Merging computational fluid dynamics and machine learning to reveal animal migration strategies

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Abstract

1. Understanding how migratory animals interact with dynamic physical environments remains a major challenge in migration biology. Interactions between migrants and wind and water currents are often poorly resolved in migration models due to both the lack of a high-resolution environmental data, and a lack of understanding of how migrants respond to fine scale structure in the physical environment.

2. Here we develop a generalizable, data-driven methodology to study the migration of animals through complex physical environments. Our approach combines validated Computational Fluid Dynamic (CFD) modeling with animal tracking data to decompose migratory movements into two components: movement caused by physical forcing, and movement due to active locomotion. We then use a flexible recurrent neural network model to relate local environmental con-

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ditions to locomotion behavior of the migrating animal, allowing us to predict a migrant's force production, velocity and trajectory over time.

3. We apply this framework to a large data set containing measured trajectories of migrating Chinook salmon through a section of river in California's Sacramento-San Joaquin Delta. We show that the model is capable of describing fish migratory movements as a function of local flow variables, and that it is possible to accurately forecast migratory movements on which the model was not trained.
4. After validating our model, we show how our framework can be used to understand how migrants respond to local flow conditions, how migratory behavior changes as overall conditions in the system change, and how the energetic cost of migratory movements depend on environmental conditions in space and time. Our framework is flexible and can readily be applied to other species and systems.

Computational Fluid Dynamics; Migration; Bionergetics; Machine Learning.

1 Introduction

Migration is an essential part of many animal life cycles (Dingle 2015). For animals that swim and fly, migration often involves not only long-distance navigation and ecological interactions with conspecifics and predators, but also complex interactions with the physical environment in the form of air and water currents (Smith, 2012, Dingle, 2015, Flack et al., 2018). The way migratory animals interact with abiotic currents can determine the energetic cost of migration (Pennycuick, 2008) and even whether migration is feasible at all (Alexander, 1998, Pennycuick, 2003). Because climate change and anthropogenic habitat alteration are modifying air and water currents at both small and large scales (Boning et al., 2008, Kling and Ackerly, 2020, Silva et al., 2018), management

plans must increasingly consider how human activities influence the physical environment through which migrants travel (Thorstad et al., 2008). There is a growing recognition that managing migratory species must involve managing landscapes to facilitate successful migration (Silva et al., 2018, De Lucas, Janss, and Ferrer, 2004). However, to make informed decisions about how changes to the environment will alter the ability of animals to migrate, we need a deeper understanding of how air and water currents influence migratory physiology and also migratory behavior.

In the past, efforts to understand how migrants interact with abiotic forcing have tended to take a migration physiology perspective, where the emphasis has been on combining biomechanical models with physiological data to understand the cost of migration in flows (e.g., Martin et al., 2015). For example, classic work on animal migration considered the energetic costs of large-scale mean wind or water currents on the cost of a migratory journey and on the fuel loads required at stopovers, as well as the ranges migrants could achieve under favorable and unfavorable currents (Pennycuick, 2003, Pennycuick, 2008). More recently, several studies have analyzed physical data or models of wind or hydrodynamics in the context of animal migration (Weber et al., 2006, North et al., 2008, Arenas et al., 2015; Gao et al., 2015, Reddy et al., 2016). Nevertheless, a major outstanding challenge in migration biology is understanding how migrant behavior and physical forcing by wind and water currents interact to determine how migrants move across a landscape, and the costs they incur when doing so.

One of the limitations of many animal tracking data sets is that only the positions and movements (e.g., via animal-borne accelerometers) of the animal are recorded, and details of the physical environment through which the animal moves are unknown. Because of this, movements must often be studied and interpreted without knowledge of the physical forces and sensory cues that in-

fluenced the observed motion of the animal. This severely limits the types of questions about migration behavior that can be answered with movement data. While modern animal-borne sensors can aid in this problem (Hughey et al., 2018), at present, such sensors are often expensive and too heavy to be carried by small animals. Moreover, animal-borne sensors have the added limitation that they record conditions only in the vicinity of the sensor, leaving the range of conditions available to the animal elsewhere in the environment unknown.

Here, we present an alternative approach to the problem of inferring the physical variables an animal experiences as it moves. This approach combines animal tracking data with high-resolution physical models of the region through which the tracked animal moves. The essential data requirements are (1) animal tracking data describing the physical position of an animal or animals over time, (2) measurements of the structure of the physical environment (e.g., river bathymetry, local landscape topography), and (3) a collection of sample measurements of the physical variables one wishes to model (e.g., local water or wind velocity), preferably collected from the study region over the same range of conditions as those experienced by tracked animals. The latter two data sources are used to build a dynamic model of the physical environment that can then be used to infer the physical forces a tracked animal experienced at each location in the tracking data set. The end result of fusing animal tracking data with the physical model is a data set containing positions, velocities, and accelerations of each tracked animal (inferred from the tracking data), as well as estimates of the physical forces experienced by the animal at each point in time. Such data can then be used to infer how physical forces influence movement behavior, and to address a suite of questions related to the energetic output required to produced observed movements.

In what follows, we illustrate how to fuse animal tracking data and physi-

cal variables using, as an example, migratory juvenile Chinook salmon migrating through a section of river in the Sacramento-San Joaquin Delta in California. Tracking data consist of high spatial- and temporal-resolution tracks from salmon as they move through a key segment of the migration route. To model the flow environment these animals experience, we combine river bathymetry data with flow measurements taken in several places throughout the study region to develop a Computational Fluid Dynamics (CFD) model of water flow through the entire study domain. We use the CFD model to estimate the dynamic fluid environment experienced by each individual along its migratory trajectory. We show how this data set can then be used to estimate the force exerted on the animal by moving water as well as the force produced by the animal through locomotion. Finally, to explore how cues from the physical environment – in this case the flow cues experienced by fish – influence active swimming behavior, we develop a recurrent neural network model to predict active locomotion as a function of flow cues, and to forecast fish movement trajectories over the near term. Taken together, the elements of our methodology allow one to explore a broad suite of questions about how migrants interact with environmental flows that have been challenging to address in past studies of animal migration. We illustrate several applications of our approach by applying it to questions about navigation behavior and migratory energetics over a wide dynamic range of flow conditions.

2 Materials and Methods

The methodology we use to integrate tracking data with estimates of the flows animals experience is illustrated in Fig. 1. In addition to estimating physical variables at each point in time, the framework includes a step to predict movement behavior of animals as a function of these physical variables

(Fig. 1e,f) to determine the extent to which physical variables affect movement decisions. The data inputs to the modeling framework are animal trajectories and the bathymetry and hydrodynamic data needed to build the CFD model (Fig. 1a and 1b). The hydrodynamic data consist of two-dimensional (along-stream and lateral) near-surface river water velocity measurements collected with four Acoustic Doppler Current Profilers (ADCPs) (see Section 2.1 below), and river bathymetry obtained from the 2010 California Department of Water Resources and the United States Geological Survey's 2m-resolution multibeam sonar survey (Wang et al., 2018). Fish trajectories consisted of two-dimensional (along-stream and lateral) tracks obtained from the California Department of Water Resources (see Section 2.1 below).

We use the hydrodynamic data as inputs to simulate the flow-field in the section of river system with sub-meter spatial resolution and one second temporal resolution using an Unsteady Reynolds-averaged Navier Stokes (URANS) CFD model (Fig. 1a-c). We use the fish trajectories to first quantify the kinematics of motion (i.e., the velocities and accelerations of the fish) and, subsequently, the hydrodynamic information to quantify the dynamics of motion, i.e., the drag forces experienced by the fish and the locomotion forces exerted by the fish (Fig. 1d). We then model the locomotion force of each individual using the information from the fish trajectories and local hydrodynamic forces by training the neural network model describing fish locomotion behavior. Subsequently, we employ the trained neural network for multivariate time-series prediction of locomotion forces as a function of the time series of hydrodynamic forces and behavioral responses (Fig. 1e). After producing predictions of locomotory behavior, we used the drag force and the locomotion force predicted by the neural network to predict each individual fish's trajectory (Fig. 1f).

