Effects of avoidance behaviour on downstream fish passage through areas of accelerating flow when light and dark

Andrew S. Vowles[a,*], James J. Anderson[b], Michael H. Gessel[c], John G. Williams[b,c] & Paul S. Kemp[a]

[a] *The International Centre for Ecohydraulics Research, Faculty of Engineering and the Environment, University of Southampton, UK.*

[b] *School of Aquatic & Fishery Sciences, University of Washington, Columbia Basin Research, Seattle, USA.*

[c] *National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Seattle, USA.*

[*] Author to whom correspondence should be addressed: E-mail: asv104@soton.ac.uk Tel: +44 (0)23 8059 2700 Fax: +44 (0)23 8059 3166.

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To mitigate for negative impacts of delayed migration it is necessary to understand the causes of avoidance exhibited by animals at behavioural barriers. For downstream migrating juvenile salmon, avoidance of velocity gradients at anthropogenic structures may compromise fitness. Building on previous experimental investigations on salmonid response to velocity gradients, this study aimed to quantify impacts of behaviour on subsequent passage in the presence and absence of visual cues. In an experimental flume, downstream moving juvenile Chinook salmon (*Oncorhynchus tshawytscha*) encountered either a high or low velocity gradient created by an orifice weir, under light (95 lux) or dark (infrared illumination only) conditions. The majority of fish exhibited an observable response on encountering accelerating velocity, with avoidance behaviour elevated when light (45%), in comparison to when dark (12%). More time was spent facing the flow when the velocity gradient was high. Fish that exhibited avoidance were delayed by approximately 8 fold, travelled 3.5 times farther, and experienced a higher mean cumulative velocity gradient across the body length (spatial velocity gradient) prior to successful downstream passage. This study highlights the impact of variation in behaviour on fish passage, and the potential for combined multimodal signals (in this instance visual and mechanosensory) to be used to repel fish, e.g. from hazardous areas, such as turbine intakes. Conversely, by limiting information available, undesirable delay, e.g. at entrances to downstream fish bypasses, may be reduced.

Key words: Environmental stimuli, habitat fragmentation, migration, salmon, smolt, velocity gradient

Periodic or seasonal movements between habitats are common for many terrestrial and aquatic taxa (McFarland, 1999; Skov et al., 2010). In a physically diverse environment, barriers may fragment habitats by impeding migration and dispersal of individuals. Under severe cases, often as a result of anthropogenic development, populations can become small and genetically isolated, increasing their risk of extirpation (Morita & Yamamoto, 2001; Newmark, 1991; Winston, Taylor, & Pigg, 1991). Barriers to animal movements are most often perceived as physical structures such as fences (e.g. for Wildebeest [*Connochaetes* spp.], Williamson & Williamson, 1984), roads (e.g. for foraging hedgehogs [*Erinaceus europaeus*], Rondinini & Doncaster, 2002), and dams (e.g. for migratory fishes, Fukushima, Kameyama, Kaneko, Nakao, & Steel, 2007; Pringle, 2003). However, non-physical features associated with anthropogenic structures or activities that inhibit the dispersal ability of animals by behavioural means can also have profound ecological effects. For example, artificial lights have been shown to hinder the sea-finding performance of hatchling turtles (Witherington & Bjorndal, 1991) and disorient migratory birds (Ogden, 1996). These behavioural barriers may prevent, limit, confuse, and delay movements of animals; leading to increased energetic costs, predation risk, and fragmentation of populations (Garcia de Leaniz, 2008). While mitigation of the negative impacts of physical barriers (e.g. fish passes at hydroelectric dams and wildlife passes under highways) has been widely developed, greater understanding of how associated environmental conditions influence migratory behaviour is needed to enhance conservation efforts to restore habitat connectivity.

Fish are frequently selected as models in behavioural research due to their short generation time providing easy access to subjects at the life stage of interest (e.g. zebrafish *Danio rerio*, Blaser & Goldsteinholm, 2012; Miklósi & Andrew, 2006), because they can be readily bred or obtained from wild stocks, and their use does not generally require large laboratories and sophisticated, expensive equipment (Gouveia et al., 2005). Fish also present discernible behavioural repertoires that are not unmanageably complex (Huntingford, 1986). For anadromous salmonids, the juvenile life-stage is of particular interest as their ability to pass barriers in the downstream direction during seaward migration is not dictated by swimming performance (a significant factor for upstream migrating adults returning to spawn) and hence behaviour is the key determinant of success (Williams, Armstrong, Katopodis, Larinier, & Travade, 2012). They therefore provide an ideal candidate for exploring behavioural avoidance to environmental stimuli encountered during migration.

