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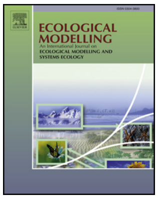

A physiologically inspired agent-based approach to model upstream passage of invasive fish at a lock-and-dam

D.P. Zielinski[a,b,*,1], VR. Voller[c], P.W. Sorensen[a]

[a] *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN, USA*
[b] *Great Lakes Fishery Commission, Ann Arbor, MI, USA*
[c] *Department of Civil, Environmental, and Geo- Engineering University of Minnesota, St. Paul, MN, USA*

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ABSTRACT

The ability of fish to swim upstream through regions of swiftly flowing water is ultimately dependent on their physiological capacity. Swimming performance, the relationship between swim speed and time-to-fatigue, has been used to design fishways and identify barriers to fish movement. However, existing numerical models do not all capture the variability in swimming abilities nor the turbulent, unsteady, and three-dimensional aspect of natural flows. This deficiency is particularly problematic for fish species whose behavior is poorly understood (i.e., invasive fish) and at sites with complex flow patterns. Here, we combine species-specific swimming performance with high resolution abstractions of fluid flow in a new agent-based framework to model fatigue of upstream swimming fish under turbulent flow conditions. Our model simulates fish paths, in the absence of information on their behavioral tendencies, based on a rules-set aimed at fish swimming as far upstream as possible before complete exhaustion by selecting the path of least fatigue. We demonstrate how this model functions by examining theoretical passage of invasive silver carp, Hypopthalmichthys molitrix, and bighead carp, H. nobilis, as well a native fish, the lake sturgeon, Acipenser fulvescens, through a typical Mississippi River lock-and-dam (Lock-and-Dam #8 near Genoa, WI). The model then tests whether passage could be reduced by altering spillway gate operations. Model results suggest that passage of all three species is low under current gate operations and that passage of both carp species could be further reduced by about half through minor changes in spillway gate operation without apparent impacts on navigation, scour, or lake sturgeon passage. Model results are qualitatively consistent with observed passage rates monitored by other studies at similar lock-and-dams and are consistent with the possibility that the model likely overestimates passage rates by relying on physiological data only. This approach could be exported to other applications and fish species to help manage and control fish migration and dispersal, especially for fish whose behavior and ecology are poorly understood and not presently quantifiable.

1. Introduction

Fish migration and dispersal are key life history traits that are highly susceptible to disruption by natural and man-made obstructions like waterfalls, dams, and culverts. Upstream movement in particular is heavily impacted by hydraulic challenges (i.e., regions of flow that exceed a fish's locomotor capacity). However, while understanding how fish movement is influenced by water flow is vital to the design of fishways and identification of barriers to movement, relating fish movement to the naturally unsteady, turbulent, and three-dimensional flow conditions found in these situations is not straightforward (Liao et al., 2003). Accordingly, fisheries managers and engineers have developed computer models to help bridge the gap between water flow and fish movement. Preferably, models of fish movement would incorporate environmental stimuli (e.g., velocity, temperature, etc.) with data on physiology (e.g., swimming performance) and key information on behavioral attributes (e.g., when and why particular fish move). However, while both environmental stimuli and physiological traits of certain species of fish are often either well understood or readily obtained using laboratory instrumentation (e.g., swim tunnels); fish behavior, especially in situ, is inherently difficult to obtain and usually unavailable. Thus, with the exception of a handful of economically important species (e.g., Pacific salmon, freshwater eels), behavioral traits of upstream swimming fish in the field are largely unknown. This

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[*] Corresponding author at: Great Lakes Fishery Commission, Ann Arbor, MI, USA.
E-mail address: dzielinski@usgs.gov (D.P. Zielinski).
[1] Current address: Great Lakes Fishery Commission, 11188 Ray Road, Millersburg, Michigan, 49759-9481, USA.

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is especially the case for non-native fishes, some of which are invasive. Since many existing models require information on behavioral traits, which is lacking for invasive species, new models that emphasize physiological limits of fish swimming (i.e., how fast and how long can fish swim before exhaustion) to examine barriers to fish passage and estimate movement ranges are needed.

One area where modelling of the physiological limits of fish movement in complex flows would be especially beneficial is the control of invasive species such as the Asian or bigheaded carps (a genus with two key species, the silver carp, Hypopthalmichthys molitrix and bighead carp, H. nobilis). The bigheaded carps are large, voracious microphagous fish that were introduced to North America in the 1970s (Kolar et al., 2007) and are now disrupting food webs and negatively impacting fisheries across the Mississippi River Basin (Carlson et al., 1995; Schrank et al., 2003; Sass et al., 2014; Pendleton et al., 2017). However, while they are ubiquitous in much of this large watershed, they have not yet invaded many peripheral and interconnected areas including the Mississippi River headwaters area, upper Illinois River, and the Great Lakes (USFWS, 2014). Identifying new ways to block upstream movement of bigheaded carp is a key objective of state, regional, and federal management strategies in these regions (Tsehaye et al., 2013). The set of 29 Mississippi River navigational lock-and-dams located in this river network and managed by the U.S. Army Corps of Engineers (USACE) offers a possible avenue to block bigheaded carp passage as all fish must pass through them. Water velocities increase as a result of passing through the lock-and-dam spillway gates which are also fully adjustable and have already been suggested to reduce passage of native migratory species in the Mississippi River (Knights et al., 2002; Zigler et al., 2003, 2004). Further, a recent swim study on bigheaded carp swimming performance (Hoover et al., 2017) showed that bigheaded carps are relatively weak swimmers. The possibility that lock-and-dams could be used to block passage has also been supported by telemetry studies at lock-and-dams in the Mississippi River (Tripp et al., 2014) and Illinois River (Lubejko et al., 2017), which found bigheaded carp passage rates to be low and occur largely during open-river conditions (i.e., all spillway gates are raised out of the water and velocities are relatively low). Lock-and-dams near the headwaters of the Mississippi River, where bigheaded carp have not yet reached, rarely experience open-river conditions (FishPro, 2004) and represent the greatest likely impediment to fish passage (depending on when specific fishes naturally move relative to open-river conditions). If gate operations could be modified in appropriate ways that do not increase scour near the structure or impair navigation, these lock-and-dams would offer great potential to further restrict bigheaded carp passage. However, flows through these structures are complex and not easily measured, and there are presently no data on carp behavior or movement near these structures. Models must therefore rely on swimming performance and hydraulic data alone. A common approach to such models is to assume fish will swim to their maximum physiological capacity (e.g., exhaustion), resulting in conservative estimates of passage as fish are not naturally expected to swim to complete exhaustion. Models that calculate the highest number of fish passing a hydraulic challenge are of great value as a first step to evaluate whether and how to stop undesirable invasive species while allowing for the possible passage of other species like the lake sturgeon, Acipenser fulvescens, a native fish of ecological and cultural importance that makes prolonged migrations throughout the Mississippi River Basin.

