turbines unless screens intercept that flow or else alternative surface flow routes can attract and pass these surface-oriented fish (e.g. see Johnson *et al*., 2000; Johnson and Moursund, 2000; Johnson *et al*., 2005; Johnson and Dauble, 2006). Adult eels migrating downstream also appear to follow the route with the highest flow but, depending on size and quantity of flow and trashrack spacing, may seek alternate routes to turbine passage (Travade and Larinier, 2006; Travade *et al*., 2010). Fish may also try to avoid areas with rapid changes in water velocity (either acceleration or deceleration) (Haro *et al*., 1998; Kemp *et al*., 2005, 2008; Enders *et al*., 2009) and areas created by screens or surface flows designed to divert them from turbines, and instead they may move to areas of flow with less turbulence/lower velocity gradients; in other words, they move with the bulk flow that goes through the turbines. On the other hand, adult eels migrate near the river bed and do not respond to changes in velocity until they physically encounter an obstruction (Gosset *et al*., 2005; Russon *et al*., 2010). Based on recovery of lamprey juveniles in fyke nets placed in turbine units at Columbia River dams during research to develop turbine screening systems for juvenile salmon (data on lamprey from unpublished National Marine Fisheries Service research, but see Long (1968) for details on nets for vertical distribution studies and Gessel *et al*., (1991) for details on screen studies), it appears that the majority of juvenile lamprey (macrophthalmia and ammocoetes) also migrate near the bottom. However, in these stages, because of their small size, almost nothing is known about their downstream behaviour or orientation to flow. Finally, the fate of potamodromous species is often ignored despite the fact that they may undergo considerable movements downstream as juveniles or adults (Pavlov, 1994; Larinier and Travade, 2002; Zitek *et al*., 2004; Katopodis, 2005; Pavlov *et al*., 2008).

Downstream-migrant fish, particularly juvenile salmonids, if they behaviourally seek areas of bulk flow, need to swim relatively little other than to maintain orientation or water flow across their gills to maximize downstream distance travelled with minimal energy expenditures. If a fish moves little relative to the flow in which it migrates, its speed with respect to non-moving objects nearly equals the velocity of the water. The observation that juvenile salmon appear to travel at the speed of water at one time suggested that they may float passively downstream (Thorpe *et al*., 1988). Recent research has shown this assumption false as juvenile salmon and shad have very distinct reactions to changes in water velocity and react to avoid conditions they deem unsuitable (Peake and McKinley, 1998; Castro-Santos, 2005; Kraabøl *et al*., 2008; Pedersen *et al*., 2008). If they encounter conditions where the velocity begins to change, decreasing velocity will occur as flow approaches a barrier or increasing velocity will occur where flow begins to constrict or water starts to free fall, they may choose to alter their position in the water body in which they are migrating. If they swim in a downstream direction, and recent research has shown that juvenile salmon sometimes actively migrate headfirst with the current (Johnson *et al*., 2000; Kemp *et al*., 2005; Kemp *et al*., 2006; Enders *et al*., 2009), they will increase the encounter rate with downstream conditions that changed the velocity gradient in the first place. Thus, they will have less time to make a decision about whether or not to try to avoid the condition they are encountering. Whereas if a fish swims slowly into the current while moving downstream, and this is considered by some as the only orientation to current for downstream-migrant Pacific salmonids (Coutant, 2001b; Coutant and Whitney, 2006), they can increase their tail-beat speed to slow their downstream travel and possibly move upstream to avoid the changing velocity areas.