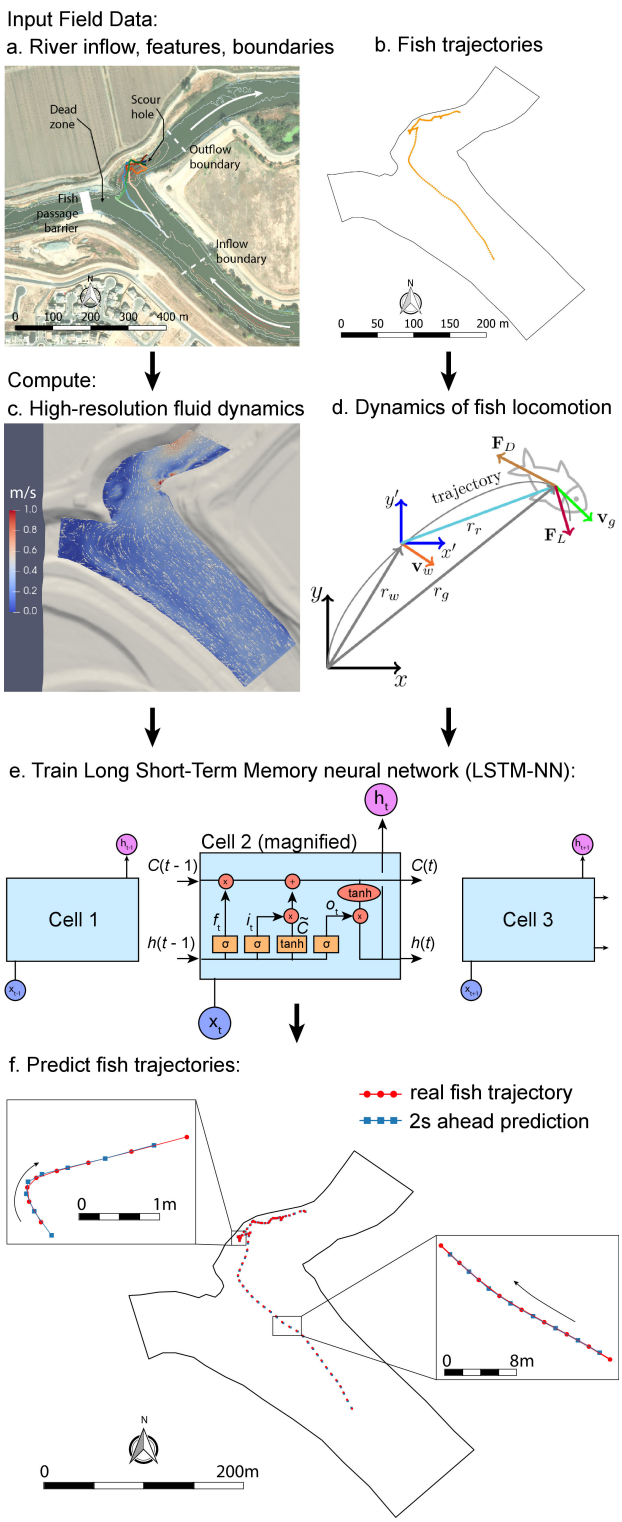


Figure 1: Modeling framework. a) Physical features of the environment and inflow data are collected along with b) migrant movement trajectories. c) Physical data are used to build Computational fluid dynamic (CFD) modeling of water flow. d) CFD predictions are combined with observed fish movements used to decompose motion into drag-induced forcing by the flow and active locomotion. e) The Long Short-Term Memory Neural Network (LSTM-NN) model is developed to forecast locomotion. f) Locomotion predictions and flow are combined to forecast movement trajectories and predictions are compared to out-of-sample data.

2.1 Field data

Flow and animal tracking data were provided by the California Department of Water Resources. These data were collected through a large collaborative study of a segment of the San Joaquin River within an agricultural and urban watershed in the California Central Valley (study details provided in AECOM, 2015). The spatial locations of fish implanted with acoustic transmitters were inferred using tag detections by a hydrophone array extending over roughly $1km$ of the San Joaquin River at the junction with Old River – a tributary – and immediately downstream of the Southernmost extent of the Sacramento-San Joaquin Delta. The Delta is an inverted alluvial fan estuary formed at the confluence of the Sacramento River from the North and the San Joaquin River from the South, as well as numerous tributaries. This watershed is used by several species of salmonids of high conservation concern. Subpopulations of Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*O. mykiss*) traverse portions of the San Joaquin River and the Delta during their juvenile migration to the Pacific Ocean (Williams, 2006), where they mature before returning as adults (Sridharan et al., 2006 for a detailed description of the hydrometeorology and hydrodynamics in the Delta).

Our study domain includes distinct regions as shown in Fig. 1a: (i) a $500m$ long reasonably straight prismatic section of the mainstem San Joaquin River about $150m$ downstream of a meandering section where the flow is Southeast to Northwest, (ii) a junction at the Northwestern region of the straight section where the Old River bifurcates to the West, and (iii) a sharp $90°$ bend Eastward in the mainstem San Joaquin River. During the period when the study was conducted, the bifurcation into Old River was blocked by a temporary earthen barrier (white box in Fig. 1a). The Eastward bend at the northern end of the domain is characterized by an approximately $10m$ deep scour hole along the

North bank where the flow separates and strongly recirculates before rejoining the freestream along the San Joaquin River (see Appendix D for the bathymetry of study domain).

Two-dimensional near-surface velocity fields were acquired by AECOM Technical Services between 23 April and 30 May, 2012 using moored RDI Channel Master side-looking broadband Acoustic Doppler Current Profilers (ADCPs) operating at 600 Khz. Each cross-section was comprised of 2m-bins, over which point velocity measurements were averaged over several minutes. A 5m-resolution flow field was reconstructed at fifteen-minute intervals throughout the study domain by first numerically computing the streamlines from the Southermost ADCP cross-section and performing an inverse distance weighting interpolation using the velocity vectors obtained from the instrumented cross-sections (Stumpner, 2013a, Stumpner, 2013b). Fish trajectories were obtained from 424 Fall-run Chinook salmon implanted with injectable HTI hydroacoustic tags (M800 and 795Lm models) which were detected at thirteen HTI hydroacoustic detectors (model 590) deployed in an two-dimensional array throughout the system. By colocating fish position using a minimum of four detectors, fish positions were typically estimated at a precision of within 1m every two seconds (AECOM, 2015). In the present study, we used 184 of these tracks that were sufficiently long to be included in the neural network analysis. We applied our own post-processing pipeline to raw tag detections. This consisted of breaking tracks from each fish into sub-segments if subsequent locations were separated by more than 30 seconds in time. Within each sub-segment, we smoothed tracks using a third-order Savitzky-Golay filter with filter length of 22 seconds. Positions were also interpolated to a regular time interval of 2 seconds between subsequent locations.

2.2 Fish behavior

2.2.1 Movement Kinematics

The first step in our workflow is describing the kinematics of fish movement. The accuracy of position data in the depth dimension was poor, likely due to constraints on the positioning of hydrophones determined by the relatively shallow average depth of the study region (AECOM, 2015). As a result, we were unable to study movements of fish in the depth dimension, and we retained only the horizontal coordinates of the position of each fish. Accordingly, tracks are represented as 2-dimensional trajectories through the river section, and we consider only horizontal components of the fish kinematics and dynamics. Henceforth, we assign the East-West direction as the x-dimension and the North-South direction as the y-dimension. To keep track of the relative motion of fish and flowing water, we define two reference frames: an inertial frame (x, y) fixed at a point on the river bank and a relative frame (x', y') moving along the fish trajectory with water velocity $\mathbf{v}_w$, see Fig. 1d. Given these reference frames, the position of a fish can be defined as follows:

$$\mathbf{r}_g = \mathbf{r}_r + \mathbf{r}_w. \tag{1}$$

Here, $\mathbf{r}_g$ is the fish position with respect to the inertial frame (x, y), $\mathbf{r}_r$ is the fish position with respect to the relative frame (x', y') and $\mathbf{r}_w$ is the position of the relative frame with respect to the inertial frame. By recursively differentiating Eq. 1 with respect to time we obtain the velocity $\mathbf{v}_g$ and acceleration $\mathbf{a}_g$ of each fish as follows

$$\mathbf{v}_g = \mathbf{v}_r + \mathbf{v}_w, \tag{2}$$

$$\mathbf{a}_g = \mathbf{a}_r + \mathbf{a}_w. \tag{3}$$

$\mathbf{v}_g$ and $\mathbf{a}_g$ are the fish's velocity (or overground velocity) and acceleration with respect to the inertial frame, $\mathbf{v}_r$ and $\mathbf{a}_r$ are the fish relative velocity and acceleration with respect to the relative frame and $\mathbf{v}_w$ and $\mathbf{a}_w$ are the velocity and acceleration of the relative frame with respect to the inertial frame. The latter quantities can also be interpreted as velocity and acceleration of a water parcel along the fish's trajectory. Eq. 2 and Eq. 3 are useful to decompose the fish motion (see Section 2.2.2 below).