Actively migrating juvenile salmonids (smolts) have previously been observed to avoid constant and strobe light (Fjeldstad et al., 2012; Nemeth & Anderson, 1992), sound (Knudsen, Schreck, Knapp, Enger, & Sand, 2005), overhead cover (Greenberg, Calles, Andersson, & Engqvist, 2012; Kemp, Gessel, & Williams, 2005a), and combinations of stimuli (e.g. bubbles and sound, Welton, Beaumont, & Clarke, 2002). Hydrodynamic signals also play a prominent role, and smolts have demonstrated avoidance of velocity gradients created by structures (Haro, Odeh, Noreika, & Castro-Santos, 1998 for Atlantic salmon smolts [*Salmo salar*], Enders, Gessel, & Williams, 2009; Enders, Gessel, Anderson, & Williams, 2012; Kemp, Gessel, & Williams, 2005b for Pacific salmon smolts [*Oncorhynchus* spp.]). As smolts are typically observed to migrate down river head first (Davidsen et al., 2005; Kemp, Gessel, & Williams, 2008; Martin et al., 2012), reactions are expressed as a switch from a negative (facing downstream) to positive (facing upstream) rheotactic orientation as a threshold velocity gradient along the body length (spatial velocity gradient) is encountered (Enders et al., 2009; 2012; Vowles & Kemp, 2012). Subsequent responses are variable and include continued progression downstream, or retreating upstream away from the gradient followed by further approaches, and either rejection or continued downstream movement (Kemp & Williams, 2009; Vowles & Kemp, 2012). This oscillatory or milling behaviour, where fish move in and out of areas of hydrodynamic transition, has been described in the field for salmonids (e.g. Johnson & Moursund, 2000 for Pacific salmon smolts in the vicinity of bypass entrances; Svendsen et al., 2011 for Atlantic salmon smolts at water abstraction sites), as well as other migratory fish (e.g. Behrmann-Godel & Eckman, 2003; Winter, Jansen, & Bruijis, 2006 for European eel [*Anguilla anguilla*] approaching hydropower facilities).

For fish, the importance of hydrodynamic relative to other sensory stimuli (e.g. auditory, visual, olfactory; Evans, 1998) remains unclear. For example, overhead cover has induced avoidance in Pacific salmon smolts irrespective of discharge under experimental conditions (Kemp et al. 2005a), and in the wild has been used to enhance guidance of downstream migrant brown trout (*Salmo trutta*) towards preferred passage routes at hydroelectric power dams (Greenberg et al. 2012). Vowles and Kemp (2012) describe elevated avoidance of velocity gradients when presented with a strong light stimulus, suggesting that visual cues may supplement information supplied by the mechanosensory system to enhance responsiveness to hydrodynamic signals. However, the nature of response to single or combinations of stimuli can be highly variable, influenced by factors such as signal strength, external "noise", and internal motivational state (Kemp, Anderson, & Vowles, 2012). Despite the numerous experimental investigations of the behaviour of salmonids at velocity gradients, the extent to which variation in response impacts subsequent passage is yet to be quantified.

Building on the results of Vowles and Kemp (2012) and Kemp et al. (2012), the aim of this study was to determine how variation in behaviour exhibited by juvenile salmonids encountering accelerating velocity gradients, when light and dark, influenced subsequent downstream migration. It was predicted that under a more abrupt accelerating velocity gradient and when light, downstream moving fish would: 1) exhibit greater avoidance by expressing more oscillatory behaviours, and 2) spend a greater proportion of time positively rheotactic. Further, fish that exhibit greater avoidance were expected to: 3) travel greater distances while assessing the gradient, 4) take longer to pass downstream, and 5) experience a higher mean cumulative spatial velocity gradient along the body prior to passage. In this experimental study downstream migrating juvenile Chinook salmon (*O. tshawytscha*) encountered either a low or high velocity gradient created under two discharge regimes. The hydrodynamic signals were presented both when dark and light, the latter providing the opportunity to employ both mechanosensory and visual modalities. The study findings highlight the impact variation in response exhibited by downstream moving fish encountering behavioural barriers has on subsequent migration, and the requirement to manipulate stimuli to influence behaviour in a manner desirable from a fisheries management perspective.

METHODS

Study Area and Flume Setup

At McNary Dam on the Columbia River, USA (45°55' N, 119°17' W) a Perspex barrier (152 cm wide, 45.8 cm high) with a rectangular orifice (45.8 cm wide, 7.7 cm high) was centrally positioned perpendicular to the flow on the channel floor of a through-flow flume (12.0 x 1.52 x 0.75 m; Fig. 1). The flume was supplied with water from the McNary Dam forebay and an accelerating velocity gradient was created upstream of the orifice. A high (30 litres s^{-1}) or low (10 litres s^{-1}) discharge created two different velocity gradients which are subsequently referred to as high-light, high-dark, low-light or low-dark treatments dependent on whether the trial was conducted under light (mean level = 95.4 lux) or dark (infrared illumination only) conditions. When dark, observers were unable to see, and as salmonids have a similar spectral sensitivity to humans (Ali, 1961) it is assumed that this was the case for the test fish also.

Within the flume, a test area was created using a wire mesh screen spanning the channel width placed 1.20 m upstream of the barrier at a point where there was no discernible velocity gradient. A 0.15 m diameter PVC pipe entered the test area 1.10 m upstream of the barrier. The pipe extended 0.91 m upstream of the mesh screen and into a 1.20 x 1.20 m perforated and submerged acclimation tank, into which the fish were placed prior to the start of each trial (Fig. 1).

The water depth within the test area was maintained constant and equal to barrier height independent of discharge by placing a weir 3.6 m downstream of the barrier under the low velocity gradient treatment. Mean (± SD) water velocity was measured using an Acoustic Doppler Velocimeter (ADV) (Vectrino+, Nortek AS), sampling at 25 Hz for 60 seconds with a sample volume set at 0.31 cm^3. Microsoft Office Excel (2007) was used to post process ADV data, and incorporated a maximum / minimum threshold filter (as described in Cea, Puertas, Pena, 2007). The three planes of water velocity were measured simultaneously allowing the mean velocity vector (*V*) to be calculated as:

$$V = \sqrt{\bar{u}^2 + \bar{v}^2 + \bar{w}^2} \tag{1}$$

where $\overline{u}$, $\overline{v}$ and $\overline{w}$ are the mean longitudinal, lateral and vertical velocity components (m s^{-1}), respectively. Mean velocity vectors were plotted using spline interpolation in the Spatial Analyst tool in ArcGIS 10 (ESRI, Redlands, CA, USA).

