

Fish navigation of large dams emerges from their modulation of flow field experience

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Navigating obstacles is innate to fish in rivers, but fragmentation of the world's rivers by more than 50,000 large dams threatens many of the fish migrations these waterways support. One limitation to mitigating the impacts of dams on fish is that we have a poor understanding of why some fish enter routes engineered for their safe travel around the dam but others pass through more dangerous routes. To understand fish movement through hydro-power dam environments, we combine a computational fluid dynamics model of the flow field at a dam and a behavioral model in which simulated fish adjust swim orientation and speed to modulate their experience to water acceleration and pressure (depth). We fit the model to data on the passage of juvenile Pacific salmonids (*Oncorhynchus* spp.) at seven dams in the Columbia/Snake River system. Our findings from reproducing observed fish movement and passage patterns across 47 flow field conditions sampled over 14 y emphasize the role of experience and perception in the decision making of animals that can inform opportunities and limitations in living resources management and engineering design.

fish movement behavior | hydraulic pattern | individual-based model | fish passage | ecohydraulics

Understanding how the design and management of civil infrastructure modifies the outcome of naturally evolved behavior in animals is critical for sustainably using limited environmental resources to spur economic development and maintain native species. The issue is particularly relevant for rivers, which make up only 0.0002% of water on Earth (1) but support more than 40% of the world's human population (2, 3). River regulation to meet society's needs has accelerated in the past two centuries (4), leaving over half of the world's major rivers now fragmented by >50,000 large dams providing water, energy, flood control, and transportation (3, 5, 6). The demand for large hydro-power continues, spurred by the need for economic development while limiting carbon use (7). However, dams impede the dispersal and migration of fish, a problem that, along with other factors, has contributed to the loss of populations and entire species (5). These losses have cultural, economic, and geopolitical repercussions (3, 8), because more than 40% of the world's human population lives in internationally shared river basins (9) and declines in fish populations jeopardize the food security of hundreds of millions worldwide (10–12).

In North America, the tension between economic development and living resource conservation is evident in the Columbia River basin. Flowing from Canada to the United States, the river once supported one of the world's largest salmon runs, with annual returns of 10–16 million fish (13) sustaining tribal nations and ecosystems far from the ocean (14). However, years of overharvesting, land-use changes, ocean conditions, and dams have contributed to a decline in the annual return of salmon (15). To reverse the decline, millions of dollars are spent each year seeking a durable hydroelectric strategy to improve annual returns (1–2 million fish). A major emphasis in restoration is ensuring that millions

of downstream migrating juvenile salmon reach the ocean where they grow before returning to the river as adults.

Hydropower dams on the river provide three general routes of passage for downstream migrating fish: powerhouse turbines, a spillway, and often a bypass specifically designed for fish. These routes differ in their mortality effects on fish, so an understanding of how fish behavior determines route selection is important for mitigating the impacts of dams on the populations. However, route selection behavior is poorly understood. Not only has it been difficult to explain route passage patterns at one dam, but it has been even more difficult to explain why the pattern may be different at another dam with similar routes.

Assumptions

Monitoring all environmental and internal factors (16–19) that could contribute to fish movement in a large open system is not possible, so the following assumptions underlie our analysis. First, although fish migration between habitats involves many factors (e.g., physiological, life cycle, feeding), over the temporal and spatial scales it takes a fish to transit a dam environment, we assume movement is hydraulically mediated.

Our second assumption stems from the need to describe a fish's perception of hydraulics, which is difficult in open flowing environments because our understanding is still limited (20). One challenge is selecting a stimulus variable, because “hydraulics”

Significance

Whereas adult salmon swimming upstream through a ladder visibly illustrates the challenge a dam presents to fish returning home to spawn, the downstream passage of juveniles swimming toward the ocean is often a greater, although more unseen, challenge to their survival. Decades of work have identified many factors that affect fish behavior near dams, but why downstream passage structures may work well at one dam but not at another is poorly understood. We use a computer model to show that observed downstream passage patterns could result from a generic strategy that fish may use to navigate flow field obstacles. Our findings identify environmental and biological factors warranting further evaluation for sustaining native species amid economic development.