2.2.2 Movement Dynamics

Once the kinematics are defined, we subsequently apply the momentum equation (i.e., Newton's second law of motion) to each fish to quantify its movement dynamics. In the horizontal plane, we identify two forces for each fish: locomotion force $\mathbf{F}_L$ and drag force $\mathbf{F}_D$, see Fig 1d. We assumed that vertical forces such as gravitational force and buoyancy balance each other resulting in null vertical acceleration. Defining the fish's mass as m_{fish}, the fish dynamics can be summarized as

$$m_{fish}\mathbf{a}_g = \mathbf{F}_L + \mathbf{F}_D. \tag{4}$$

The drag force acts opposite to the relative motion of the fish moving with respect to the surrounding flow and it can be defined (Hoerner, 1965) as

$$\mathbf{F}_D = -\frac{1}{2}\rho_w A_f C_d ||\mathbf{v}_g - \mathbf{v}_w||(\mathbf{v}_g - \mathbf{v}_w), \tag{5}$$

where ρ_w is the water density, A_f is the fish's wetted area and C_d is the drag coefficient, see Appendix A for how we calculate C_d and A_f. The term $\mathbf{v}_g - \mathbf{v}_w$ is the fish relative velocity $\mathbf{v}_r$ with respect to the relative frame (see Eq. 2). The locomotion force can then be calculated by inverting the momentum equation, see Eq. 4. For this approach to be useful for understanding how instantaneous

fish behaviors contribute to their overall migration trajectories, we need information on the drag force at a spatial and temporal resolution commensurate with the tracking data. While m_{fish} can be obtained from the metadata associated with the tracking experiments and $\mathbf{a}_g$ can be directly obtained from the tracking data, $\mathbf{F}_D$ cannot be calculated at the desired resolution from the fifteen-minute 5m-resolution interpolated ADCP $\mathbf{v}_w$ fields. We therefore developed the CFD model of the river system to estimate $\mathbf{v}_w$, and used this estimate to infer $\mathbf{F}_D$ and compute $\mathbf{F}_L$. The details of the CFD modeling are described in the following sections.

The tracking data consist of 184 fish tracks for a total of $129,830$ location points with a standardized temporal resolution of $2s$. We show several example tracks in Fig 1b. Given the fish position $\mathbf{x}_g(t_n)$ from each track, the fish velocity with respect to the inertial frame (see section 2.2.1) is $\mathbf{v}_g(t_n) \approx (\mathbf{x}_g(t_{n+1}) - \mathbf{x}_g(t_n))/\Delta t$, where $t_n = [2, 4, 6, \dots]$ and $\Delta t = 2s$. The fish velocity with respect to the relative frame is obtained by reversing Eq. 2 such that $\mathbf{v}_r(t_n) = \mathbf{v}_g(t_n) - \mathbf{v}_w(t_n)$. $\mathbf{v}_w(t_n)$ is computed from the CFD results for each fish track (see section 2.3). Consequently $\mathbf{a}_r(t_n) \approx (\mathbf{v}_r(t_n) - \mathbf{v}_r(t_{n-1}))/\Delta t$. With the kinematics defined thus, it is now possible to calculate the locomotion force for each fish by combining Eq. 4 and Eq. 5 such that

$$\mathbf{F}_L(t_n) = \frac{1}{2}\rho_w A_f C_d ||\mathbf{v}_r(t_n)||\mathbf{v}_r(t_n) + m_{fish}\mathbf{a}_g(t_n) = f(\mathbf{v}_g(t_n), \mathbf{v}_w(t_n)). \quad (6)$$

It is important to notice that $\mathbf{F}_L(t_n)$ is a function of $\mathbf{v}_g(t_n)$ and $\mathbf{v}_w(t_n)$ as shown in Eq. 6.

2.3 Hydrodynamic variables

The next step in our workflow is to compute the drag force $\mathbf{F}_D$ on the fish. Since $\mathbf{F}_D$ is a function of $\mathbf{v}_w$ (see Eq. 5) we simulated the flow dynamics of the river

using a three-dimensional CFD model based on Unsteady Reynolds-Averaged Navier-Stokes (URANS) equations. The river flow is considered incompressible and isothermal with the deflection of the water surface being represented by a two-phase water-air Volume of Fluid (VOF) model. We used the openFOAM solver interFoam (Deshpande, Anumolu, and Trujillo, 2012) to develop this model. Although the tracking data we used are two-dimensional, we constructed a three-dimensional CFD model to realistically represent the statistics of the turbulence and the flow dynamics at the scour hole and in regions near the channel banks. We assumed tracks were located within the uppermost cell of the CFD volume corresponding to approximately 0.3 meters below the water surface.

2.3.1 Solver and Model Parameters

The interFoam solver in openFoam implements the continuity and momentum equations for isothermal and incompressible flows along with an additional equation tracking the fraction of air within each parcel of water. The URANS models requires turbulence closure equations in order to be a well-posed PDE system (Menter, 1994). We used the $k - \omega$ equations to represent the statistics of the unresolved turbulence. The boundary conditions for the velocity and the water elevation are based on field measurements, see Section 2.1. The empirical flow velocity time-series is available at the inlet section for the three-month period from March to May with a time resolution of 15 minutes supersampled linearly at 2s intervals.

2.3.2 Modeling active locomotion: a neural network approach

The final step in our workflow (Fig. 1e,f) is to develop a model describing how fish locomotion depends on features of the environment, including the hydrodynamic forces the animal experiences as it moves through the water. The details

of sensory integration, processing, and decision-making during navigation are poorly understood for most migratory species, including migratory fishes. To avoid making *ad hoc* assumptions that might arbitrarily restrict the form of the relationship between physical variables and movement behavior, we modeled effects of flow on movement behavior using a flexible approach for time-series prediction, the Long Short-Term Memory Neural Network (LSTM-NN).

We selected the LSTM-NN as a reasonable model of movement behavior for two reasons: first, in the past, LSTMs have been used successfully to model movements of vehicles and pedestrians (e.g., Xue, Huynh, and Reynolds, 2018, Altché and De La Fortelle, 2017). Second, there is detailed documentation in the literature (Kang and Choi, 2005) on how LSTMs are implemented in TensorFlow (Abadi et al., 2015). This existing software implementation makes LSTMs a convenient modeling tool for describing the relationship between physical variables and migrant behavior when no *a priori* model exists. Details of the underlying structure of the LSTM and how it maps inputs to outputs is given in the Appendix D. In the Discussion, we further elaborate on the *pros* and *cons* of LSTM and the situations in which it is likely to provide a good model of navigation behavior.

In the current application, we use the LSTM to predict the locomotory force produced by migrating fish at each time step. We take, as input to the network, the fish's overground velocity, $\mathbf{v}_g$, and the water velocity, $\mathbf{v}_w$, because $\mathbf{F}_L = f(\mathbf{v}_g, \mathbf{v}_w)$ as shown in Eq. 6. This assumes the fish could measure overground velocity, which could be accomplished, for example, through visual means, by estimating the optic flow of visual features on the benthos (e.g., the river bed itself, submerged debris or aquatic vegetation). In the past, environmental variables such as water acceleration, hydrostatic pressure (Goodwin et al., 2014), turbulent structures (Lacey et al., 2012), turbulent kinetic energy

intensity (Gao et al., 2015), and circulation around the fish (Oteiza et al., 2017) have been used to explain fish movement behaviors. We decided to use the water velocity experienced by the fish because the river system under consideration is characterized by a relatively low turbulent kinetic energy content, and because other mechanisms of behavior response to variables such as the local shear or circulation are not understood in complex environmental flows. Moreover, exploratory analyses including other variables in LSTM-NN training did not indicate improved performance.

The resulting trained LSTM-NN is a function that relates the overground velocity and water velocity experienced by a migrating fish at some time t_{n-1} to the locomotion force produced by that fish at time t_n:

$$\mathbf{F}_L(t_n) = LSTM(\mathbf{v}_g(t_{n-1}), \mathbf{v}_w(t_{n-1})), \tag{7}$$

where t_n is the discrete time-step with $n = [0, 1, ..., N-1, N]$. We note that the use of $\mathbf{v}_g$ in this formulation allows us to explicitly model the locomotion of the fish as a function of its memory of its response to the local environment, as well as its current sensory experience. Details of LSTM-NN structure and how inputs map to predictions are given in Appendix C.