Reactions of fish to changing water velocities with variable turbulence differ between migrating and non-migrating fish. Where a resident fish works to hold its position in flowing water, downstream-migrating fish, at least anadromous Pacific salmon that need to travel long distances to arrive during optimal ocean conditions, actively seek to move with the flow because they have a relatively narrow window in which to migrate these distances successfully. Thus, research to develop systems to guide fish toward benign passage routes or repel them from deleterious routes as fish approach river obstructions requires the use of fish actually in a positive migratory phase to understand how they will react to different flow conditions. This presents one of the greatest challenges to researchers trying to develop effective fishway systems because the migratory phase is short-lived. The life stages of diadromous fish that spend their time in freshwater usually do so to feed and grow until they reach some stage at which they begin to migrate toward the sea. One cannot simply raise fish in a hatchery for testing or capture fish and presume they are in an active migratory state that will provide meaningful indications of migratory behaviour. Further, even holding known migratory fish for an extended time period may alter their migratory behaviour and they will thus not express the same behaviour as fish that have naturally migrated for some distance or time in a river. Although few laboratory facilities have this capability, laboratory research on migration behaviour of Pacific salmon juveniles at McNary Dam, Columbia River, USA has been able to use actively migrating fish (Kemp *et al*., 2005; Enders *et al*., 2009). Large-scale river studies using radio or acoustic tags implanted in actively migrating fish or else fish tracked with sensitive acoustic gear, such as a DIDSON camera, may also provide needed information (e.g., see Hockersmith *et al*., 2003; Johnson *et al*., 2005).

Yet, while not using migratory fish, basic laboratory research has shown that velocity that is chaotic and with wide fluctuations can repel fish, whereas flows that have a component of predictability can attract fish (Liao, 2007). Our experience with migratory fish suggests that they react similarly. To develop effective passage systems, however, requires a quantification of migratory fish behaviour to changing flow; data needed for engineers to design the systems. For juvenile Pacific salmon, studies to determine how migratory fish react to variable flow/velocity conditions within rivers began in earnest in the last decade following improvements and downsizing in acoustic tags that have allowed for tagging and monitoring movement of individual migrant fish. Results have led to models that predict juvenile behaviour as smolts approach dams or diversions where variable water velocity conditions exist (Goodwin *et al*., 2006; Goodwin *et al*., 2007; Lemasson *et al*., 2008; Nestler *et al*., 2008). Results from these large-scale studies are based on positions of fish generally within cells of water with a volume of 0.5–1.0 m^3. Likewise, the ability to estimate velocity components that the fish experience has about the same resolution. To develop information on fine-scale resolution of fish behaviour, recent laboratory studies have been able to determine how fish react to variable velocity with a resolution in cm (Kemp *et al*., 2005, 2006, 2008; Enders *et al*., 2009).

Although a laboratory setting may have the ability to provide choices of hydraulic conditions that mirror those that fish may encounter in a real situation, it becomes much more difficult to determine how they might react when given multiple choices. For instance, downstream-migrating salmonid smolts in a river might reject an area with decreasing velocity caused by screens in a turbine intake and choose to move to another area where they find more acceptable velocity conditions. Providing choices in the laboratory on a scale equivalent to those that a juvenile fish might encounter at a dam and to which it could react poses exceptional challenges. For adult fish, this particularly holds true. Inevitably, the combination of laboratory studies and field studies will provide the best set of information needed for effective fishway systems.

With the exception of the recent work on juvenile salmonids identified above in the last 10 years, and as a consequence of the difficulty in testing behaviour of downstream migrants, much less research has been carried out in this area when compared to upstream-migrating adults. Further, outside of considerable efforts to develop effective fish screening systems for downstream migrating for salmonid smolts at dams on the Columbia River, much less attention has gone toward developing means to divert or guide downstream migrants away from turbines at hydroelectric dams in other places (Larinier and Travade, 2002).

For both upstream-migrating and downstream-migrating fish, where the biological knowledge of their behaviour or engineering components for an effective fishway (or both) are missing, development of effective passage facilities has often taken on trial and error approaches that have required years (to decades) to attain success…even where resources, funding, time and the will have existed.

