



Context-dependent responses to turbulence for an anguilliform swimming fish, Pacific lamprey, during passage of an experimental vertical-slot weir



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ABSTRACT

Fish passage systems (fishways) have become the most common mitigation tool for improving the connectivity of migratory fish populations in ecosystems with barriers to movement. Because fishways often have high-velocity and high-turbulence environments, fish should seek low-energy movement paths during passage. We tested this hypothesis by analyzing the swimming paths of 90 adult Pacific lamprey (*Entosphenus tridentatus*) in response to hydraulic conditions when passing a vertical-slot weir in an experimental fishway. Varying hydraulic conditions were achieved by manipulating three variables: water velocity (1.2, 1.8, 2.4 m/s), vertical-slot length (0.33 m, 0.66 m, 1.00 m), and presence or absence of a turbulence-inducing structure. Turbulence parameters, such as turbulent kinetic energy (*TKE*), were quantified using an Acoustic Doppler Velocimeter (*ADV*). Pacific lamprey exhibited context-dependent behaviors in response to turbulence whereby lamprey were more likely to move towards areas of lower turbulence along their swimming paths, but only as the surrounding turbulence within the vertical-slot increased. In contrast, when the surrounding turbulence within the vertical-slot was low, Pacific lamprey became more likely to move towards areas of higher turbulence. The ‘turbulence-avoidance’ behaviors likely allowed passage of the hydraulic obstacle by reducing energy expenditure or physiological stress, while the ‘turbulence-attraction’ behaviors may have resulted from lamprey using turbulence as a mechanism for upstream orientation. Overall, our results provide new insight into how fish may use turbulence as an important sensory modality for perceiving the aquatic environment.

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1. Introduction

Evaluating how fish respond to their hydraulic environment can be challenging because fish behavior is often as dynamic as the environment. The biological consequences of hydraulic parameters can often be a “double-edged” sword with both positive and negative consequences (Liao 2007; Lacey et al., 2012). Water velocity, for example, has been frequently cited as an important factor that affects swimming performance and limits upstream distribution because passing through high velocities requires intensive energy use or may exceed fish swimming speed (Haro et al., 2004; Rodriguez et al., 2006; Sanz-Ronda et al., 2015). Turbulence also negatively influences swimming performance because increased work is required to traverse chaotic flows (Hinch and Rand 1998;

Enders et al., 2003; Hockley et al., 2013). Notably, both water velocity and turbulence can also positively influence fish behavior by creating attraction cues (i.e., rheotaxis; Bunt et al., 2012; Silva et al., 2012), increasing individual motivation (Castro-Santos 2004), and providing potential energy to assist in upstream propulsion in complex flows (Lindberg et al., 2015). This presents an interesting trade-off for both fish and fishway designers, where hydraulic conditions have to be balanced between potential physiological limitations and the necessary sensory cues for upstream orientation.

The migration corridors for many riverine fish species have been impounded and blocked through the construction of dams. The primary solution for maintaining connectivity of river corridors has been the development of fish passage systems, or fishways (Roscoe and Hinch 2010; Bunt et al., 2012; Noonan et al., 2012). Fishways typically create environments of high velocity and turbulence, which are necessary to compensate for the often large head differential that occurs at these dams. As a result, many of

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the flow conditions and structural elements within fishways create challenging passage conditions (Marriner et al., 2014; Goettel et al., 2013). The majority of fishway designs were constructed specifically for salmonid species (e.g., *Oncorhynchus* and *Salmo* spp.) capable of high burst swim speeds and do not account for biological differences in swimming across other taxa. Hence, it is believed that these challenging environments create conditions that are simply too taxing for many non-salmonid species to overcome (Silva et al., 2011, 2012; Noonan et al., 2012).

Many anadromous fish species exhibit long distance migrations that require significant energetic investments (Dingle, 2014). Some species cease feeding during migration and thus have a finite amount of energetic reserves, and it seems likely that fish seeking to minimize energy expenditure would have an evolutionary advantage (Kemp et al., 2003; McElory et al., 2012). Additionally, avoiding strenuous swimming activity, such as prolonged burst swimming and high endurance rates (i.e., reduced aerobic capacity), can reduce the mechanisms of physiological stress (e.g., acidosis) that prevent upstream progress (Hasler et al., 2009; Pon et al., 2009). Indeed, studies with Pacific salmon (*Oncorhynchus* spp.) have documented energy conserving strategies in natural riverine environments, which include using reverse-flow currents, swimming at metabolically optimum speeds, and using burst-and-coast swimming (Hinch and Rand, 1998, 2000; Standen et al., 2002, 2004). Perhaps the most obvious strategy is simply to follow a swimming path with lower velocities and lower turbulence, in order to minimize associated transport costs (Standen et al., 2004; Lindberg et al., 2015). We suspect that such behaviors would be prevalent in environments with high swimming demands (e.g., fishways) and for species with low swimming speeds and low aerobic capacity (e.g., anguilliform swimmers; Mesa et al., 2003; Katopodis and Gervais, 2012).