2.4 LSTM-NN fitting, predictions, and out-of-sample testing

We used the LSTM-NN module available in TensorFlow (Abadi et al., 2015) for predicting $\mathbf{F}_L$. The training data set consisted of the time-series of overground velocities of fish and water velocities along the fish tracks. Furthermore, we used the time-series related to the observed components of the locomotion force $F_{L_x}(t_n)$ and $F_{L_y}(t_n)$ computed with the field data, see Eq. 6, as reference output for the LSTM-NN training. We optimized the LSTM-NN settings to

minimize the average error of ΔF_{L_x} and ΔF_{L_y}, where Δ is the difference between the predicted and actual value. We tested a number of LSTMs-NNs with an increasing number of cells and used the k-Nearest-Neighbor method (Arya et al., 1998) to select the architecture with the optimal number of cells (see Appendix C). We found an LSTM-NN with 112 cells to be the optimal configuration, because it produced ΔF_{L_x} and ΔF_{L_y} with minimal average error. After the end of the cascade of LSTM-NN cells, we included a dense layer of two rectified linear activation functions, $ReLU$, to output the model results (Abadi et al., 2015). The length of the training data set was 60% of the original data set subdivided in 72 batches; the total length of the data set consist of 129,830 data points. We trained the LSTM over 30 epochs.

2.5 Forecasting fish movements

Once the LSTM-NN model of $\mathbf{F}_L(t_n)$ is fitted to training data, it can be used to predict migrant trajectories by applying the forward Euler method to Eq. 4 as follows:

$$m_{fish}\frac{\mathbf{v}_g(t_n)-\mathbf{v}_g(t_{n-1})}{\Delta t} \approx m_{fish}\mathbf{a}_g(t_n) = \mathbf{F}_L(t_n) + \mathbf{F}_D(t_n), \tag{8}$$

Hence, considering Eq. 2 and Eq. 5

$$\begin{cases} \mathbf{F}_L(t_n) = LSTM(\mathbf{v}_g(t_{n-1}), \mathbf{v}_w(t_{n-1})) \\ \mathbf{v}_g(t_n) = \mathbf{v}_g(t_{n-1}) + (\mathbf{F}_L(t_n) + \mathbf{F}_D(t_n))\frac{\Delta t}{m_{fish}} \\ \mathbf{x}_g(t_n) = \mathbf{x}_g(t_{n-1}) + \mathbf{v}_g(t_n)\Delta t \end{cases} \tag{9}$$

The initial conditions $\mathbf{v}_g(t_0)$, $\mathbf{v}_w(t_0)$ and $\mathbf{x}_g(t_0)$ are determined from the corresponding field data. This scheme can be used both to predict fish velocities and trajectories in-sample, and to predict entirely new trajectories, given the

appropriate input data.

3 Results

3.1 CFD results

We used the CFD model of the study domain to compute flows over the duration that fish were present. In Fig. 2a, we show a snapshot of the water velocity field in the horizontal section near the water surface (where the fish trajectories are assumed to be contained). The contour colors represents the water velocity magnitude, while the vectors represent the direction of local flow. The southeast region close to the inlet is characterized by a flow that tends to be uniform. In contrast, the northwest region close to the barrier shows a large area of flow recirculation; two counter-rotating vortexes appear along the barrier Fig. 2b. A vortex rotating in the counterclockwise direction on the northern bank is visible in Fig. 2c. The formation of this vortex is due to the sharp bend of the river course and associated scour hole, causing the flow to recirculate along the north bank. We validated the CFD model by comparing the velocity profiles from the numerical simulation against the velocity profiles from the field measurement; we show in Fig. 2d and 2e that the CFD results (lines) are in good agreement with the ADCP measurements from two cross sections which include a typical variation of $\pm 5.8 cm/s$ within each velocity bin (dots; AECOM, 2015).

3.2 Fish migration behavior and LSTM model predictions

The tracking data provided is an extensive collection of fish velocity and trajectory estimates from across the study domain. By applying the velocity decomposition introduced above to the fish trajectory data and CFD-generated flow velocity predictions, we were able to estimate the distinct contributions of

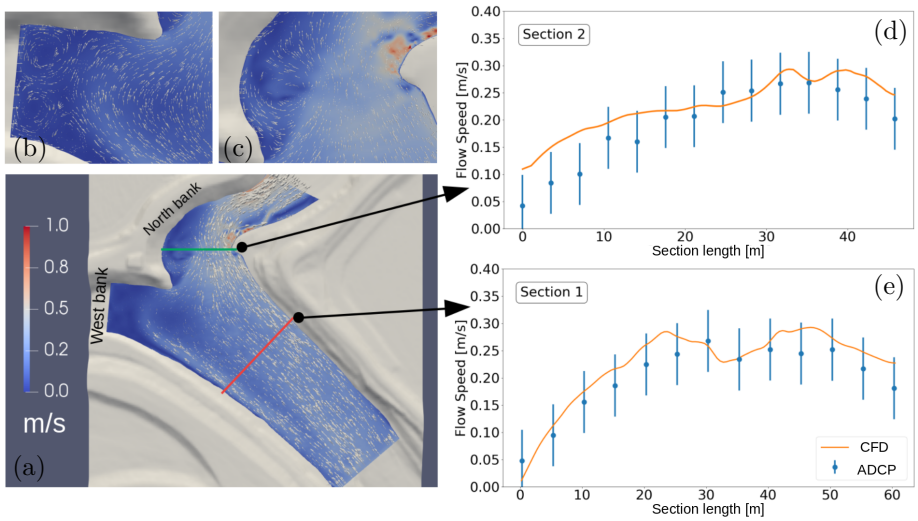
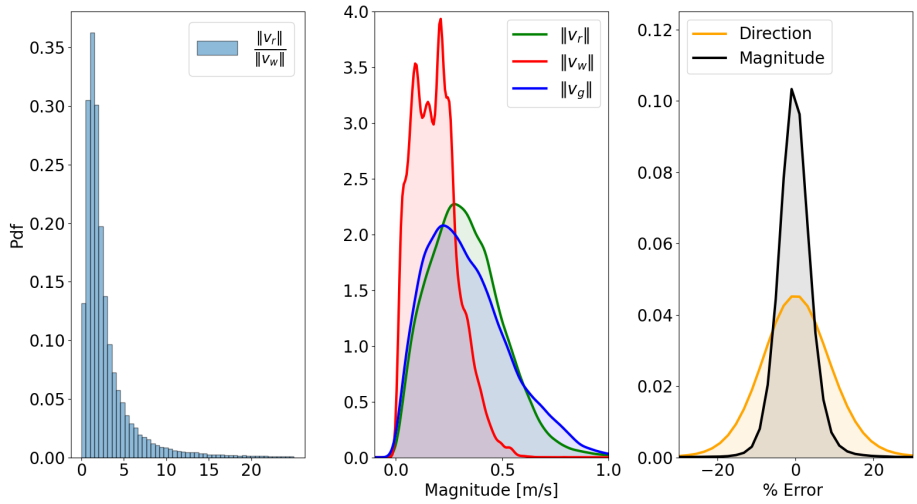


Figure 2: a) Snapshots of the velocity field magnitude at one point in time. The color bar indicates flow magnitude in units of m/s. Lines through the domain show cross-sections used for model validation. Red line: Section 1 (shown in panel e). Green line: Section 2 (shown in panel d). b) Zoomed in view of the Western bank showing regions of weak recirculation flow. c) Zoomed in view of the Northern bank showing a vortex. d) Comparison between CFD flow predictions (line) and water velocity magnitude measured by ADCP (blue dots and error bars) in Section 2. Profiles averaged over 30 minutes. e) Comparison between CFD predictions and data.

water flow and migrant locomotion to the observed overground velocity of each migrating animal. In Fig. 3b, we show the probability density function (*pdf*s) of the magnitudes of the fish overground velocity, $||\mathbf{v_g}||$, and the fish relative velocity $||\mathbf{v_r}||$ (i.e., the animal's velocity relative the the moving water), as well as the magnitude of water velocity at observed fish locations $||\mathbf{v_w}||$. Note that the overall magnitude of relative velocity of the fish – the component of velocity due to active locomotion – often exceeds the magnitude of water velocity, indicating that fish regularly swim at speeds that are higher than the speeds of the flows in which they are swimming. This can be seen more directly in the distribution of the ratio of relative velocity magnitude to the overground velocity magnitude, Fig. 3a. The right tail of this distribution shows cases where fish are swimming

at speeds that far exceed the speed of local water movement.



(a) (b) (c)

Figure 3: Empirical velocity data and LSTM-NN prediction performance. a) *Pdf* of the ratio of the magnitudes of the fish relative velocity to the water velocity. b) *Pdf*s of magnitude of the fish relative and overground velocity (green and blue distributions, respectively) and *pdf* of water speed at fish locations computed from CFD model (red distribution). c) *Pdf*s of prediction errors from the LSTM model shown as percentage error in predicted direction (orange distribution) and magnitude (grey distribution) of locomotion force.