CONCLUSIONS

Initial development of effective passage facilities at obstructions, including hydroelectric dams, was initially directed almost entirely at salmonid species, both in North America and Europe. It took decades to develop effective facilities, often based on trial and error testing of prototype installations. Recently, research has begun to focus on developing facilities for upstream non-salmonid migrants. Results from more recent studies demonstrate that 'one solution does not fit all' and that design of passage facilities that can effectively pass a wide range of species needs to take into account the preferences and swimming abilities for the specific species of interest. It requires biological knowledge about fish behaviour under the varying flow/velocity/turbulence conditions they encounter during upstream migration, development of fishways that provide flows through which fish can actively and successfully migrate and, of particular importance, installing fishways with adequate attraction flows at locations that fish will seek during their migration. We encourage and recommend actively quantifying migration behaviour of fish in the field. The ability to do so has become feasible within the last decade or so because of tremendous advancements in technology. The use of internally implantable PIT-tags (Prentice *et al*., 1990), acoustic tags (Ehrenberg and Steig, 2009) and radio tags (Aarestrup *et al*., 1999; Moser *et al*., 2002; Burke and Jepson, 2006; Keefer *et al*., 2008), along with the ability to estimate 3-D positions of fish from underwater acoustic arrays (Hockersmith *et al*., 2003; Johnson *et al*., 2005), can provide information on upstream or downsteam behaviour of fish in relation to hydrodynamic conditions as they approach river obstructions. Computational fluid dynamic models provide the ability to estimate the hydraulic characteristics in forebays and tailraces of obstructions through which tagged fish pass (Khan *et al*., 2008), and others have developed modelling tools to combine the fish behaviour with the hydraulics (Goodwin *et al*., 2006, 2007). These types of field techniques along with laboratory experimentation to develop flow conditions through which fish will pass can provide the information needed for species for which we presently have little data.

We emphasize again that construction of effective fish passage facilities will only occur if biologists and engineers work together to achieve successful environmental outcomes. Biologists need to provide engineers the knowledge on fish behaviour under different flow conditions, using all pertinent variables for the correct description of the flow conditions that engineers use in design. On the other hand, it is critical that engineers seek biological input before proceeding with design, avoiding the temptation to consider solely engineering and developer objectives in the first instance. And finally, money…costs go way beyond actual fishway construction. Most often, substantial amounts are needed for biological and hydraulic testing, engineering design and post-construction evaluation, particularly where specific knowledge of fish behaviour does not already exist. The ability to comparatively easily construct test facilities to define fish behaviour for upstream migrants under variable flow conditions has led to much greater progress in developing successful upstream fishways than downstream ones. Further innovative research is sorely required, especially in relation to fish behaviour and hydrodynamics and particularly for downstream-migrating fish.

The ability to understand how a fish species of interest will respond to micro-hydrodynamic and macro-hydrodynamic conditions upstream and downstream of obstructions, what attracts them and what repels them, is the key to the development and design of successful passage facilities. Worldwide, biologists and engineers still lack the understanding and quantification of the behaviour of all sorts of freshwater fish species for which a need to develop fishways exists. To tackle this will require multi-disciplinary approaches, particularly co-operation between biologists and engineers to ensure sound environmentally engineered solutions (i.e. the brave new world of ecohydraulics has far to go).

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REFERENCES

Aarestrup K, Jepsen N, Rasmussen G, Økland F. 1999. Movements of two strains of radio tagged Atlantic salmon, *Salmo salar* L., smolts through a reservoir. *Fisheries Management and Ecology* **6**: 97–107.

Aarestrup K, Lucas MC, Hansen JA. 2003. Efficiency of a nature-like bypass channel for sea trout (*Salmo trutta*) ascending a small Danish stream studied by PIT telemetry. *Ecology of Freshwater Fish* **12**: 160–168.

Agostinho CS, Agostinho AA, Pelicice FM, Almeida DA, Marques EE. 2007a. Fish ladder: migration on one way routes? *Neotropical Ichthyology* **5**: 121–130.

Agostinho CS, Pereira CR, de Oliveira RJ, Freitas IS, Marques EE. 2007b. Movements through a fish ladder: temporal patterns and motivations to move upstream. *Neotropical Ichthyology* **5**: 161–167.

Armstrong GS, Aprahamian MW, Fewings GA, Gough PJ, Reader NA, Varallo PV. 2004. Environment agency fish pass manual: guidance notes on the legislation, selection and approval of fish passes in England and Wales. Available on CD from Environment Agency, Llys Afon, Hawthorn Rise, Haverfordwest, Pembrokeshire, SA61 2BQ, Wales, UK. E-mail: greg.armstrong@environment-agency.gov.uk.

Arnekleiv JV, Kraabol M. 1996. Migratory behaviour of adult fast-growing brown trout (*Salmo trutta*, L) in relation to water flow in a regulated Norwegian river. *Regulated Rivers—Research & Management* **12**: 39–49.