One species that has poor passage in fishways is Pacific lamprey (*Entosphenus tridentatus*), which is an anadromous species native to western North America and the northern Pacific Rim. Only ~50% of Pacific lamprey successfully pass many dams on the Columbia River, U.S.A. and the species struggles to pass individual fishway segments at these dams (Moser et al., 2002; Keefer et al., 2009, 2013b). Studies seeking to identify the mechanisms that explain the limited passage of lamprey have provided some support for the role of velocity barriers. Specifically, passage conditions associated with high water velocity and high turbulence have been shown to exceed the swimming capabilities of lamprey and thus reduce passage at some locations (Keefer et al., 2010; Kirk et al., 2015, 2016). As a result, we hypothesize that lamprey should seek to optimize their swimming movements by selecting paths of low velocity and low turbulence in order to avoid conditions that exceed their capabilities.

Our primary objective was to evaluate how the fine-scale movement decisions of Pacific lamprey were influenced by varying levels of velocity and turbulence when passing through a single passage structure. Pacific lamprey are a good model species for asking questions about responses to flow field dynamics because the species is predominately nocturnal and is likely more dependent on flow cues (i.e., rheotaxis) during upstream migrations than visual cues (Binder and McDonald, 2007; Keefer et al., 2013a). We hypothesized that individual lamprey would be more likely to move towards areas of lower turbulence along their swimming paths when facing greater turbulence. Although we focus predominately on the increasing intensity of turbulence variables, we also used principal components analysis (PCA) to statistically control for covariation among metrics of velocity and turbulence and identify relationships among them.

A secondary objective was to identify how hydraulic variables explained the attachment behaviors (attachment probability, attachment duration) observed for Pacific lamprey, which use their

suctorial oral disc for attaching to surfaces under high flow conditions and during exhaustive swimming (Kemp et al., 2009; Keefer et al., 2010; Kirk et al., 2016). We used attachment behaviors as a marker for evaluating the relationships between hydraulic stimuli, movement behaviors, and physiological condition as recommended by Gao et al. (2016). Pacific lamprey attachments were evaluated with regards to both coarse-scale ('bulk' or mean turbulence conditions) and fine-scale (spatial differences) hydraulic patterns because results from a companion analysis found non-linear relationships in attachment behaviors that may have been associated with fine-scale hydraulics (Kirk et al., 2016). We hypothesized that: 1) the probability of attachment and attachment duration would increase with turbulence; and that 2) lamprey would select different attachment locations in response to increasing turbulence.

2. Methods

2.1. Study site and experimental procedure

We analyzed Pacific lamprey movements in relation to fine-scale hydraulics using biological data collected during a companion study (Kirk et al., 2016). Briefly, a sample of 300 adult Pacific lamprey was collected at Bonneville Dam (45.6°N, 121.9°W), which is the most downstream dam on the Columbia River, from May–July of 2014. Lamprey were anesthetized and had half-duplex passive integrated transponder tags (HD-PIT tag; 4 × 32 mm, Texas Instruments, Dallas, Texas) inserted into their body cavities. Fish were allowed 8–12 h of recovery before being used in swimming experiments. Fish were evaluated in a flume (11.6-m long, 1.2-m wide and 2.4-m high) that had a 9-m long swimming section with a single vertical-slot weir in the middle (Fig. 1A), which is a common design structure in fishways (Rodriguez et al., 2006; Gao et al., 2016). The experimental vertical-slot was intended to have a structural configuration similar to the vertical-slot (serpentine weir) sections in the upper fishways at Bonneville Dam, which Pacific lamprey have a difficult time passing (Keefer et al., 2013b). Individual fish were identified from a pair of HD-PIT antennas that were custom designed to slide into the vertical-slot structure.

A total of 54 experimental trials were conducted at night (21:00–05:20) with 5–6 lamprey used in each 90-min trial. The objective was to test the effects of three different fishway features on lamprey passage ability: water velocity, turbulence, and the length of the vertical-slot weir. Hence, the experimental design consisted of 18 different treatment combinations with three levels of bulk velocity through the slot (1.2, 1.8, and 2.4 m/s), three levels of slot length (0.33, 0.66, and 1.00 m), and two turbulence conditions that were manipulated using a turbulence-inducing structure upstream of the vertical-slot (Fig. 1A). The different slot lengths reflect differences in the lengths of individual slots in the serpentine weir sections, which allowed us to more generally test how obstacle length affects lamprey passage. Velocity at the slot was manipulated by altering total flume discharge and hydraulic head at the outflow of the flume until the target velocity was achieved.

2.2. Lamprey swimming paths

The movements of Pacific lamprey were recorded within the vertical-slot using four underwater digital cameras (SPECO CVC-320WP IR LED Bullet Camera, Amityville, New York.) lit by three infrared lamps. One camera was positioned on the floor directly upstream and one was directly downstream of the vertical-slot, which provided a lamprey-level view that oriented across the channel into the slot. The other two cameras were also located directly upstream and downstream of the vertical-slot, but were positioned

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