Employing Eq. 6, velocity estimates can be used to estimate the locomotory force produced by each fish to achieve its observed motion. The LSTM-NN model of locomotion accurately predicted this locomotory force in the 51,932 data points (40% of the original data set) that were held out during training, Fig. 3c. Typical errors for direction are within 20% of observed values, and magnitude estimates are typically accurate to well within 10% of observed values, Fig. 3c. Our results indicate that our model of fish swimming behavior is able to predict this behavior for times and locations on which the model was not trained (i.e., on the out-of-sample data).

Given a prediction for the locomotory force, the equation system in Eq. 9 can be used to predict a fish's trajectory, $\mathbf{x}_g(t_n)$, in addition to the locomotion

forces, accelerations, and velocities.

We show the distributions of error in predicting position prediction measured in body length for several time ahead predictions, e.g. from 2s up to 30s (predictions shown are for 51,932 data points held out-of-sample during training)

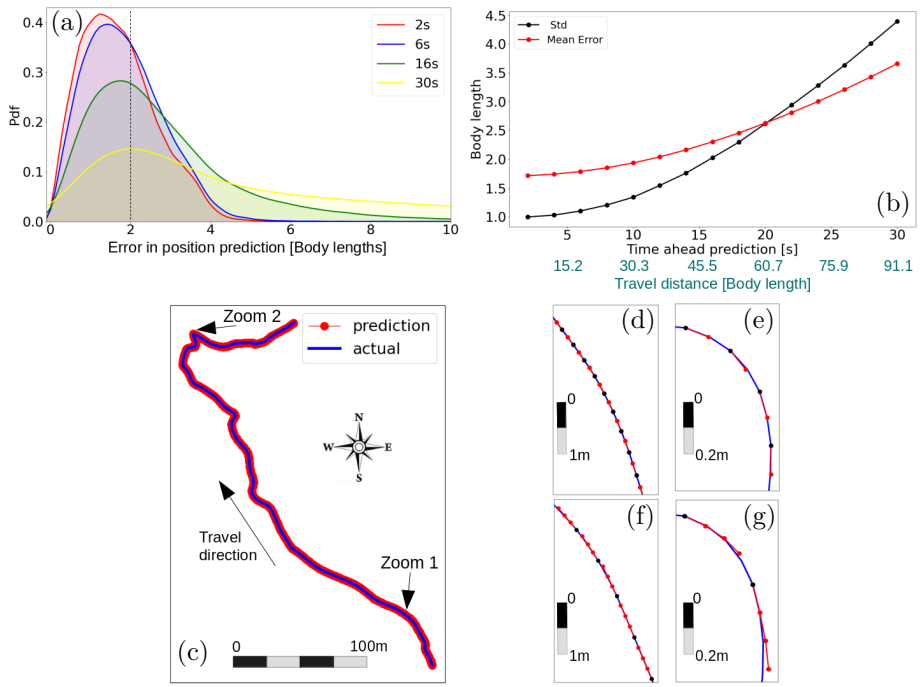


Figure 4: Trajectory prediction performance over different forecast time horizons. a) $Pdfs$ of the error in predicting the position of the fish [in body lengths] for several of the prediction horizons. The vertical line at two body lengths indicates that the mode of the error in predicting fish positions is well contained for even large forecast time horizons. b) Mean error (red) and standard deviation (black) in predicting the position over forecast horizon (time in seconds) and average distance traveled by the fish (scale in green [in body lengths]). c) Example of a single trajectory prediction. Blue line shows observed trajectory; red points show predicted trajectory for $2s$-ahead predictions. d) Zoomed into a straight section of the track (zoom 1) for $2s$-ahead prediction. Black points show an initial location of the fish from which the Eq. 9 is initialized. Red points show predicted location $2s$-later e) Zoomed into a curved section of the track (zoom 2) for $2s$-ahead prediction. f) and g) $6s$-ahead predictions zoomed into the sections shown in d) and e) respectively. Colors and symbols in e), f) and g) are as in d).

in Fig. 4a; while the tail of the error distribution includes significantly larger errors as the prediction horizon increases, the mode of the error distribution only grows by roughly one body length when moving from a prediction horizon of 2 seconds to a horizon of 30 seconds. Red and blue distributions in Fig. 4a show $2s$-ahead and $6s$-ahead predictions, illustrating that increasing the forecast horizon from 2 to 6 seconds does not result in a dramatic decrease in the quality of predictions. Nevertheless, the discrepancies between the observed and predicted trajectories do continue to grow as the prediction horizon is increased as one would expect. In Fig. 4b, we show the dependence of the mean and standard deviation of the error in predicting position on the forecast horizon. Up to forecast horizons of 30 seconds, the mean prediction error remains below four fish body lengths. It is worth noting that the mean and standard deviation of prediction error represent a small fraction of the typical travel distance during any given forecast horizon. For example, in 30s the average travel distance is 91.1 body lengths while the mean error is about 3.5 body lengths, green scale in Fig. 4b. In Fig. 4c, we show a sequence of predictions along the length of a long trajectory. In Fig. 4c the blue line is the actual trajectory of a tagged fish while the red dots are the $2s$-ahead predictions; this fish trajectory consists of 455 points corresponding to $906s$ of the fish's trajectory through our study region. We zoom into two parts of the trajectory which are structurally different from each other: a relatively straight section in Fig. 4d and a sharply curving section in Fig. 4e. In these plots, the black dots are initial locations to initialize the model in Eq. 9. In both sections of the track, there is close alignment between the observed and predicted trajectory points. In Figs. 4f - 4g, we show the same sections of the track for $6s$ ahead predictions (3 time-steps ahead); while the accuracy tends to decrease as the prediction horizon increases, errors remain reasonably bounded, even in the highly curved region of the trajectory.

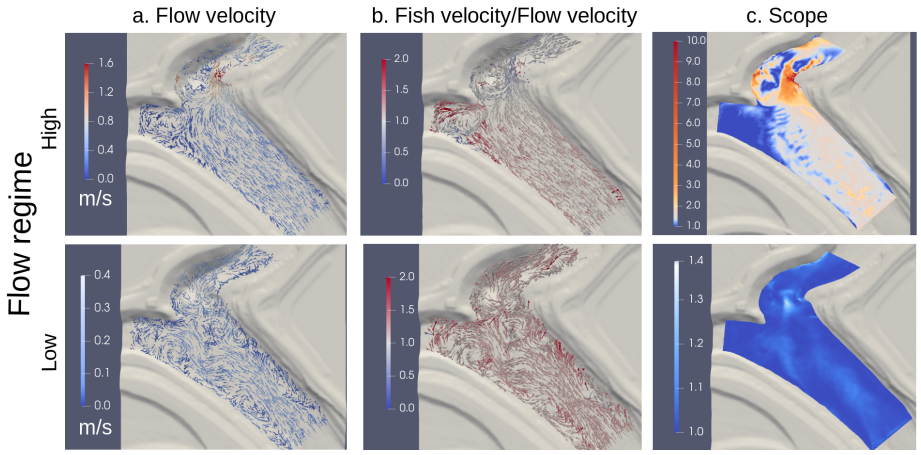


Figure 5: Predicted water flow, velocity ratio and locomotory scope under high (upper panels) and low (lower panels) net flow conditions. a) Flow velocity field. b) Ratio of the relative velocity of the fish to the water velocity. c) Locomotory scope, S_L. Note large differences in range of predicted scope between high (upper) and low (lower) flow conditions.

By combining the CFD model to predict flow, and the LSTM-NN to predict fish locomotion in response to flows, one can explore a wide range of questions about how flow and locomotory behavior of animals interact under different conditions. For example, by exploiting the first two equations in Eq. 9, it is possible to estimate the movements of fish across the entire flow domain for different environmental conditions of interest. In Fig. 5a, we show snapshots of the water velocity vector field in the river system during the period of lowest and highest outgoing flows, respectively. In Fig. 5b, we show the "relative swimming velocity", R_{fw}, defined as the ratio of the magnitudes of relative velocity of fish and the water velocity, for the same flow conditions shown in Fig. 5a. Two key patterns are immediately evident. First, the relative swimming velocities of the fish regularly exceed water velocity throughout much of the domain. This predicted spatial pattern is consistent with the empirical observation shown in Fig. 3a-b that the observed relative swimming velocities regularly exceed

water velocity. Moreover, this demonstrates the degree to which fish movements appear to be driven by active swimming behavior rather than simple passive forcing by the flows. The second pattern evident in Fig. 5b is that there is strong spatial heterogeneity in the ratio of fish to water velocities, and these spatial patterns change as the overall flow transitions from weak to strong. For example, during low flows, the relative swimming velocity is greatest in the open channel, upstream of the bend. During high flows, relative swimming velocity is much slower in this same region. During high flow, the relative velocities of fish are smaller than the water velocity in the regions of high circulation near the channel bifurcation, whereas this pattern is not evident at low flows.