Bates DW, Vinsonhaler R. 1957. Use of louvers for guiding fish. *Transactions of the American Fisheries Society* **86**: 38–57.

Baumgartner LJ, Boys CA, Stuart IG, Zampatti BP. 2010. Evaluating migratory fish behaviour and fishway performance: testing a combined assessment methodology. *Australian Journal of Zoology* **58**: 154–164.

Becker B. 1938. Where to find the big ones. In *Boys' Life*. Boy Scouts of America: New York, NY; 44.

Burke BJ, Jepson MA. 2006. Performance of passive integrated transponder tags and radio tags in determining dam passage behavior of adult Chinook salmon and steelhead. *North American Journal of Fisheries Management* **26**: 742–752.

Calderwood WJ. 1928. Hydro-electricity and salmon fisheries. *Transactions of the American Fisheries Society* **58**: 54–60.

Calles EO, Greenberg LA. 2005. Evaluation of nature-like fishways for re-establishing connectivity in fragmented salmonid populations in the river Emån. *River Research and Applications* **21**: 951–960.

Calles EO, Greenberg LA. 2007. The use of two nature-like fishways by some fish species in the Swedish River Emån. *Ecology of Freshwater Fish* **16**: 183–190.

Castro-Santos T. 2005. Optimal swim speeds for traversing velocity barriers: an analysis of volitional high-speed swimming behavior of migratory fishes. *Journal of Experimental Biology* **208**: 421–432.

Caudill CC, Daigle WR, Keefer ML, Boggs CT, Jepson MA, Burke BJ, Zabel RW, Bjornn TC, Peery CA. 2007. Slow dam passage in adult Columbia River salmonids associated with unsuccessful migration: delayed negative effects of passage obstacles or condition-dependent mortality? *Canadian Journal of Fisheries and Aquatic Sciences* **64**: 979–995.

Clay CH. 1995. *Design of Fishways and Other Fish Facilities*, 2nd edn. Boca Raton, LA: Lewis Publishers.

Collins GB, Elling CH. 1960. *Fishway Research at the Fisheries Engineering Research Laboratory*. U.S. Department of the Interior, Fish and Wildlife Service, Bureau of Commercial Fisheries, Circular 98: Washington, D.C.; 1–17.

Collins GB, Elling CH, Gauley JR, Thompson CS. 1963. Effect of fishway slope on performance and biochemistry of salmonids. *Fishery Bulletin* **63**: 221–253.

Congress of the United States/Office of Technology Assessment. 1995. *Fish Passage Technologies: Protection at Hydropower Facilities*. U.S. Government Printing Office: Washington, D.C..

Connor AR, Elling CH, Black EC, Collins GB, Gauley JR, Trevor-Smith E. 1964. Changes in glycogen and lactate levels in migrating salmonid fishes ascending experimental "endless" fishways. *Journal of the Fisheries Research Board of Canada* **21**: 255–290.

Coutant CC (ed.). 2001a. *Behavioral Technologies for Fish Guidance*. American Fisheries Society: Bethesda, MD.

Coutant CC. 2001b. Turbulent attraction flows for guiding juvenile salmonids at dams. *American Fisheries Society Symposium* **26**: 57–77.

Coutant CC, Whitney RR. 2000. Fish behavior in relation to passage through hydropower turbines: a review. *Transactions of the American Fisheries Society* **129**: 351–380.

Coutant CC, Whitney RR. 2006. Hydroelectric system development: effects on juvenile and adult migration. In *Return to the River: Restoring Salmon to the Columbia River*, Williams RN (ed.). Elsevier Academic Press: London; 249–324.

Denil G. 1909a. La genèse d'une échelle a poisons nouvelle. *Bulletin Populaire de la Pisciculture Améliorations de la Pêche* **9**: 155–183.

Denil G. 1909b. *Les échelles à poissons et leur application aux barrage de Meuse et d'Ourthe*. Annales des travaux publics de Belgique: Bruxelles.

Denil G. 1938. *La mécanique du poisson de rivière*. Annales des travaux publics de Belgique: Bruxelles.