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Data deposition: The computational fluid dynamics model and other data reported in this paper are available in the *SI Appendix*.

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manifests itself in many ways that have been implicated in fish behavior, including sound (16) and turbulence (21). Our approach is based on the simple notion that animals sensitive to gravity are generally also sensitive to other acceleratory and inertial stimuli (22). Decades of work have identified fish sensitivity to relative water velocity and acceleration fields over short ranges, as well as inertial stimuli (17, 21–36). To explore how water acceleration may shape fish movement and identify why fish avoid some flow field regions, we need descriptions of water velocity and acceleration throughout the environment. In this study, we develop Reynolds averaged Navier–Stokes computational fluid dynamics (CFD) models using hydraulic field data to describe water velocity and acceleration throughout these environments, averaged over time periods corresponding to available fish passage observations (*SI Appendix, Materials and Methods, Representing the Hydraulic Environment and Tables S1 and S2*). Although a fish can detect hydraulic signals at subbody length scales, which are far smaller than can be resolved in our hydraulic models (CFD resolution is <1 m in some locations), we assume our modeled hydraulics characterizes flow field changes important to a fish, because as the fish moves, it experiences an acceleration/deceleration where water velocity increases/decreases (i.e., where there is spatial, convective acceleration of water). Thus, we infer this experience provides the fish with a sense of larger, steady 3D water accelerations/decelerations analogous to flow field heterogeneity resolved in our CFD models.

Our third assumption stems from the observation that animals evaluate the world in relative terms (37) and may change their response to a stimulus with repeated exposure (38). At a dam, individual fish may reject a route several times before entering, and some fish never return to a route after the first encounter. Fish movement between the first encounter and eventual passage is important because it can modify the spatial distribution of the population among multiple routes. The sensory, physiological, and cognitive processes for why fish change their response may be complex. With water acceleration as our stimulus, we describe changing response over time using an analogy to Weber's just-noticeable difference (39) that allows perception of a fixed stimulus to change with experience (*SI Appendix, Materials and Methods, Perceived Change in Flow Field Experience*). In our model, the fish acclimatizes, or habituates, to acceleration it is exposed to, and we relate the acceleration that the simulated fish experiences each instant in time t to its level of acclimatization. With these assumptions, we introduce a behavioral strategy with defined responses that a fish might use to navigate flow field obstacles and, by extension, engineered structures.

Fish Movement Hypothesis

We introduce our downstream movement hypothesis by assuming that a river's bathymetry and embedded objects impose predictable patterns in the flow field (40, 41) that guide fish navigation. To illustrate, consider the passage of a fish in a channel with an embedded cube (Fig. 1), where we characterize the flow field in terms of average water velocity and spatial acceleration and the fish response to the field in terms of three mutually exclusive behavior states, $B\{j\}$, $j = 1, 2, 3$, each with a unique swimming orientation to the field (Fig. 1). The fish enters the channel with a biased correlated random walk (BCRW) in the direction of downstream flow, behavior state $B\{1\}$. Approaching the cube, the fish experiences water accelerations and decelerations that differ from its recent past, $E_1(t)$. Water acceleration and deceleration result in an exchange of force (Mass \times Acceleration) between the fish and surrounding water, akin to the force an accelerating car imposes on its driver and the reverse when decelerating. Acceleration/deceleration can trigger one of two different response behaviors, $B\{2,3\}$, that modulate $E_1(t)$ through different mechanisms (Fig. 1). Behavior $B\{2\}$ orients swimming in the direction leading to faster water, irrespective of the flow direction. This attraction to velocity may reduce inertial stimuli associated with