Mean water velocity in the test area was 0.23 (± 0.16) and 0.11 (± 0.08) m s^{-1} for the high and low velocity gradient treatments, respectively. At approximately one body length upstream from the orifice (11 cm), a distance where the orifice may be considered detectable by the fish (Coombs, 1999), the rate of water acceleration was greater during the high (9.98 m s^{-2}) compared to low (6.87 m s^{-2}) discharge. The gradient extended further upstream and a higher maximum velocity was reached during the high (1.53 m s^{-1}) compared to low (1.23 m s^{-1}) velocity gradient treatment (Fig. 2).

An overhead low light CCD video camera was placed 1.3 m above the flume and directly over the test area to monitor sub-yearling Chinook salmon behaviour during trials. Overhead artificial fluorescent lighting or four 50 W infrared lighting units (emitting infrared light at 840-1200 nm), mounted above the flume, were used during light and dark treatments, respectively. Water temperature increased from 18.2 to 19.4°C over the nine day study period.

Experimental Protocol

A total of 23 trials were conducted between 1 and 9 July 2009. Between two and four 1-hour trials were conducted per day (alternating between the four treatments) between 08.00 and 13.00 hours. This was considered acceptable because Pacific salmon spp. have been observed to migrate during both day and night (Ledgerwood, Ryan, Dawley, Nunnallee, & Ferguson, 2004; Moser, Olson, Quinn, 1991). Physical screens diverted actively migrating fish approaching the dam into a gatewell where they subsequently entered the juvenile bypass channel through one of 84 (0.3 m diameter) orifices (Gessel, Sandford, & Ferguson, 2004). At one of these orifices, water was routed to a holding tank to collect the fish which were of mixed origin (i.e. wild and hatchery), as is typical for the Columbia River Chinook salmon population. Trials commenced after collection of 30 fish, which took a maximum of approximately one hour. For each trial, five fish were randomly netted from the holding tank and transported to the test flume. Fish were then placed into the submerged acclimation tank from which they could volitionally exit via the PVC pipe. The conditions in the acclimation tank were the same as in the test area of the flume, allowing fish time to adjust to the light intensity and recover from effects of handling before they entered the test area. An additional five fish were added to the acclimation tank every 10 minutes for the first 50 minutes of each trial. All fish that passed through the orifice in the test flume were collected downstream, anaesthetized in 10 mg litre^{-1} solution of tricaine methanesulfonate (MS-222), and measured. Each fish was used once during the study and returned to the bypass system after recovering from anaesthesia (a maximum of approximately 2 hours after collection). The experimental protocol was assessed and approved by the University of Southampton Ethics Committee. Permission to handle fish protected under the U.S. Endangered Species Act was provided from Washington (permit no: 09-198) and Oregon (permit no: 14550) State, and under National Oceanic and Atmospheric Administration Permit 2-09-NWFSC9.

Fish Behaviour

Video footage was post processed at a rate of 30 frames per second using either custom written software (FishTrack, Matlab v7.9; Mathworks, Natick, MA, USA) or Logger Pro Version 3.8.2 (Vernier Software, Beaverton, OR, USA). FishTrack automatically tracked head and tail locations for each video frame during passage through the test area. Automated tracking operated on a colour contrast principle and was not possible for all trials (e.g. due to image quality during dark treatments). Logger Pro was used to manually (also on a frame wise basis) track head and tail locations for fish under conditions where automated tracking was not possible. A sample comparison of an automated and manually tracked video indicated little difference (< 5%) in coordinate position between methods.

Nature of response

Five distinct responses were expressed as fish initially encountered the accelerating velocity gradients. These were defined as either avoidance, and consisted of 1) 'Retreat' and 2) 'Reject'; or non-avoidance behaviours, which consisted of 3) 'React', 4) 'Drift-with-bulk-flow', and 5) 'Swim-with-bulk-flow'. Behaviours were ranked in terms of magnitude of avoidance (Fig. 3).

Orientation

Using the coordinates derived from the tracking software, the rheotactic orientation (*RO*) of the fish was calculated for each frame as:

$$RO = arctan\left((Head_x - Tail_x)/(Head_y - Tail_y)\right)180/\pi \qquad (2)$$

where *arctan* is the inverse tangent trigonomic function used to calculate the angle between head and tail locations. $Head_x$, $Tail_x$, $Head_y$, and $Tail_y$ represent head and tail coordinates on the x and y axis, respectively. Based on the angle between head and tail locations, the proportion of time spent positively or negatively rheotactic during trials was calculated. Fish were only observed to be perpendicular to the flow as they switched orientation, and were deemed to be positively oriented until the point their head was further downstream than their tail.

Distance travelled

The ground distance (i.e. not accounting for flow velocity) fish travelled (*D*), relative to the earth frame of reference, between successive frames was calculated as:

$$D = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2} \tag{3}$$

where x_1 and y_1 are the head coordinates on the x and y axis respectively for a specific video frame, and x_2 and y_2 are the head coordinates for the following frame. The distance travelled prior to passing the barrier was calculated for each trial by summing the distances between consecutive points.

Time to pass

Time to pass was the period between a fish's head entering the test area and exiting through the orifice.