Ebel WJ. 1985. Review of effects of environmental degradation on the freshwater stages of anadromous fish. In *Habitat Modification and Freshwater Fisheries*, Alabaster JS (ed.). Butterworths: London; 62–79

Ehrenberg JE, Steig TW. 2009. A study of the relationship between tag-signal characteristics and achievable performances in acoustic fish-tag studies. *ICES Journal of Marine Science* **66**: 1278–1283.

Enders EC, Gessel MH, Williams JG. 2009. Development of successful fish passage structures for downstream migrants requires knowledge of their behavioural response to accelerating flow. *Canadian Journal of Fisheries and Aquatic Sciences* **66**: 2109–2117.

Fields P. 1957. Guiding migrant salmon. *The Scientific Monthly* **85**: 10–22.

Francis F. 1870. *Reports on Salmon Ladders: With Original Drawings, Plans, and Sections*. Horace Cox: London.

Gessel MH, Williams JG, Brege DA, Krcma RF, Chambers DR. 1991. Juvenile salmonid guidance at Bonneville Second Powerhouse, 1983–89. *North American Journal of Fisheries Management* **11**: 400–412.

Goodwin RA, Nestler JM, Anderson JJ, Weber LJ. 2007. A new tool to forecast fish movement and passage. *Hydro Review* **26**: 2–8.

Goodwin RA, Nestler JM, Anderson JJ, Weber LJ, Loucks DP. 2006. Forecasting 3-D fish movement behavior using a Eulerian–Lagrangian-agent method (ELAM). *Ecological Modelling* **192**: 197–223.

Gosset C, Travade F, Durif C, Rives J, Elie P. 2005. Tests of two types of bypass for downstream migration of eels at a small hydroelectric power plant. *River Research and Applications* **21**: 1095–1105.

Griffin LE. 1935. Certainties and risks affecting fisheries connected with damming the Columbia River. *Northwest Science* **9**: 25–30.

Haro A, Castro-Santos T, Noreika J, Odeh M. 2004. Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 1590–1601.

Haro A, Odeh M, Noreika J, Castro-Santos T. 1998. Effect of water acceleration on downstream migratory behavior and passage of Atlantic salmon smolts and juvenile American shad at surface bypasses. *Transactions of the American Fisheries Society* **127**: 118–127.

Hockersmith EE, Muir WD, Smith SG, Sandford BP, Perry RW, Adams NS, Rondorf DW. 2003. Comparison of migration rate and survival between radio-tagged and PIT-tagged migrant yearling Chinook salmon in the Snake and Columbia rivers. *North American Journal of Fisheries Management* **23**: 404–413.

Holmes HB, Morton FG. 1939. The success of the Bonneville fishways during their first year of operation. *The Progressive Fish Culturist* **6**: 1–11.

Iwata M. 1995. Downstream migratory behavior of salmonids and its relationship with cortisol and thyroid hormones: a review. *Aquaculture* **135**: 131–139.

Johnson GE, Adams NS, Johnson RL, Rondorf DW, Dauble DD, Barila TY. 2000. Evaluation of the prototype surface bypass for salmonid smolts in spring 1996 and 1997 at Lower Granite Dam on the Snake River, Washington. *Transactions of the American Fisheries Society* **129**: 381–397.

Johnson GE, Anglea SM, Adams NS, Wik TO. 2005. Evaluation of a prototype surface flow bypass for juvenile salmon and steelhead at the powerhouse of Lower Granite Dam, Snake River, Washington, 1996–2000. *North American Journal of Fisheries Management* **25**: 138–151.

Johnson GE, Dauble DD. 2006. Surface flow outlets to protect juvenile salmonids passing through hydropower dams. *Reviews in Fisheries Science* **14**: 213–244.

Johnson RL, Moursund RA. 2000. Evaluation of juvenile salmon behavior at Bonneville Dam, Columbia River, using a multibeam technique. *Aquatic Living Resources* **13**: 313–318.

Karppinen P, Makinen TS, Erkinaro J, Kostin VV, Sadkovskij RV, Lupandin AI, Kaukoranta M. 2002. Migratory and route-seeking behaviour of ascending Atlantic salmon in the regulated River Tuloma. *Hydrobiologia* **483**: 23–30.