To determine the impact this spatial and flow-dependent variation in behavior has on migration energetics, we can estimate the rate of power output required to achieve predicted movements across the domain. We do this by defining a quantity we will call "locomotory scope," $S_L = 1 + \mathbf{F}_L \cdot \mathbf{v}_r / RMR$, which characterizes the power output required to fuel resting metabolism and locomotion, normalized by the resting metabolic rate (RMR) (see Appendix A for RMR calculation). The locomotory scope is a measure of the power output of an animal measured in units of resting metabolic rate. Thus, a locomotory scope of one corresponds to a case where an individual devotes no power to locomotion, whereas a value of five corresponds to a case where the total rate of power output (including resting metabolism) is five times resting metabolic rate. Note that locomotory scope as it is defined here is not the same as aerobic scope because we neglect any power loss due to inefficiencies in force production, and we do not consider other sources of power consumption (e.g., specific dynamic action) that could be relevant during migration. Thus, locomotory scope should be taken as a lower bound on the relative power output required during movements.

Our analysis of predicted locomotory scope reveals strong spatial patterns in power output as well as strong differences in patterns across specific instances of low and high flow conditions, Fig. 5c. Under low flow conditions, locomotory scope was generally below 1.5, indicating that the power required to produce predicted migratory movements across the domain was generally less than half of the resting metabolic rate of migrants. The highest relative power outputs were predicted to be along the center of the main channel, upstream of the channel bend, and in a region of relatively high circulation near the eastward channel bend, Fig. 5c. In strong contrast to these patterns, locomotory scope during high flows was as large as 10 in some regions of the domain, indicating that predicted movements in those regions required total power outputs 10 times higher than resting metabolic rate. The highest rates of power output were predicted to be in the region of strong flow recirculation near the eastward channel bend and along the eastern bank in the same region. However, even outside of these regions the locomotory scope exceeded a value of 1.5 throughout much of the domain. One might expect migrants to take advantage of strong oceanward flows in the high flow conditions by drifting passively rather than swimming actively. To the contrary, our model suggests that migrants generally use far more power under high flow scenarios, particularly in local regions of strong unsteady flow. This is due, at least in part, to the fact that in weak flows, the locomotion force tends to be biased in alignment with the direction of local water flow (Appendix A), whereas in more powerful flows, fish locomotion is aligned opposite or orthogonal to the direction of local water flow.

4 Discussion

Here, we have developed a general methodology to combine quantitative estimates of a turbulent environment with measurements of the movements of

animals to better understand migratory behavior in the wild. Our methodology combines animal tracking data with high resolution physical modeling of environmental flows – here achieved using computational fluid dynamics – to estimate the dynamic flow environment migrants experience and determine the component of force of migratory movements due to active locomotion by the animal. Finally, we employ recurrent neural network methods to relate the physical conditions experienced by the migrant to locomotion behavior, and use this model to forecast movements over times and conditions outside those included in the training data.

Reconstruction of the local physical environment and decomposition of active and passive components of movement have the potential to offer new insights into the processes that influence the movements of migrating animals in complex environments. This approach extends recent work to characterize how migrants move in relation to coarser-scale environmental flows such as water currents and regional wind patterns (e.g. the use of favorable prevailing winds and fast air streams by migrating insects, Alerstam et al., 2011). Our approach also holds significant promise as a tool for management of migratory species because, after careful testing on out-of-sample data, our framework allows one to make predictions about both the physical *and* behavioral consequences of modifying the migratory environment, for example by raising or lowering flow, altering the bathymetry or course of the river, or installing equipment such as water diversion facilities along the migration route (Thorstad et al., 2008, Silva et al., 2018). Although we have applied our framework to migratory fish in a river system, the same methods could be used to understand migratory strategies of flying species by combining high-fidelity tracking during flight (Ling et al., 2018) with CFD modeling of environmental features of interest (e.g. wind turbines, Martin et al., 2017) or physical modeling of turbulent convective flow in the atmospheric

boundary layer (Reddy et al., 2016). It is well known that flying animals also respond to local air flows (Scacco et al., 2019, Shepard, Ross, and Portugal, 2016 and Dabiri, 1993); however, constructing and validating models of air flow poses some unique challenges. For example, it is often challenging to collect high-resolution time-varying data on air currents in the atmosphere that can be used during model validation. For small-scale flow phenomena such as boundary layer flows over localized topography and built-up areas on the order of a few hundred square-meters to a few square kilometers, wind-tunnel experiments over downscaled models can provide validation data sets for high-resolution URANS and LES models of atmospheric flow (e.g., Kellnerová et al., 2018 and Jimenez and Moser, 1998). For flows distributed over larger open areas, on the order of tens of square kilometers, a combination of wind-vane, flux tower and LiDAR and Radar measurements may be used to produce reliable estimates of the air currents (Friedrich et al., 2012 and Madala et al., 2015). An alternate strategy more recently has been to dynamically or statistically downscale global circulation models to spatial-temporal resolutions required for regional-scale analysis and validate these downscaled models using a regional network of weather stations (Winstral, Jonas, and Helbig, 2017 and Wagenbrenner et al., 2016). For many physical modeling methods, open source software packages are readily available (e.g., openFoam), as are packages for constructing statistical models (e.g., R, TensorFlow) of migration behavior once the locomotion component of migratory movements has been computed (Fig. 1e,f).

Computational fluid dynamics, and computational modeling of the flow environment more generally, have already proven to be useful for studying environmental flows in the context of animal migrations. For example, Gisen, Weichert, and Nestler (2016) developed a 3D CFD model of a hydropower dam tailrace using a Detached-Eddy Simulation turbulence model to evaluate impacts on

migrants. Reddy et al. (2016) developed a computational model of thermals in the atmospheric boundary layer to study how soaring birds navigate complex turbulent motion of air. Gualtieri et al. (2019) modeled fish migration through a river system as particles characterized by two bioenergetic parameters, one related to the drag force a fish experienced and one related to the energy needed by a fish to remain in a specific location. Similar assumptions were adopted by Ramón, Acosta, and Rueda (2018) who studied the hydrodynamic drivers of juvenile salmon movements using CFD to compute the flow field across a river system. Although Gualtieri et al. (2019) and Ramón, Acosta, and Rueda (2018) modeled fish as passive particles dragged by the river flow, as we show here, even small migratory fish can swim very actively, and in many cases, their locomotion force production is significant. Indeed, our analysis of relative velocity of fish and water (Fig. 5) shows that the component of ground speed due to active locomotion is often greater in magnitude than the water speed, even in relatively fast flows. Our findings corroborate results from other systems (e.g., Arenas et al., 2015), and suggests more generally that even small migratory animals such as the juvenile salmon considered here (mean length 112 mm) spend significant amounts of energy on locomotion, even when the net direction of environmental flow aligns with the direction of migration.

Several researchers have begun using CFD models to attempt to understand how migrants navigate complex physical environments at spatial and temporal resolutions similar to those considered in our study. For instance, Goodwin et al. (2014) used a steady-state RANS CFD model to compute water field velocity in combination with an *ad hoc* fish behavioral model to represent fish movements in the vicinity of hydropower facilities. Gao et al. (2015) used a similar approach for a slot fishway, applying a parametric model of fish movement. Martin et al. (2017) combined a CFD model of a wind turbine and aerody-

namic modeling of bat flight to understand how flying bats might interact with the forces produced by wind turbines. In the present study, we extended the approaches of these past models by developing a URANS CFD model to compute time-dependent flow variables. We employed a time-dependent CFD model because the flow-field through complex channel morphologies like the one studied here can be extremely dynamic, particularly in river and estuary systems where flows can change due to a variety of reasons including precipitation, effects of tides, sudden storms and floods and local water diversions and runoff. A dynamic, time-varying CFD model allows us to model changes in flows that occur as inflows change. In general, a dynamic model will be necessary to correctly decompose drag and locomotion forces when the flow field changes appreciably over time. Not accounting for changes in flow will lead to biased estimates of these components.

After we validated that model against empirical flow measurements, we used flow estimates, along with observed fish migration trajectories, to infer the drag and locomotory forces that produced observed fish accelerations. Rather than prescribing an *ad hoc* model of locomotion behavior, we used a flexible recurrent neural network model (the LSTM-NN) to describe how flow cues and past behavior influence locomotion behavior in the near future. Importantly, this approach provides accurate near-term forecasts of migrant behavior on out-of-sample data. Thus, our model both captures observed patterns of locomotion in complex flows, and is capable of making accurate out-of-sample predictions to evaluate hypothesis about the implications of migratory behavior across space and over ranges of environmental conditions (e.g., Fig. 5).