In this study we develop a new numeric model to describe fish swimming upstream through a hydraulic challenge by incorporating species-specific data on fish swimming performance and hydraulic data around and through structures such as locks-and-dams. We then use the model to both evaluate, and then simulate, fish passage through a typical lock-and-dam under various scenarios while comparing findings with known data at similar structures. It is novel because of the manner in which we merge two attributes, swimming performance and hydraulic conditions, the first of which we now introduce. Fish swimming performance (i.e., the relationship between swim speed and time-to-fatigue) is generally categorized by two distinct modes: sustainable and unsustainable swimming. While fish can maintain relatively slow swim speeds almost indefinitely by relying on aerobic metabolism (i.e., sustainable swimming), they cannot do this at higher speeds as their ability to swim become limited by the contribution of anaerobic metabolism (i.e., unsustainable swimming). Further, fish can only maintain unsustainable swim speeds for limited durations that are inversely related to swim speed (Beamish, 1978). Thus, after bouts of unsustainable swimming, fish completely fatigue, and may require several hours to recover (see review in Kieffer (2000)). Relationships between swim speed and time-to-fatigue are readily quantified through laboratory swim tunnel / flume trials (Beamish, 1978; Castro-Santos, 2005; Hoover et al., 2017).

Hydraulic conditions are the second key component of our model. They can be generated using well-established computational fluid dynamics (CFD), computer models that simulate water flows by solving the governing equations of fluid flow, and is a practical method to model the complex flows in and around lock-and-dams in a framework that fish passage can be readily incorporated. Since CFD models provide fine-scale resolution (i.e., sub-meter, seconds/minutes) hydraulic data over a wide range of conditions, it is already widely incorporated into modelling applications focused on the interface of hydraulics and ecology (Daraio et al., 2010; Harvey and Clifford, 2009). Generating fine-scale simulations of flow fields experienced by fish is critical as the efficacy of any model or assessment of fish movement is inexorably linked to the scale at which spatiotemporal changes in water velocity are modeled (Tullos et al., 2016). Our approach is driven by the need to expand upon existing fish passage models which either are limited by reliance upon simplified hydraulics and homogenized swimming performance (ex. FishXing; Furniss et al., 2006) or require extensive (usually nonexistent) telemetry data (Gao et al., 2016; Arenas et al., 2015; Goodwin et al., 2014, 2006; Haefner and Bowen, 2002) Also, with the exception of Gao et al. (2016), all extant behavioral models are intended to describe downstream movement of fish where the influence of swimming fatigue is minimized.

In this study, we develop and describe a new agent-based approach, a mathematical model that simulates the interactions of individuals, or agents, with each other and/or their environment. Our model incorporates swimming performance data with high resolution abstractions of complex fluid environments to evaluate fish swimming fatigue. Agent-based approaches similar to this have proven to be effective in simulating many complex ecological phenomena like larval fish navigation (Staaterman and Paris, 2004), fish aggregations and movement (Gao et al., 2016; Arenas et al., 2015; Goodwin et al., 2014, 2006; Nestler et al., 2002; Huth and Wissel, 1992), and mussel dispersal (Daraio et al., 2010), but they have not been deployed to understand invasive fish passage at lock-and-dams before. Our model makes three primary assumptions: (1) fish are only motivated to move upstream (i.e., no backtracking); (2) fish swim at their distance-maximizing ground speed; and (3) fish select a path of least energetic cost. The percent endurance model, developed by Castro-Santos (2005) and partially used in other fish passage evaluations (Neary, 2012) is used as a proxy for energy expenditure. Stochasticity is introduced by varying individual fish swimming performance and hydraulic fields based on turbulent fluctuations.

We describe the framework of a new agent-based swimming fatigue model and discuss its general characteristics and intrinsic models. We then demonstrate the applicability of the model by simulating bigheaded carp passage at Lock-and-Dam #8 (Genoa, WI) on the Mississippi River, a structure with similar geometry and hydrologic features to many other lock-and-dams and located upstream of the bigheaded carp invasion front. We examine whether these invasive species are likely being blocked by current spillway gate operations at this typical lock-and-dam and whether changes to gate operating procedures (i.e., gate opening height) could enhance this feature without