Katopodis C. 1992. *Introduction to Fishway Design*. Freshwater Institute, Department of Fisheries and Oceans Canada: Winnipeg, Manitoba; 68

Katopodis C. 2005. Developing a toolkit for fish passage, ecological flow management and fish habitat works. *Journal of Hydraulic Research* **43**: 451–467.

Katopodis C, Derksen AJ, Christensen BL. 1991. Assessment of two Denil fishways for passage of freshwater species. *American Fisheries Society Symposium* **10**: 306–324.

Katopodis C, Ead SA, Straden G, Rajaratnam N. 2005. Structure of flow upstream of vertical angled screens in open channels. *Journal of Hydraulic Engineering* **131**: 294–304.

Keefer ML, Daigle WR, Peery CA, Pennington HT, Lee SR, Moser ML. 2010. Testing adult pacific lamprey performance at structural challenges in fishways. *North American Journal of Fisheries Management* **30**: 376–385.

Keefer ML, Peery CA, Heinrich MJ, Bjornn TC. 2008. Behavior and survival of radio-tagged sockeye salmon during adult migration in the Snake and Salmon rivers. p. 16: Report by U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, University of Idaho. (Available online at: http://www.cnr.uidaho.edu/uiferl/pdf%20reports/2008-6_SNR%20Sockeye%20Report.pdf.) [Accessed October, 2010]

Kemp PS, Gessel MH, Sandford BP, Williams JG. 2006. The behaviour of Pacific salmonid smolts during passage over two experimental weirs under light and dark conditions. *River Research and Applications* **22**: 429–440.

Kemp PS, Gessel MH, Williams JG. 2005. Fine-scale behavioral responses of Pacific salmonid smolts as they encounter divergence and acceleration of flow. *Transactions of the American Fisheries Society* **134**: 390–398.

Kemp PS, Gessel MH, Williams JG. 2008. Response of downstream migrant juvenile Pacific salmonids to accelerating flow and overhead cover. *Hydrobiologia* **609**: 205–217.

Khan LA, Roy EW, Rashid M. 2008. Computational fluid dynamics modelling of forebay hydrodynamics created by a floating juvenile fish collection facility at the Upper Baker River dam, Washington. *River Research and Applications* **24**: 1288–1309.

Knaepkens G, Baekelandt K, Eens M. 2006. Fish pass effectiveness for bullhead (*Cottus gobio*), perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in a regulated lowland river. *Ecology of Freshwater Fish* **15**: 20–29.

Kraabøl M, Arnekleiv JV, Museth J. 2008. Emigration patterns among trout, *Salmo trutta* (L.), kelts and smolts through spillways in a hydroelectric dam. *Fisheries Management and Ecology* **15**: 417–423.

Larinier M. 2002a. Baffle fishways. *Bulletin Francais de la Peche et de la Pisciculture* **364**: 83–101.

Larinier M. 2002b. Biological factors to be taken into account in the design of fishways, the concept of obstruction to upstream migration. *Bulletin Francais de la Peche et de la Pisciculture* **364**: 28–38.

Larinier M. 2002c. Location of fishways. *Bulletin Francais de la Peche et de la Pisciculture* **364**: 39–53.

Larinier M, Travade F. 2002. Downstream migration: problems and facilities. *Bulletin Francais de la Peche et de la Pisciculture* **364**: 181–207.

Lemasson BH, Haefner JW, Bowen MD. 2008. The effect of avoidance behavior on predicting fish passage rates through water diversion structures. *Ecological Modelling* **219**: 178–188.

Liao J. 2007. A review of fish swimming mechanics and behaviour in altered flows. *Philosophical Transactions of the Royal Society, B*. DOI: 10.1098/rstb.2007.2082.

Long CW. 1968. Diel movement and vertical distribution of juvenile anadromous fish in turbine intakes. *Fishery Bulletin* **66**: 599–609.

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.

Mallen-Cooper M. 1999. Developing fishways for nonsalmonid fishes: a case study from the Murray River in Australia. In *Innovations in Fish Passage Technology*, Odeh M (ed.). American Fisheries Society: Bethesda, Maryland; 173–195.

Mallen-Cooper M, Brand DA. 2007. Non-salmonids in a salmonid fishway: what do 50 years of data tell us about past and future fish passage? *Fisheries Management and Ecology* **14**: 319–332.