To predict swimming behavior, we relied on a flexible multivariate time series method. Multivariate time series analysis methods such as the LSTM-NN have become popular in many fields including healthcare (Kang and Choi,

2014), phoneme classification (Kang and Choi, 2005), and activity and action recognition (Pavlovic, Frey, and Huang, 1999, Geurts, 2001, Fu, 2015, Yu and Lee, 2015). In our analysis, the LSTM-NN model of swimming behavior revealed that knowledge of the flow environment the animal experiences as it moves can allow one to make accurate out-of-sample forecasts of a fish's future movements, at least over short timescales (e.g. 2s-30s). This suggests not only that features of the flow influence the movement decisions animals make as they migrate (Liao, 2007, Oteiza et al., 2017), but also that the behavioral rules or "behavioral algorithms" (Hein et al., 2020) that relate flow to locomotion behavior are at least reasonably similar, both across individual animals, and over the range of time periods included in our study. We believe this workflow of building data-driven models of behavior and validating predictions of those models on out-of-sample data is crucial, given that our understanding of how animals perceive and respond to sensory cues during migration is still far from complete. The flexibility of recurrent neural networks frees our approach, at least to some extent, from assumptions about the precise functional form relating flow variables to the swimming behavior of migrants. However, one disadvantage of using a highly flexible framework like LSTM-NN to relate environmental variables to fish behavior is that, due to the complexity of the neural network model structure, there is no compact symbolic representation of the functional relationships between input and output variables (Martin, Munch, and Hein, 2018). We expect future studies will unpack the patterns described phenomenologically by our LSTM-NN model of movement behavior. In particular, it will be insightful to determine whether migration behavior, like some other animal behaviors including predator evasion (Hein et al., 2018) and prey interception (Brighton, Thomas, and Taylor, 2017), can be described accurately by a set of relatively simple control algorithms (Hein et al., 2020). Future work

could apply other modeling paradigms (e.g., control theory, neuro-ecological modeling, Brighton, Thomas, and Taylor, 2017, Bar et al., 2015) to address this and other fundamental questions, including (i) which variables most influence locomotion, (ii) whether migratory behavior varies appreciably over time, and (iii) the extent to which different individuals respond to environmental variables in different ways. Notably, all of these questions require estimates of both the behavioral actions taken by individual migrants and the environmental variables experienced by those individuals. Our methodology provides a way to acquire such estimates.

While the overall methodology presented here holds much promise, it nevertheless has important limitations. Firstly, due to computational limitations on the simulation of turbulent flow, the spatial and temporal resolution of our CFD model is limited. This means that we cannot resolve fine-scale flow at the scale of the migrating fish's body, nor can we fully resolve temporal fluctuations in flow due to turbulence. This makes it challenging to directly link our model of locomotion behavior with biomechanical (e.g., Lighthill, 1971, Bandyopadhyay, 2002; Cui et al., 2017) or behavioral models (e.g. Oteiza et al., 2017) that describe movement of the migrant's body. Nevertheless, our model does have the ability to resolve larger features in the flow on the spatial scale of tens of body lengths. Such features include gradients in water velocity near channel banks and zones of strong recirculation (e.g., see Fig. 2). This allowed us to conclude, for example, that effects of these features on migratory behavior can be significant (Fig. 5). A second limitation of our approach is due to the tracking data themselves. Tracking data were acquired through hydrophone detections of animals implanted with acoustic transmitters. These data therefore have limited spatial resolution and the status of tagged animals are unknown (e.g., tags from fish consumed by larger predatory fish can still be detected by

the hydrophone array). Such limitations are worth considering when choosing a tag technology to use for studies that will combine tracking and physical modeling to study migratory movement behavior. Another important consideration is that our framework cannot fully address the question of whether high or low flow conditions are more favorable for migration because it does not consider how energy use trades off with other potentially important quantities related to migration success such as the travel time through regions of high predation risk (Anderson, Gurarie, and Zabel, 2005). The times taken by fish to traverse our entire study region were longer, on average, when overall flow was weak (mean of 63 minutes for trajectories experiencing the weakest 10% of flows) than when overall flow was strong (51 minutes for trajectories experiencing strongest 10% of flows). However, variability in this trend was significant. Nevertheless, travel time and other tradeoffs could be included in our framework by integrating additional data sources (e.g. predation risk data).

Despite its limitations, our framework can be used to gain traction on questions that have fascinated migration biologists for many years. Many such questions relate to how migrants use energy as they move through a landscape. As demonstrated in Fig. 5, our methodology has much potential to address these types of questions. For example, when applied to distinct environmental conditions observed in our data set, locomotion force predictions revealed that fish generally spend far more energy moving through the landscape when the overall rate of flow is high than when the rate of flow is low, despite the fact that the net flow direction is aligned with the direction of migration. Our analysis provides additional insights into the cause of this pattern; when fish swim in slow currents their movements are generally oriented uniformly relative to the flow with a slight bias toward alignment in the direction of flow (see Appendix A). On the other hand, when migrants move through high speed currents, their

movements are primarily oriented against the flow or laterally relative to the direction of flow. These lateral and opposing movements require greater power output. It is also important to note our methodology is in no way limited to the study of migratory movements. Both swimming and flying animals modulate short-term movement behavior in response to local environmental flows (Scacco et al., 2019, Shepard, Ross, and Portugal, 2016 and James, 2007). The same methodology presented here can be applied to study animal movement behaviors beyond the context of migration.

In this work, we have presented a general methodology for merging data and modeling of environmental currents with tracking data to understand animal migratory behavior. Our approach extends more traditional methods in migration biology, which have often either ignored interactions with wind and water currents, or modeled these interactions in simple ways that are not fully informed by physical data (e.g., Alexander, 1998, Pennycuick, 2003, Hein, Hou, and Gillooly, 2012, Stier et al., 2014). We believe our framework has the potential to shed new light on how migrants interact with wind and water currents and how behavior and biophysics interact to determine the costs and benefits of different migratory strategies and environmental conditions.

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Data Accessibility Statement

Intended location for data archive: https://datadryad.org/

Authors' contributions statement

Simone Olivetti, Michael A. Gil, Vamsi K. Sridharan, and Andrew M. Hein conceived the ideas and designed methodology; Vamsi K. Sridharan and Andrew M. Hein pre-processed movement and hydrologic datasets; Simone Olivetti constructed CFD and LSTM models and carried out all analyses with input from all authors. Simone Olivetti and Andrew M. Hein led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Appendix A: Drag coefficient, resting metabolic rate, and swimming orientation relative to flow

To estimate the dragging force on each fish, we required an estimate of the drag coefficient for these animals. The average fish length was $L = 0.112m$ (AECOM, 2015). The drag coefficient was estimated using a formula for Reynolds numbers $R_e > 2000$ based on fish length and fish relative velocity, $C_d = 493.9/R_e^{0.922}$ (Arenas et al., 2015). Given the average fish relative velocity, $v_r = 0.34m/s$, average fish length $L = 0.112m$ and water density $\rho_w = 999.06kg/m^3$ we have $C_d = 0.033$. The fish wetted area A_f is estimated using the formula $A_f = 0.28L^{2.11} = 0.0026m^2$ (Webb, 1976).

Mean fish length was also used to estimate resting metabolic rate for the locomotory scope calculation. We first used length to estimate average mass using scaling a scaling relationship for juvenile Chinook Salmon (Kimmerer et al., 2005): $m_{fish} = (10^{-3})(1.8 \times 10^{-3})L^{3.44}$, which gave an estimate of $m_{fish} \approx 0.02kg$. The resting metabolic rate was calculated using the formula: RMR $= m_{fish}^{0.95} 10^{-1.385+0.021T}$, where T is the water temperature (degrees Celsius, Killen et al., 2016).