Spatial velocity gradient

Fish tracks, generated from the coordinates derived from the tracking software, were overlain onto hydraulic profiles to enable the extraction of underlying velocity data (i.e. the mean velocity vector [*V*] at head and tail locations) for each coordinate position. This allowed the spatial velocity gradient (SVG) across a fish's body to be calculated, using the formula described by Enders et al. (2009):

$$\mathrm{SVG} = \frac{|V_H - V_T|}{L} \tag{4}$$

where V_H and V_T represent the velocity at the fish's head and tail position respectively, and L is the total length of the fish. The SVG experienced by smolts while passing through the flume was quantified as the cumulative SVG prior to passage, and was calculated by summing SVG values for each fish prior to passage through the orifice.

Statistical Analysis

Tests of normality and homogeneity of variance were performed using a Shapiro-Wilk and Levene's test, respectively. Non-normal data were normalized using Box-Cox transformation; when this was unsuccessful non-parametric tests were performed. Proportion of time spent positively rheotactic was arcsine square root transformed prior to statistical analysis. Binary logistic regression determined the influence of velocity gradient and illumination on (1) nature of response. A Mann-Whitney U or Independent samples *t*-test (dependent on distribution of the data) determined the influence of velocity gradient and illumination on (2) orientation; and nature of response on (3) distance travelled, (4) time to pass, and (5) spatial velocity gradient.

RESULTS

Not all fish entered the test area (39%, 53%, 21%, and 67% for the high-light, high-dark, low-light, and low-dark treatments, respectively, did not exit the acclimation tank). Of those that entered, 19.5%, 48%, 16%, and 52% of fish for the aforementioned treatments were included in the analysis (mean fork length ± SD = 107.6 ± 9.7 mm; Table 1), with the remaining fish either not passing the orifice or exhibiting group behaviour (i.e. the aggregation of two or more fish that forms when they react to each other by remaining in close proximity, Keenleyside, 1955).

For the 111 fish included in the analysis, illumination (Wald = 6.20, $P < 0.05$) rather than velocity gradient (Wald = 0.15, $P = 0.697$) predicted nature of response (avoidance or non-avoidance) (Logistic Regression: Nagelkerke $R^2 = .21$, $\chi^2_3 = 16.66$, $P = 0.001$). Non-avoidance was more common than avoidance during all treatments, but the percentage of avoidance responses increased when light (Fig. 4). When dark, 88% of responses were non-avoidant, compared to 55% when light. The most common response expressed as smolts initially encountered the gradient under the high-light treatment was 'Retreat'. 'React' was more common during high-dark and low-dark, while 'Retreat' and 'React' were expressed equally during the low-light treatment (Table 1).

Under the high velocity gradient treatment, more time on average (mean ± SD: 25.6 ± 72.1 s or 42 ± 36%) was spent positively rheotactic compared to fish passing through the low velocity gradient (mean ± SD: 6.3 ± 15.0 s or 22 ± 24%) (Mann-Whitney U: $U = 1020$, $N_1 = 66$, $N_2 = 45$, $P < 0.01$). Illumination had no effect on orientation (Mann-Whitney U: $U = 1238$, $N_1 = 44$, $N_2 = 67$, $P = 0.153$).

Fish that exhibited an avoidance response travelled on average 3.5 times farther than those that did not (Mann-Whitney U: $U = 323$, $N_1 = 28$, $N_2 = 83$, $P < 0.001$; Fig. 5).

The time taken to pass the test area was highly skewed (Fig. 6), with most (85.6%) fish doing so within the first 30 seconds of entering (mean time ± SD = 8.14 ± 6.19 s). Fish taking more than 30 seconds were delayed by an average of 14 times (mean time ± SD = 114.11 ± 117.38 s). Fish were delayed approximately 8 times longer when expressing avoidance responses compared to those exhibiting non-avoidance behaviours (Independent samples *t* test: $t_{109} = 7.431$, $P < 0.001$; Fig. 7).

Fish experienced a higher mean SVG prior to passage when expressing avoidance rather than non-avoidance behaviours (Independent samples *t* test: $t_{109} = 6.514$, $P < 0.001$; Fig. 8).

DISCUSSION

This study assessed the response of downstream moving juvenile Chinook salmon to velocity gradients, behavioural barriers commonly encountered during the migration to the ocean, in the presence and absences of visual cues, and quantified the influence of response type on passage. It was predicted that avoidance, and thus the impediment to downstream migration, would be greater on encountering a stronger hydrodynamic signal and when reinforced by visual cues when light. The results obtained support the findings of others; smolts exhibited avoidance on encountering velocity gradients (Enders et al., 2009; Haro et al., 1998; Kemp et al., 2005b; Kemp & Williams, 2009) and this effect was reinforced when multimodal signals were presented (as demonstrated by Vowles & Kemp, 2012). Further progress was made through the identification of a hierarchy of behaviours that describes magnitude of avoidance, and that the variation in response type, influenced primarily by visual signals, impacted migratory (passage) progress.

During this study not all fish entered the test area, with a larger proportion remaining in the acclimation tank when dark. For those in the test area, a higher proportion passed the orifice as singletons when dark, while there was a greater propensity to school when light. These broad behavioural patterns were also observed by Kemp and Williams (2009), who show Pacific salmon smolts to be more active and form schools when under illuminated conditions in an experimental flume. The degree to which schooling influences migratory progress (and overall fitness) for an individual group member encountering behavioural barriers presents a substantial challenge for future research in this area of behavioural ecology.

