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

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To mitigate 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 a low velocity gradient created by an orifice weir, under light (95 lx) 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 eight-fold, travelled 3.5 times further, 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, for example from hazardous areas such as turbine intakes. Conversely, by limiting information available, undesirable delay, for example at entrances to downstream fish bypasses, may be reduced.

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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. In 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, nonphysical 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 owing 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,

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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, Anderson, & Williams, 2012; Enders, Gessel, & Williams, 2009; 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 when 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 & Eckmann, 2003; Winter, Jansen, & Bruijs, 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) described 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 increase 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 affects 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. We 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. Furthermore, fish that exhibited 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, *Oncorhynchus 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 Set-up

At McNary Dam on the Columbia River, U.S.A. (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 × 1.52 and 0.75 m high; 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) or low (10 litres/s) 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 lx) 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 × 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, Rud, Norway), sampling at 25 Hz for 60 s with a sample volume set at 0.31 cm³. 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:

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

where $\overline{u}$, $\overline{v}$ and $\overline{w}$ are the mean longitudinal, lateral and vertical velocity components (m/s), respectively. Mean velocity vectors