Mallen-Cooper M, Stuart IG. 2007. Optimising Denil fishways for passage of small and large fishes. *Fisheries Management and Ecology* **14**: 61–71.

McLeod AM, Nemenyi P. 1941. An investigation of fishways. *University of Iowa Studies in Engineering Bulletin* **24**: 1–63.

Monan GE. 1967. Efficiency of a combined electrode and louver array in guiding juvenile steelhead trout (*Salmo gairdneri*). *Transactions of the American Fisheries Society* **96**: 422–423.

Monk BH, Weaver D, Thompson CS, Ossiander FJ. 1989. Effects of flow and weir design on the passage behavior of American shad and salmonids in an experimental fish ladder. *North American Journal of Fisheries Management* **9**: 60–67.

Moser ML, Darazsdi AM, Hall JR. 2000. Improving passage efficiency of adult American shad at low-elevation dams with navigation locks. *North American Journal of Fisheries Management* **20**: 376–385.

Moser ML, Matter AL, Stuehrenberg LC, Bjornn TC. 2002. Use of an extensive radio receiver network to document Pacific lamprey (*Lampetra tridentata*) entrance efficiency at fishways in the Lower Columbia River, USA. *Hydrobiologia* **483**: 45–53.

Nestler JM, Goodwin RA, Smith DL, Anderson JJ, Li S. 2008. Optimum fish passage and guidance designs are based in the hydrogeomorphology of natural rivers. *River Research and Applications* **24**: 148–168.

NMFS. 2004. Anadromous salmonid passage facility guidelines and criteria. National Marine Fisheries Service, Northwest Regional Office, Hydro Division. (Available at ≤http://www.nwr.noaa.gov/1hydrop/hydroweb/ferc.htm≥—Fish Passage Criteria and Guidelines.)

Oldani NO, Baigún CRM. 2002. Performance of a fishway system in a major South American dam on the Parana River (Argentina–Paraguay). *River Research and Applications* **18**: 171–183.

Otterstrøm CV. 1936. Die Turbinen und die abwärts wandernden jungen Lachse und Forellen (sowie Aale) 3. *Teil Journal du Conseil* **11**: 72–93.

Otterstrøm CV. 1942. Turbines and descending salmon and trout smolt (and eels). In *Report of the Danish Biological Station to the Ministry of Agriculture and Fisheries*, Blegvad H (ed.). Dansk Biologisk Station: Copenhagen; 27–37.

Parasiewicz P, Eberstaller J, Weiss S, Schmutz S. 1998. Conceptual guidelines for nature-like bypass channels. In *Fish Migration and Fish Bypasses*, Jungwirth M, Schmutz S, Weiss S (eds.). Fishing News Books: Oxford, UK; 348–362.

Pavlov DS. 1994. The downstream migration of young fishes in rivers—mechanisms and distribution. *Folia Zoologica* **43**: 193–208.

Pavlov DS, Mikheev VN, Lupandin AI, Skorobogatov MA. 2008. Ecological and behavioural influences on juvenile fish migrations in regulated rivers: a review of experimental and field studies. *Hydrobiologia* **609**: 125–138.

Peake S, McKinley RS. 1998. A re-evaluation of swimming performance in juvenile salmonids relative to downstream migration. *Canadian Journal of Fisheries and Aquatic Sciences* **55**: 682–687.

Pedersen LF, Koed A, Malte H. 2008. Swimming performance of wild and F1-hatchery-reared Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) smolts. *Ecology of Freshwater Fish* **17**: 425–431.

Pelicice FM, Agostinho AA. 2008. Fish-passage facilities as ecological traps in large neotropical rivers. *Conservation Biology* **22**: 180–188.

Pompeu PdS, Martinez CB. 2007. Efficiency and selectivity of a trap and truck fish passage system in Brazil. *Neotropical Ichthyology* **5**: 169–176.

Prentice EF, Flagg TA, McCutcheon CS. 1990. Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *American Fisheries Society Symposium* **7**: 317–322.

Pugh JR, Monan GE, Smith JR. 1970. Effect of water velocity on the fish-guiding efficiency of an electrical guiding system. *Fishery Bulletin* **68**: 307–324.