Although the number of fish that encountered the hydrodynamic signal (accelerating velocity) varied between treatment, their response was largely predictable. The smolts tended to move downstream head first and then switch orientation on experiencing a change in velocity along their body (a strategy also observed by Enders et al., 2009 and Kemp et al., 2005b), although when dark passive movement through the orifice was more common than when light. The proportion of time spent facing the flow was higher when the velocity gradient was more abrupt. By maintaining positive rheotaxis, control over downstream movement is enhanced, enabling fish to maintain position while acquiring information about their surroundings, and to burst upstream should potentially harmful conditions be encountered (Enders et al., 2009; Kemp et al., 2005b). However, there are costs as well as benefits, as the delay at barriers may elevate predation risk (Poe, Hansel, Vigg, Palmer, & Prendergast, 1991), energy expenditure (Schilt, 2007), risk of disease if fish congregate at high densities (Garcia de Leaniz, 2008), and propensity to pass through suboptimal routes (Castro-Santos & Haro, 2003; Svendsen et al., 2011).

Fish were more responsive when visual in addition to hydrodynamic signals were presented, supporting the findings of Vowles and Kemp (2012) for downstream moving brown trout. While fish are highly dependent on the mechanosensory system when dark, this study indicated that visual cues, when available, may have been more important than the hydrodynamic signals. Combined multisensory stimuli can enhance detectability, discriminability and memorability of a stimulus within the receiving animal (Rowe, 1999). For example, multimodal signals enhance predator avoidance (e.g. Rowe & Guilford, 1999; Ward & Mehner, 2010), mate selection (e.g. Uetz, Roberts, & Taylor, 2009), and communication (e.g. Partan, Larco, & Owens, 2009). The importance of multimodal cues during animal migrations has received little attention, but based on the findings presented here is an important factor to consider when mitigating for impeded movement of fish at anthropogenic barriers.

Despite a broad predictability, the nature of response to the velocity gradient varied when considered at a fine-scale, reflecting a hierarchy of behaviour. Avoidance behaviours were more common when fish were able to visually fix on their surroundings. Conversely, strength of the hydrodynamic signal did not influence response type exhibited. Oscillatory or milling behaviour (retreat), during which fish moved in and out of areas of hydrodynamic transition, was the most common response type when the acceleration of velocity was abrupt under illuminated conditions (supporting the findings of Kemp & Williams, 2009). Switches in orientation ('React'), often from negative to positive rheotaxis, was equally as common as milling in response to a low velocity gradient when light, and more frequent when dark. Milling behaviour may facilitate habituation to the hydrodynamic gradient, a process suggested to take longer with increasing signal strength in which conditions created deviate further from the background levels (Goodwin, Nestler, Anderson, Weber, & Loucks, 2006;

Nestler, Goodwin, Smith, Anderson, & Li, 2008). By milling, habituation will be achieved through exposure to the gradient, until some threshold is exceeded at which point avoidance is no longer induced. Indeed, fish expressing avoidance encountered a higher mean cumulative spatial velocity gradient (SVG) along their body length prior to passage. To date, the idea that fish must habituate to hydrodynamic conditions at behavioural barriers prior to continued downstream movement remains an untested hypothesis. However, it may, in part, explain the variable behaviour observed during the current study, and why the fish passed at locations they initially rejected.

The findings of this experimental study, in which behaviour is quantified at a fine-resolution under controlled conditions, provides an explanation for several observations made in the field (see below) and thus has important application for management. The exhibition of avoidance behaviour had a dramatic impact on subsequent passage. Fish that avoided the velocity gradients were delayed by approximately 8 fold, travelled 3.5 times farther, and encountered a higher mean cumulative SVG along their body length. Likewise, downstream migrating fish are commonly impeded at river infrastructure. For example, up to 20% of radio tagged Chinook salmon suffered extensive delay (for 7 or more days) within a hydropower dam forebay, during which time they exhibited considerable lateral and upstream movement (Venditti, Rondorf, & Kraut, 2000). Further, increased avoidance and delay in the presence of both hydrodynamic and visual cues may explain greater delay observed for tagged Chinook salmon smolts at a hydropower dam during daylight hours, despite travelling through the reservoir during both day and night (Beeman & Maule, 2001).

The current study will contribute to development of mitigation technology and strategies to reduce unwanted delay (e.g. at the entrance to fish bypass systems) where environmental factors, such as hydrodynamics, induce avoidance. As multimodal signals increase delay, one approach might be to reduce the information received, e.g. limit access to visual cues. An alternative may be to provide additional antagonistic sensory information that masks the target stimuli and reduces sensitivity through provision of exogenous noise (see Kemp et al., 2012). Conversely, the information obtained may help design technology to repel fish from hazardous areas, such as at turbine intakes, by using multimodal signals in combination to enhance avoidance.

There is much potential for future fundamental research in this area of behavioural ecology to provide the information needed on which to base sound application to environmental engineering and management. First, the response of multiple species of migrating fish to a suite of environmental stimuli operating through different sensory modalities (e.g. visual, mechanosensory, olfactory, auditory), in isolation and in combination should be quantified under controlled experimental conditions (Kemp, 2012). Once this has been defined, there is a need to investigate the influence of more complex biotic factors, particularly the presence / density of schooling conspecifics, but also the health and motivational status of the individual, on the nature of response exhibited. The research should be validated through robust field studies, culminating in the development and testing of devices that allow migratory trajectories of fish encountering river infrastructure to be manipulated.