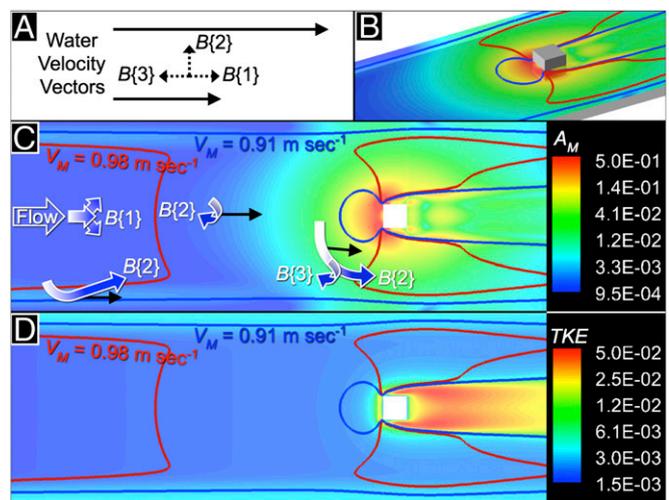


Fig. 1. Illustration of fish behavior responses $B\{1,2,3\}$ to hydraulic pattern. (A) Direction of oriented swimming for each behavior (dashed black arrows) using two water flow velocity vectors (solid black arrows), where the longer vector represents faster water. Mean orientations of $B\{1,3\}$ are with and opposite to the water flow direction, respectively, but $B\{2\}$ orientation points toward faster flow, which is often in a direction different from water flow (streamline). (B) In heterogeneous flow, such as around a cube, distinguishing the contributions of fish swimming and passive transport is not straightforward. (C) For example, white-to-blue arrows illustrate the resultant fish movement (swimming + transport) in response to acceleration magnitude (A_M , in meters per square second) for behaviors $B\{1,2,3\}$. (B–D) Note slow (blue) and fast (red) water speed [velocity magnitude (V_M) in meters per second] contour lines. In C, solid black arrows depict the general water flow direction. Behavior $B\{2\}$ can result in localized holding (milling) when faster water (red V_M contour line) is upstream of the fish. Upstream movement or milling resulting from $B\{2\}$ can resemble upstream movement from $B\{3\}$ even though the two behaviors are different. $B\{3\}$ is generally more prolonged in the direction opposite to the flow vector. In contrast, $B\{1\}$ orients swimming with the flow vector in the absence of $B\{2,3\}$. Mean patterns of V_M and A_M arise predictably in rivers from form resistance (e.g., rock, woody debris) and skin friction (e.g., water/boundary interface) (40, 41). (D) Turbulence is represented as TKE (square meters per square second). A horizontal slice at the midpoint of a 1-m cube placed at the bottom-center of an 8-m wide by 4-m deep channel is depicted in B–D. Flow was rendered using Reynolds averaged Navier–Stokes (RANS) CFD with an upstream boundary inflow of $32 \text{ m}^3 \cdot \text{s}^{-1}$ for an average water velocity of $1 \text{ m} \cdot \text{s}^{-1}$, which was selected to visualize hydraulic pattern easily. The CFD model was developed by staff at IIHR–Hydroscience and Engineering, University of Iowa.

pulsations in flow (28) from eddies and turbulence [turbulent kinetic energy (TKE); Fig. 1] near obstacles and the water's edge. Following the car analogy, the behavior is akin to steering the car into a faster traffic lane with fewer accelerations/decelerations (hereafter acceleration), and therefore reduces exchanges of force. Behavior $B\{2\}$ facilitates downstream migration through hydraulically mediated obstacle avoidance. Behavior $B\{2\}$ also limits exposure to turbulence (TKE; Fig. 1), which can reduce swimming efficiency (42) and predator detection. With behavior $B\{3\}$, the fish temporarily abandons downstream migration and swims upstream. When the relative change in acceleration, $E_1(t)$, exceeds a threshold intensity, $k_{B\{j\}}$, $j = 2, 3$, the utility of the related response, $B\{2,3\}$, increases; otherwise, it decreases (*SI Appendix, Materials and Methods, Behavior State Transitions and Fig. S1*). The utilities of $B\{2,3\}$ fluctuate as the fish transits the flow field, but the utility of downstream movement, $B\{1\}$, remains constant. In an increment of time, the behavior with the highest utility is active.