Roscoe DW, Hinch SG. 2010. Effectiveness monitoring of fish passage facilities: historical trends, geographic patterns and future directions. *Fish and Fisheries* **11**: 12–33.

Russon IJ, Kemp PS, Calles O. 2010. Response of downstream migrating adult European eels (*Anguilla anguilla*) to bar racks under experimental conditions. *Ecology of Freshwater Fish* **19**: 197–205. DOI: 10.1111/j.1600-0633.2009.00404.x.

Santos HA, Pompeu PS, Vicentini GS, Martinez CB. 2008. Swimming performance of the freshwater neotropical fish: *Pimelodus maculatus* Lacepede, 1803. *Brazilian Journal of Biology* **68**: 433–439.

Santos HdAe, Pompeu PdS, Martinez CB. 2007. Swimming performance of the migratory Neotropical fish *Leporinus reinhardti* (Characiformes: Anostomidae). *Neotropical Ichthyology* **5**: 139–146.

Schmutz S, Giefing C, Wiesner C. 1998. The efficiency of a nature-like bypass channel for pike-perch (*Stizostedion lucioperca*) in the Marchfeldkanalsystem. *Hydrobiologia* **372**: 355–360.

Schoeneman DE, Pressey RT, Junge CO. 1961. Mortalities of downstream migrant salmon at McNary Dam. *Transactions of the American Fisheries Society* **90**: 58–72.

Silva AT, Santos JM, Ferreira MT, Pinheiro AN, Katopodis C. 2010. Effects of water velocity and turbulence on the behaviour of Iberian barbel (*Luciobarbus bocagei*, Steindachner 1864) in an experimental pool-type fishway. *River Research and Applications*. DOI: 10.1002/rra.1363.

Silva AT, Santos JM, Franco AC, Ferreira MT, Pinheiro AN. 2009. Selection of Iberian barbel *Barbus bocagei* (Steindachner, 1864) for orifices and notches upon different hydraulic configurations in an experimental pool-type fishway. *Journal of Applied Ichthyology* **25**: 173–177.

Smith JR. 1974. Distribution of seaward-migrating Chinook salmon and steelhead trout in the Snake River above Lower Monumental Dam. *Marine Fisheries Review* **36**: 42–45.

Stevenson CH. 1897. The restricted range of shad due to artificial obstructions and its effect on natural reproduction. *Bulletin of the Bureau of Fisheries* **17**: 265–271.

Talbot GB. 1950. A biological study of the effectiveness of the Hell's Gate Fishways. *International Pacific Salmon Fisheries Commission Bulletin* **3**: 1–80.

Tarrade L, Texier A, David L, Larinier M. 2008. Topologies and measurements of turbulent flow in vertical slot fishways. *Hydrobiologia* **609**: 177–188.

Thorpe JE, Morgan RIG, Pretswell D, Higgins PJ. 1988. Movement rhythms in juvenile Atlantic salmon, *Salmo salar* L. *Journal of Fish Biology* **33**: 931–940.

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

Travade F, Larinier M. 2006. French experience in downstream migration devices. In *Free Passage for Aquatic Fauna in Rivers and Other Water Bodies. International DWA-Symposium on Water Resources Management*. Deutsche Vereinigung für Wasserwirtschaft, Abwasser und Abfall: Berlin; 91–99. ISBN 978-3-939057-19-2.

Travade F, Larinier M, Subra S, Gomes P, De-Oliveira E. 2010. Behaviour and passage of European silver eels (*Anguilla anguilla*) at a small hydropower plant during their downstream migration. *Knowledge and Management of Aquatic Ecosystems* **398**: 01–19. DOI: 10.1051/kmae/2010022.

Von Raben K. 1955. Kaplanturbinen und Fische. *Die Wasserwirtschaft* **45**: 196–200.

Williams JG. 2008. Mitigating the effects of high-head dams on the Columbia River, USA: experience from the trenches. *Hydrobiologia* **609**: 241–251.

Zitek A, Schmutz S, Ploner A. 2004. Fish drift in a Danube sidearm-system: II. Seasonal and diurnal patterns. *Journal of Fish Biology* **65**: 1339–1357.