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Figure Captions:

Figure 1.(a) Plan view of the experimental channel used to observe migrant juvenile salmon behaviour under two velocity gradients during both dark and light conditions, (b) side view of orifice weir, opening 7.7 cm high.

Figure 2. Velocity (*V*) profile upstream of a weir and orifice installed in an experimental flume during (a) high and (b) low velocity gradient treatments. Lines indicate (a) 'Reject' and (b) 'Retreat' behaviours exhibited by downstream moving juvenile Chinook salmon, respectively.

Figure 3. Hierarchy of behavioural avoidance expressed as smolts initially encountered an accelerating flow created by an orifice weir in an experimental flume. Grey and clear segments indicate avoidance and non-avoidance behaviours, respectively.

Figure 4. Percentage of smolts exhibiting avoidance behaviours when first approaching an orifice weir in an experimental flume.

Figure 5. Mean distance travelled by smolts prior to passing the test area (+ 1 SE) in relation to the nature of response expressed on first encountering accelerating velocity created by the orifice weir in an experimental flume.

Figure 6. Frequency distribution of time taken for smolts to pass through the orifice weir located within an experimental flume under (a) low-dark, (b) low-light, (c) high-dark, and (d)

high-light treatments. An Inverse Gaussian distribution probability density for the different treatments overlying the histograms illustrates the skew in passage time.

Figure 7. Time taken for smolts to pass the test area of flume (+ 1 SE) in relation to the nature of response expressed on first encountering the accelerating velocity gradients.

Figure 8. Mean cumulative spatial velocity gradient (SVG) across the body length (cm s^{-1} cm^{-1}) prior to passage, (+ 1 SE) in relation to the response type expressed on encountering the accelerating velocity gradients.

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Figure 1

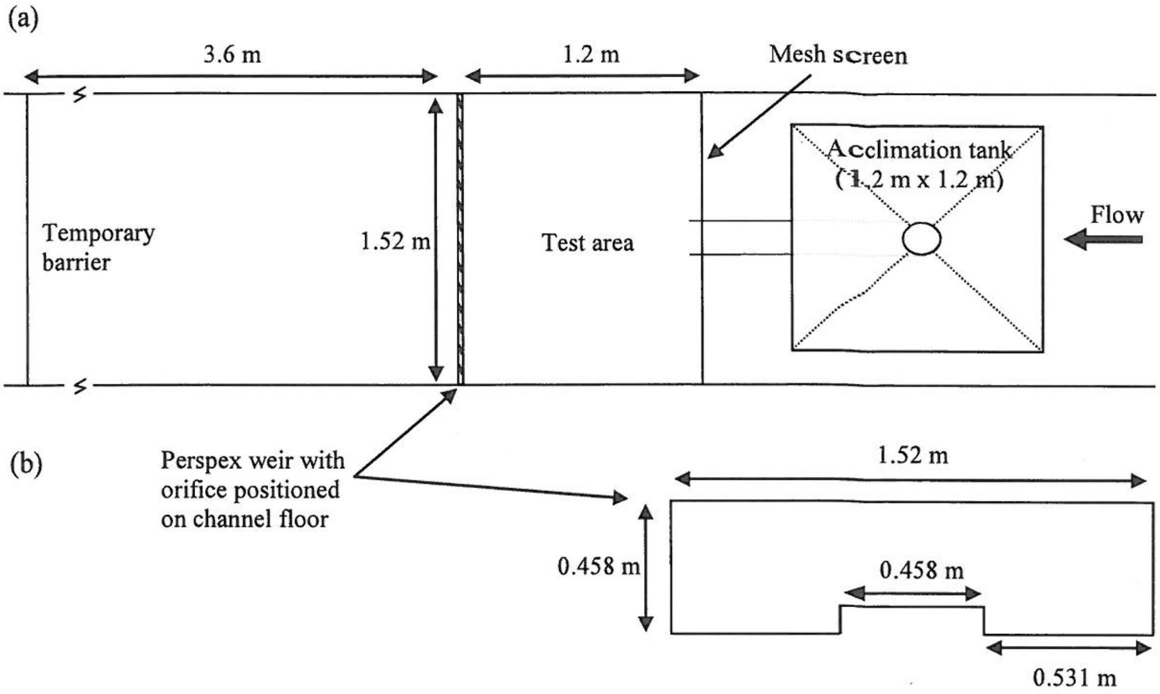

(a)
3.6 m
1.2 m
Mesh screen
Acclimation tank
(1.2 m x 1.2 m)
Flow
Temporary barrier
1.52 m
Test area
(b)
Perspex weir with orifice positioned on channel floor
1.52 m
0.458 m
0.458 m
0.531 m