Salmon and steelhead possess a swim bladder sensitive to pressure (17), so we separately encode a vertical orientation using change in depth as a simple measure of change in pressure

that a fish experiences through its swim bladder. Fish with swim bladders are known to acclimatize to new pressures over time, and, for simplicity, we treat this acclimatization using the same equation we use for water acceleration (*SI Appendix, Materials and Methods, Perceived Change in Flow Field Experience*). If fish depth exceeds a threshold range above or below the depth to which the swim bladder is acclimatized, $E_2(t) > k_{B\{4\}}$, then the vertical component of swimming orients toward the acclimatized depth, $B\{4\}$, if not already accomplished through $B\{1,2,3\}$.

Fish Movement Model

Behaviors, $B\{j\}$, $j = 1,2,3,4$, are simple small-scale, goal-oriented movement responses that depend on a fish's unique experience in space and time. Acclimatization integrating past conditions along the simulated fish's trajectory and the behavior thresholds, $k_{B\{j\}}$, $j = 2,3,4$, control its sensitivity to flow field heterogeneity. To describe how perceived changes in our stimuli, $E_i(t)$, $i = 1,2$, result in simulated behavior transition and duration, we use an event-based decision model (43) that tracks the expected utility of each alternative behavior. Each expected utility is the product of the behavior's intrinsic utility and a dynamic weighting computed as a moving average of Boolean events defined as $e_{B\{j\}} = 1$ if $E_i(t) > k_{B\{j\}}$ and as $e_{B\{j\}} = 0$ otherwise (*SI Appendix, Fig. S1*). In other words, changes that exceed thresholds drive weights of evidence for which swimming response is most likely to reduce flow field change back to within the simulated fish's tolerance for a time increment, $E_i(t) \leq k_{B\{j\}}$.

To implement this model, we use an Eulerian–Lagrangian-agent method (ELAM) (44) (*SI Appendix, Materials and Methods*). An ELAM first represents the environment as a computational mesh (Eulerian component), which comes from our CFD model. Numerical particles are then simulated (Lagrangian component) in the domain, with behaviors (agent component) representing responses to variables stored in the mesh. Releasing simulated fish upstream of each dam with a spatial distribution similar to observed fish (*SI Appendix, Materials and Methods, Simulated*

Fish Release Locations), we test the hypothesis that fish movement through hydropower dams can be reproduced by assuming fish modulate their flow field experience. To find the simplest viable model of the hypothesis, we fit the ELAM model using different combinations of the four behaviors, $B\{1-4\}$, and three other hypotheses to site data from seven Columbia/Snake River dams. The site data consist of the passage proportions of juvenile Pacific salmonids (*Oncorhynchus* spp.) through bypass, powerhouse turbines, and spillway routes for 47 flow field configurations sampled over 14 y. To identify the simplest viable set of behaviors, we compare the simulated fish passage proportions for each behavior combination with the observed passage proportions (Fig. 2), with an arbitrary goal of describing the proportions within an rms error of ≤ 10 .

Results

We evaluate 11 hypotheses ranging from random passage to the full “general” model that contains all four behaviors, $B\{1-4\}$ (Fig. 2). The simplest assumptions that fish passage is random and that it is proportional to water flow through the routes do not correspond with observed fish passage patterns (Fig. 2). Simulated fish passively moving with the flow or with a BCRW, $B\{1\}$, also poorly match the observed passage data. Simulations with $B\{1\}$ and one other behavior measurably reduce the error between the model and observations, and inclusion of two behaviors with $B\{1\}$ reduces error further. Finally, the general model, $B\{1-4\}$, yields the closest fit to observed data (Fig. 2). Although there is variation in the monitoring methods and the types of juvenile salmonids observed (*SI Appendix, Tables S1 and S2*), with the exceptions of the Lower Granite Dam and Priest Rapids Dam, two or three behaviors are generally sufficient to match the observed passage data (Fig. 2). The Lower Granite Dam includes a floating guidance wall [behavioral guidance structure (BGS)] and trash boom that extend away from the dam and create a more complex hydraulic regime, which requires the general model to fit. The Priest Rapids Dam is also unique, with

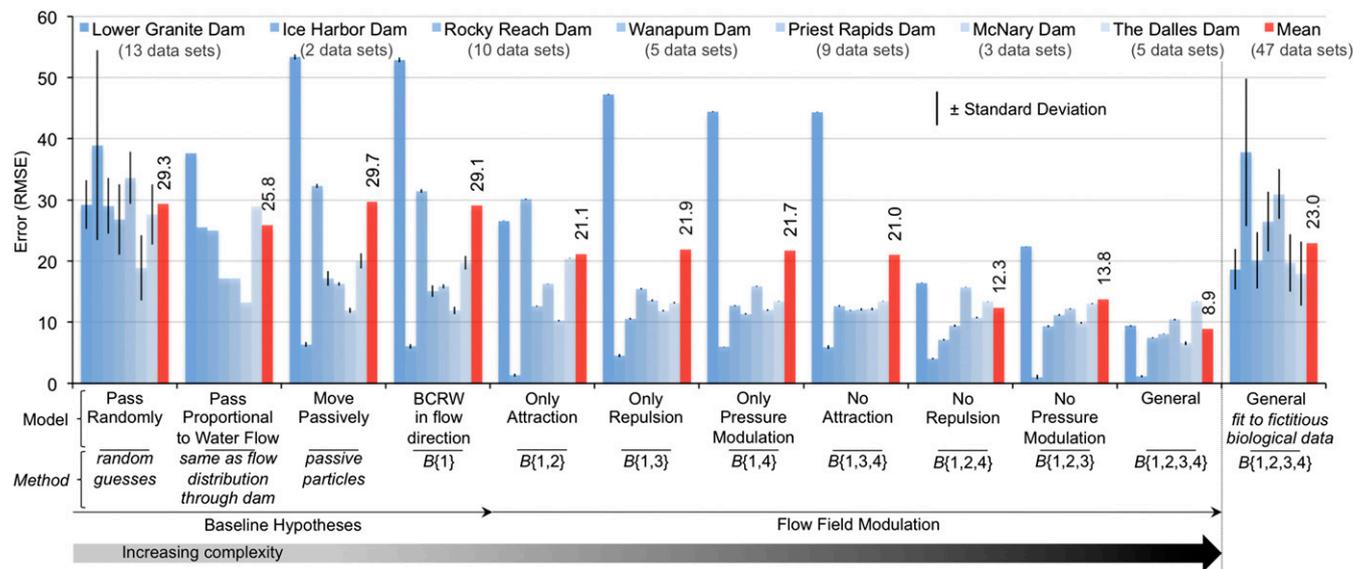


Fig. 2. Root-mean-square error (RMSE) values of the alternative models evaluated in our exploration of factors describing observed patterns of juvenile salmonids passing through routes (bypass, turbines, spillway) at seven large dams. Models increase in complexity from left to right, where pass randomly is the simplest model and general is the most complex model. (*Far Right*) General model is also fit to fictitious data as a test for whether the number of parameters, as opposed to the movement hypothesis, is primarily responsible for the model's ability to fit data. The RMSE values (*SI Appendix, Table S3*) reflect the mean differences in modeled vs. observed proportions through the routes. For each model, RMSE values for the seven dams are grouped together as blue bars (Lower Granite Dam is the left-most blue bar and The Dalles Dam is the right-most blue bar). The equally weighted mean RMSE across all 47 datasets is shown as red bars. The SD is based on 10 random number seeds (*SI Appendix, Model Evaluation*). Routes with zero passage, such as closed routes having the same zero observed and modeled passage, are not factored into RMSE values.