Figure 2

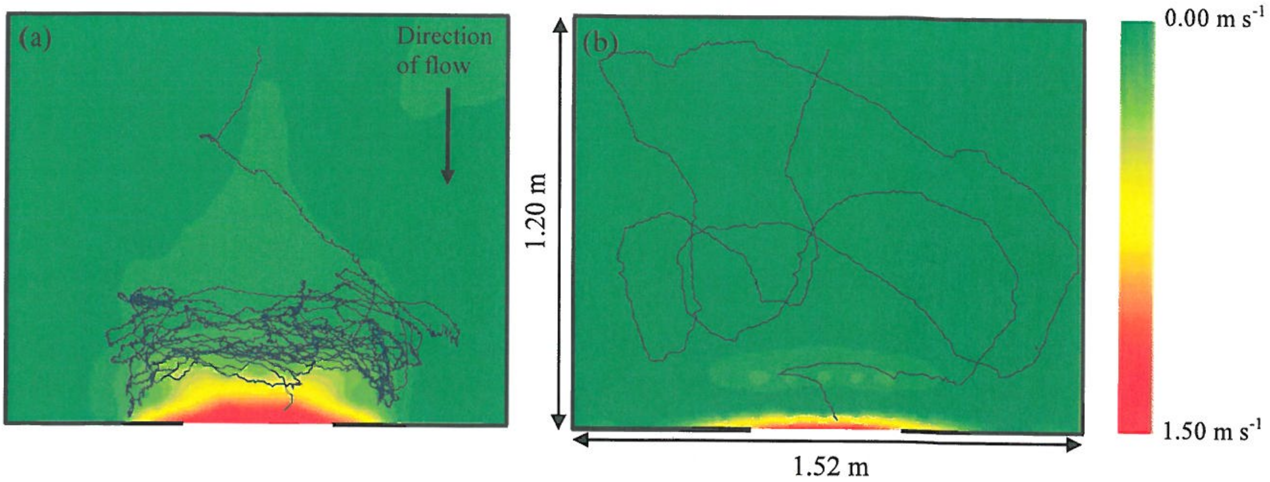


Figure 3

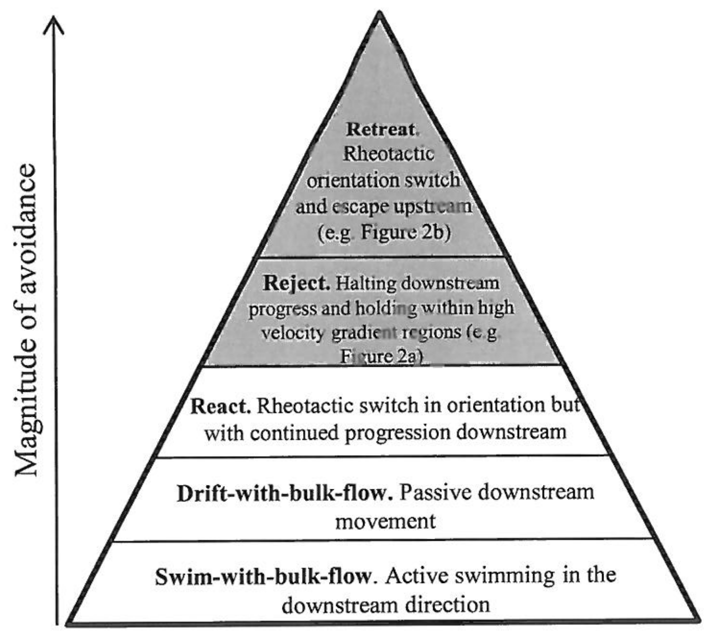

Magnitude of avoidance
Retreat. Rheotactic orientation switch and escape upstream (e.g. Figure 2b)
Reject. Halting downstream progress and holding within high velocity gradient regions (e.g. Figure 2a)
React. Rheotactic switch in orientation but with continued progression downstream
Drift-with-bulk-flow. Passive downstream movement
Swim-with-bulk-flow. Active swimming in the downstream direction

Figure 4

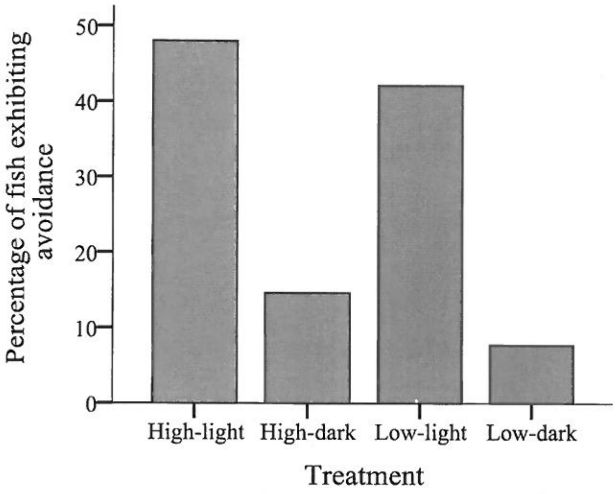

Percentage of fish exhibiting avoidance
50
40
30
20
10
0
High-light
High-dark
Low-light
Low-dark
Treatment