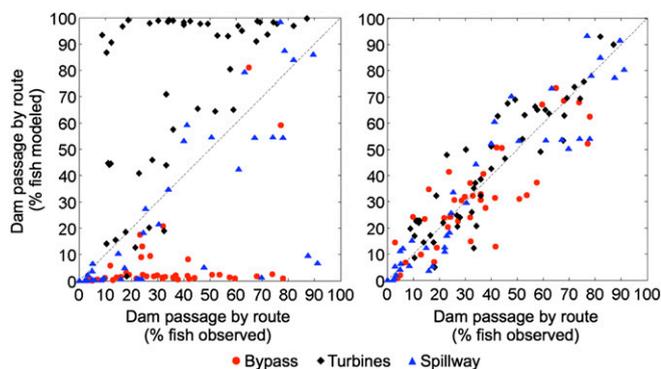


Fig. 3. Observed vs. modeled passage proportions through bypass, turbines, and spillway routes for passive particle (*Left*, no fish behavior) and simulated fish (*Right*, general model) using identical simulation attributes. Linear regression of observations vs. general model passage proportions (46, 47) for bypass ($n = 41$), turbine ($n = 46$), and spillway ($n = 38$) routes are, respectively, slope (0.76, 0.95, 0.94), intercept (5.98, 5.00, 0.82), and r^2 (0.70, 0.82, 0.89). Routes with zero passage and scenario C2 are not included (*SI Appendix, Model Evaluation*). Plots of simpler variants of the model are shown in *SI Appendix, Fig. S2*.

the smallest and largest bypass flow rates of the dams monitored (*SI Appendix, Table S1a*). These exceptions suggest the full “general” model, $B\{1,2,3,4\}$, is necessary at sites exhibiting greater flow range or where hydraulic complexity results from an engineered structure, such as a boom or wall, that protrudes away from the dam into fish approach paths.

Fit of the general model to observed fish passage across all seven dams is shown in a pattern-oriented analysis (45) (Figs. 2 and 3). Importantly, the general model is unable to fit randomly generated fish passage proportions for any dam (Fig. 2). This finding supports the notion that explanatory power of the model does not stem primarily from model complexity, such as the number of tunable parameters. Individual fish trajectories also support this notion. At the Lower Granite Dam, all four behaviors, $B\{1-4\}$, are necessary to match trajectory patterns of individual acoustically tagged fish (Fig. 4 and *SI Appendix, Fig. S3*). Of particular importance, the general model captures common patterns of fish passing through routes they previously rejected multiple times and shows how velocity attraction, $B\{2\}$, may work to separate fish from the mean flow pattern (Fig. 4*B*) and guide them along a boom (Fig. 4*C* and *D*) in a manner that is not purely vision-mediated.

Discussion

Our results suggest that fish behavior drives the passage performance of observed engineered routes. In the real world, fish swimming works in context with many factors, including light and vision (16, 24, 30), sound (16), social interactions (49), feeding, predators, water quality, chemical cues, fish size and age, and hydraulics at scales smaller than considered here. Differences between modeled and actual environments could have implications on what we infer about fish behavior (50); however, at minimum, our study suggests that abstractions of the real world from hydraulic and behavioral modeling may inform how engineered features function with the cue responses that fish have naturally evolved. With a limited evolutionary history of navigating dams, fish choices should reflect their behavioral adaptation to natural rivers. Thus, our findings should apply to fish downstream movement through natural settings and, by extension, near other types of engineered infrastructure.

The considerable resources and efforts in the Columbia River system to mitigate the mortality of fish at dams (51) are unlikely to be allocated in other systems worldwide, but our

findings reported here can inform hypotheses and design of passage systems elsewhere. Specifically, routes that elicit attraction, $B\{2\}$, without triggering repulsion, $B\{3\}$, appear effective when fish discover a passage route. However, facilitating route discovery and passage is not trivial in complex environments and may depend on a fish’s prior experience. We show how a simple structure may guide fish in some contexts by stimulating attraction, $B\{2\}$, assuming that swimming along the Lower Granite Dam’s boom and BGS (Fig. 4 and *SI Appendix, Fig. S3*) is hydraulically mediated. Our results suggest boom-like structures aligned parallel to the water flow vector, or otherwise placed in environments where the signal is difficult to perceive relative to the background, may not separate fish from mean flow. Other structure alignments, such as perpendicular to the flow vector, may disrupt guidance if they locally decrease water speed (velocity magnitude) in the direction in which fish transit the structure.

Although a single site may not require all behaviors to describe observed passage patterns, describing fish behavior in a more complex setting may improve the portability of findings to other sites. This notion is supported by Lower Granite Dam model parameters that work better at other dams than parameters from other dams work at the Lower Granite Dam (*SI Appendix, Table S5*). Also, the need for behavior $B\{3\}$ to describe patterns at the Lower Granite Dam supports our assumption that some form of acclimatization/habituation or, more generally, changing response to a route over time and its effect of redistributing the fish population along the dam can be important to emergence of passage patterns where multiple routes are available.

The hierarchy of information that influences animal movement is complex, and context changes between settings. Many stimuli (e.g., food, predators, visual) play a role in the setting of broader navigation goals and also intervene in the moment-to-moment decisions of individuals. Although we do not presume that fish respond only to water acceleration and pressure, which can sometimes result in injury (52), these two stimuli provide a viable means to identify strategies fish use to position themselves within heterogeneous flow fields.

There are contexts beyond fish passage where our findings might be relevant. First, the hydraulic imaging of river bathymetry and embedded objects that we use appears to be, at a conceptual level, informative for interpreting some of the behavior patterns observed for upstream movement and feeding. Inverting responses within the behavioral repertoire, $B\{1-3\}$, would appear to orient a fish toward the river’s edge (e.g., shoreline, riverbed, water surface), obstacles, and shallow water habitat across a broad range of ecogeomorphic contexts. In these locations, energetic costs of upstream movement and holding position are reduced (53–57) and fish often feed (58) and seek refuge (59, 60). By cueing on acceleration phenomena and their duration at multiple scales, fish could be sensitive to analogous phenomena implicated in sediment motion (61) that elicit invertebrate drift. In ocean currents, turtles (62) and fish (63, 64) could use acceleration phenomena as cues in navigation. Behaviors $B\{1-3\}$, or their inverted forms, could be used to position fish within the moving media at locations that confer the greatest advantage for their life stage. Second, hydraulic imaging of water has strong analogies in air currents, where birds (65–67) and insects (68) might use similar strategies to navigate local heterogeneity in winds reflecting landscape topology and meteorological conditions.

In summary, incorporating even simple principles of perception and decision making of animals into quantitative tools already supporting management and engineering design, as shown here, can elucidate new perspectives through which a species’ movement behavior and outcomes to management might be better evaluated.