Figure 5

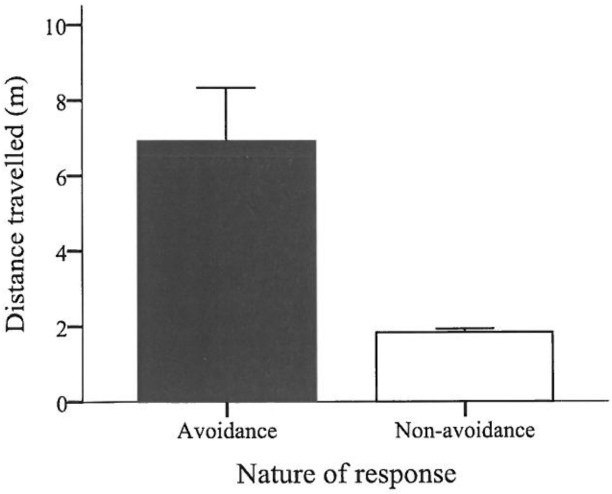

Distance travelled (m)
10
8
6
4
2
0
Avoidance
Non-avoidance
Nature of response

Figure 6

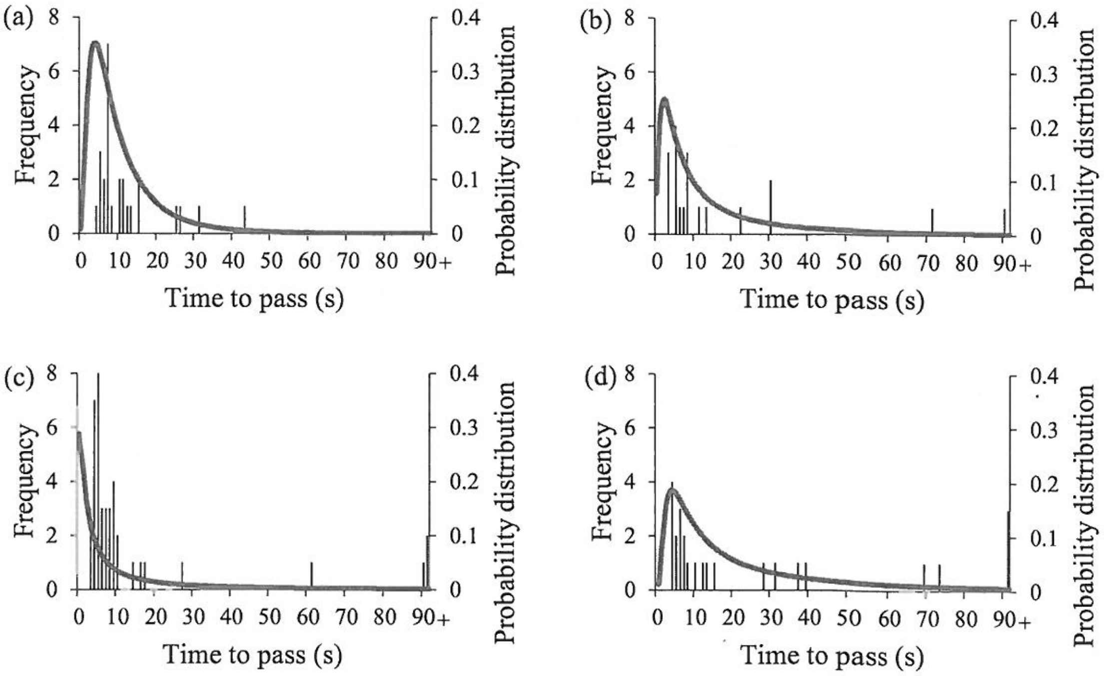
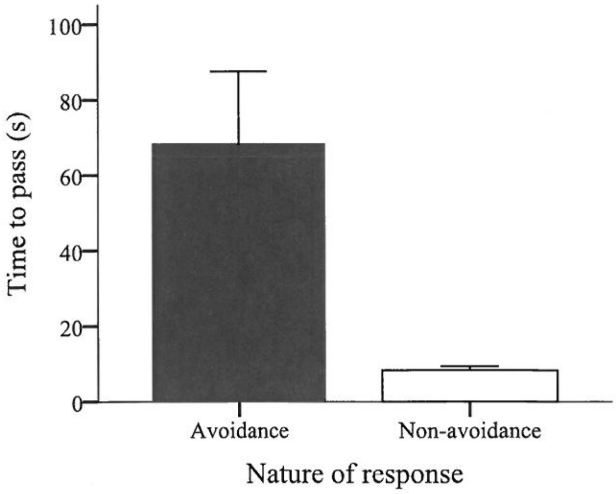
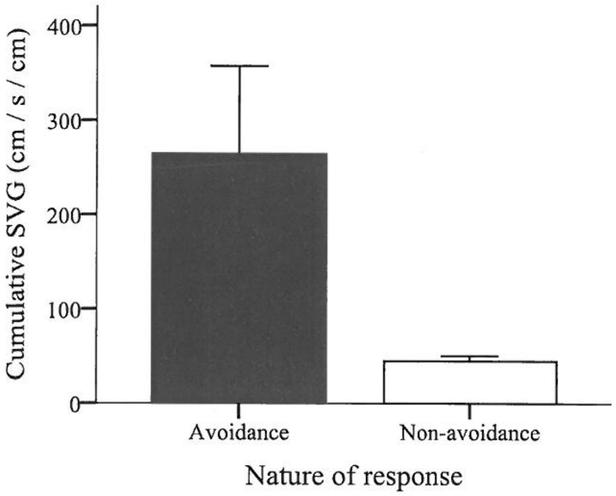

(a)
8
6
4
2
0
Frequency
0.4
0.3
0.2
0.1
0
Probability distribution
0 10 20 30 40 50 60 70 80 90+
Time to pass (s)
(b)
8
6
4
2
0
Frequency
0.4
0.3
0.2
0.1
0
Probability distribution
0 10 20 30 40 50 60 70 80 90+
Time to pass (s)
(c)
8
6
4
2
0
Frequency
0.4
0.3
0.2
0.1
0
Probability distribution
0 10 20 30 40 50 60 70 80 90+
Time to pass (s)
(d)
8
6
4
2
0
Frequency
0.4
0.3
0.2
0.1
0
Probability distribution
0 10 20 30 40 50 60 70 80 90+
Time to pass (s)

Figure 7


Time to pass (s)
100
80
60
40
20
0
Avoidance
Non-avoidance
Nature of response


Cumulative SVG (cm / s / cm)
400
300
200
100
0
Avoidance
Non-avoidance
Nature of response