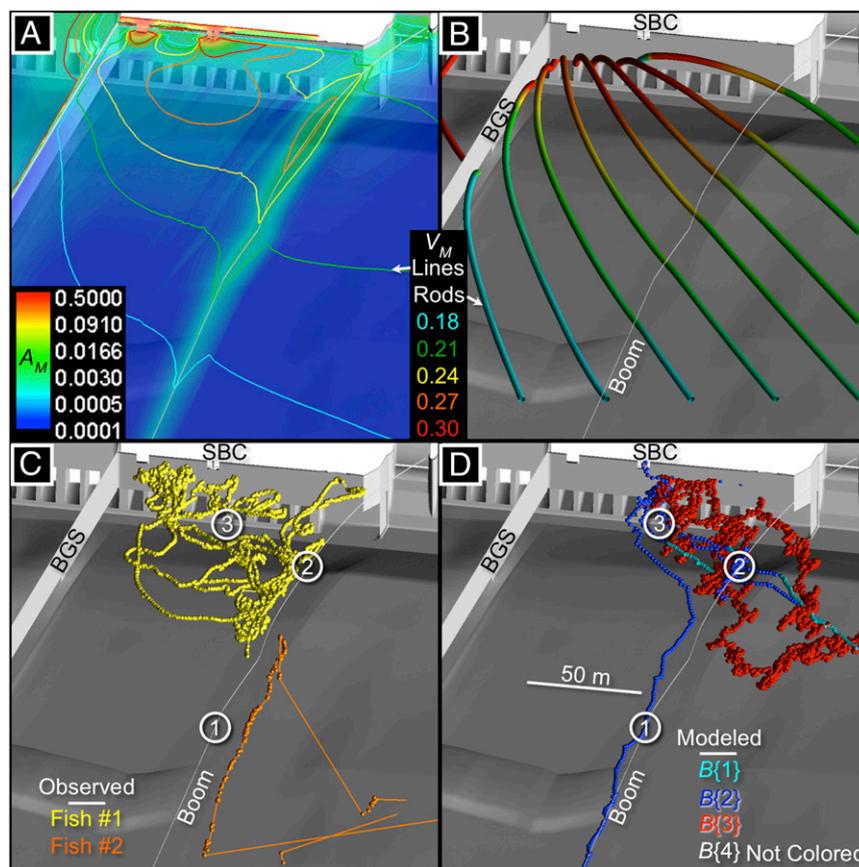


Fig. 4. Patterns of water speed (V_M , meters per second; contour lines) and acceleration (A_M , meters per square second; contour fill) (A) used in the general model generate a single fish path (D) similar to the patterns of observed fish movements (C) (48). Neutrally buoyant, nonswimming particles follow water flow paths or streamlines (B) after release at depth similar to that of observed fish (C), 3.7 m below water surface. Fish movement differs substantially from mean flow (B), and the difference between flow paths (B) and fish (C and D) illustrates the contribution of fish behavior in dam passage. Swimming effort is not trivial, because $V_M > 0.18 \text{ m}\cdot\text{s}^{-1}$ in front of the dam, as shown in A, can exceed the cruise speed of a 90-mm long fish. A shallow, $\sim 1\text{-m}$ deep floating boom can elevate A_M sufficient to trigger B{2}, resulting in movement parallel to the boom (location 1). Elevated A_M surrounding the surface bypass collector (SBC) can trigger prolonged upstream movement, B{3}, to the boom (location 2) and exploratory milling (location 3) through recursive cycles between B{3} and B{1,2}. Acclimatization over time diminishes the response to the A_M contour, resulting in eventual passage. The CFD model was developed by staff at IIHR-Hydroscience and Engineering, University of Iowa, and acoustic tag telemetry data (48) were provided by the US Geological Survey, Columbia River Research Laboratory (SI Appendix, Fig. S6).

Materials and Methods

The movement of downstream migrating juvenile Pacific salmonids through seven dams along the mainstem Columbia and Snake Rivers of the Pacific Northwest of the United States was monitored using one or more of the following field instrumentations: fixed-location hydroacoustics, radio-tag telemetry, and acoustic-tag telemetry (SI Appendix, Figs. S5–S12 and Table S1). The configurations of the dams during monitoring are illustrated in SI Appendix, Figs. S6–S12. Further details on the materials used and our analysis of fish behavior responses, B , to the water flow fields are provided in SI Appendix.

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