Fig. 5c (main text) illustrates that fish swim in ways that can cause them to expend far more energy on locomotion when swimming in strong flows than when the overall rate of flow through the system is weak. To better understand the source of this pattern, we can use the observed tracks along with CFD-derived estimates of flow direction to determine how fish orient to local flow in low versus high flow conditions. Fig. 1 shows that when the overall rate of flow through the system is relatively low, fish movements tend to be oriented more or less uniformly with respect to the direction of flow, with a slight bias in the direction of the flow (Fig. 1, left circular histogram). When water currents are

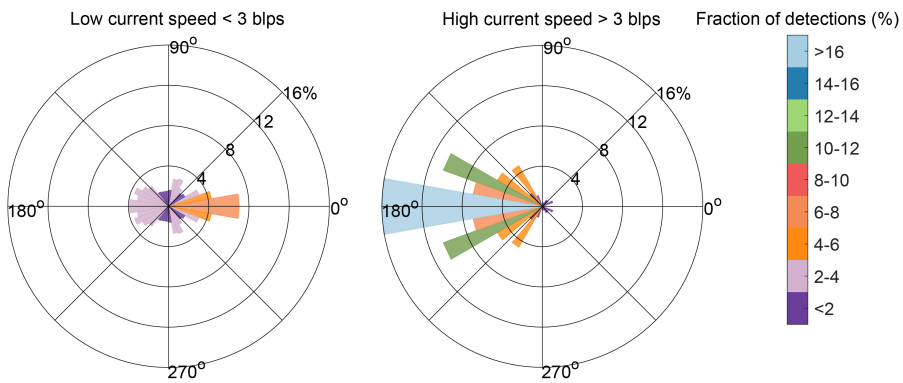

Figure 1: Orientation of fish relative velocity with respect to direction of water flow; low flow regime (left) high flow regime (right). An angle of 0 corresponds to alignment with local water velocity, whereas 180 corresponds to alignment directly against local water velocity. Color scale shows fraction of observations falling into each orientation bin.

fast, fish movements tend to be oriented opposite the flow or at at angles that would move them laterally relative to the flow direction (Fig. 1, right circular histogram). Thus, rather than moving in the same way under different flow conditions, fish tend to move in ways that oppose powerful local flows when the overall rate of flow through the system is high, leading to the high predicted costs of locomotion under such conditions (Fig. 5 in main text).

Appendix B: CFD mesh generation and modeling details

In this Appendix we give more details regarding the mesh generation and boundary conditions used for the CFD simulations. We used SnappyHexMesh (Weller and Tabor, 1998), the openFOAM meshing tool to generate a preliminary mesh which we subsequently trimmed to conform to the bathymetry. The preliminary mesh consisted of four blocks (Fig. 2a). Each block comprises of a specific

number of cells (Table 1). Block one is characterized by hexahedral cells with dimensions $0.8m \times 0.64m \times 0.3m$ respectively in the along-stream, lateral and vertical direction. Blocks two and three are characterized by hexahedral cells with dimensions $0.64m \times 0.45m \times 0.3m$ (Fig. 2b). Blocks two and three have a slightly finer mash in comparison with block one because most of the large coherent structures in the flow occur in the regions spanned by these blocks. Block four is at the outlet of the flow domain, and we therefore applied a gentle

	nx×ny×nz	Total
Block 1	150×210×38	1145700
Block 2	150×210×38	1145700
Block 3	150×210×38	1145700
Block 4	15×210×38	114570

Table 1: Number of cells for preliminary mesh. $nx \times ny \times nz$: number of cells in x, y and z direction respectively.

stretch to the cells towards the outlet, Fig. 2c. The resulting cells dimensions at the outlet are $2.3m \times 0.45m \times 0.3m$. All the blocks together form a preliminary mesh of 3,551,670 cells. We then adapted the preliminary mesh to the topography of the river using the openFOAM tool snappyHexMesh (Fig. 2d and Fig. 2e). Snapped cells are subject to three consecutive mesh refinements. Hence, the refined snapped cells are three time smaller than the cells from the preliminary mesh. The refined snapped cells are arbitrary polyhedral cells bounded by arbitrary polygonal faces. Eventually, after the snapping process, the final mesh consists of 17,474,654 cells. Fig. 2f and 2g show the air-water phases initialized; the red and blue colors are the water and the air media respectively; the white color represents the water-air interface. We applied a zero-gradient for the velocity field on the outlet and the atmosphere boundaries, see Fig.2f.

In the CFD simulations, we apply no-slip conditions to the velocity field on the riverbed and on the barrier, see Fig. 2g. We initialize the turbulent kinetic energy k at $5.4 \times 10^{-5} m^2/s^2$ and the turbulent kinetic energy dissipation rate ω

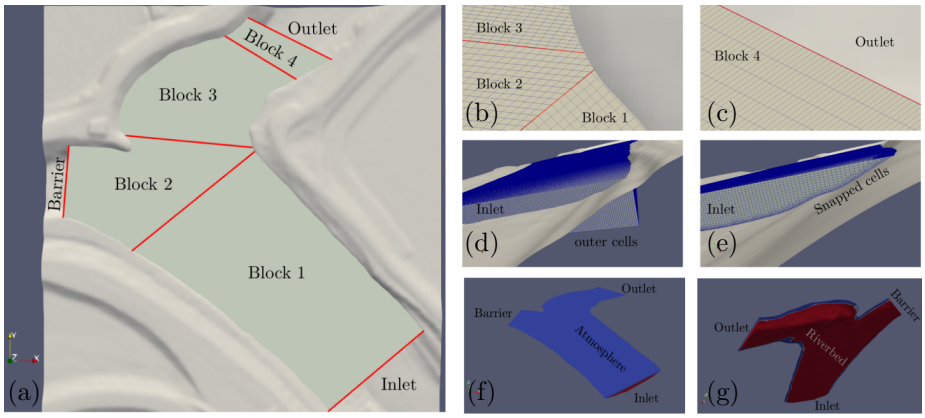

Figure 2: a) Flow domain subdivided in four blocks. b) First 3 contiguous blocks with different mesh resolution. c) Block 4 with a stretch mesh towards the outlet. d) Preliminary mesh with outer cells. d) Final mesh with snapped cells. Boundary and initial conditions: f) Top-down view. g) Down-top view.

at $2s^{-2}$ over the flow domain. We set the physical properties of the air and water media, such as kinematic viscosity and density for a constant temperature of $15°C$ (the system is considered isothermal). The density and kinematic viscosity for the air layer are $\rho_a = 1.225kg/m^3$ and $\mu_a = 1.48 \times 10^{-5}m^2/s$, respectively. The density and kinematic viscosity for the water layer are $\rho_w = 999.06kg/m^3$ and $\mu_w = 1.138\times10^{-6}m^2/s$, respectively. We set the time step for the simulation to $1s$ to ensure numerical stability.

Appendix C. LSTM-NN parameterization and structure selection

To select the structure of the LSTM architecture, one must select the number of cells to include. We did this by evaluating a range of cell counts and measuring the prediction bias of models with these different structures. In Fig. 3 each dot represents a LSTM-NN architecture with an assigned number of cells while the corresponding mean values of ΔF_{Lx} and ΔF_{Ly} are displayed on the

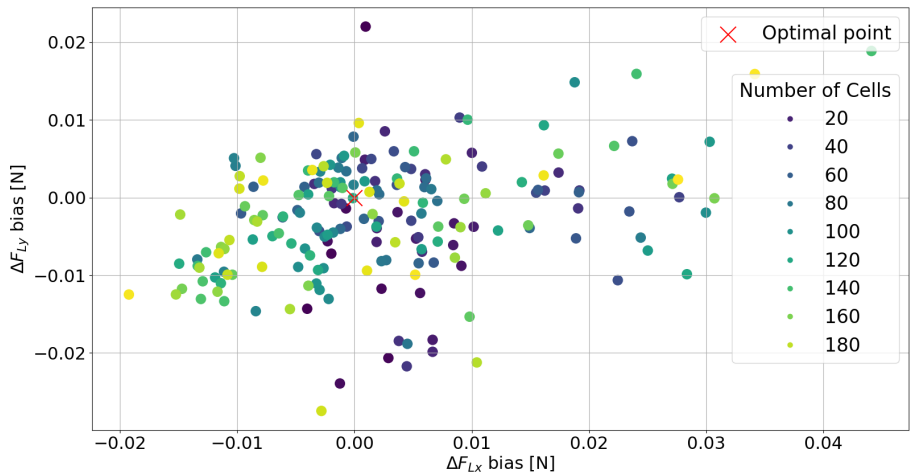

Figure 3: Optimal architecture based on kNN test. Average error for the x locomotion component on the horizontal axes; average error for the y locomotion component on the vertical axes. Every dot corresponds to a specific number of cell in the LSTM architecture. Red cross is the optimal configuration with zero error for both error locomotion components.

horizontal and vertical axis respectively. The optimal architecture correspond to the number of cells that produce the minimum error for ΔF_{Lx} and ΔF_{Ly}. In this case an LSTM with 122 cells is the optimal configuration, red cross in Fig. 3.

An LSTM-NN consists of a cascade of interconnected LSTM cells (Fig. 1e main text). A key feature of LSTM cells is the presence of an internal state which serves as a "memory", $C(t)$, associated with each cell in the network. A generic cell receives three variables: the previous cell's memory state $C(t-1)$, the previous cell's output $h(t-1)$ and the current sensory input variables, $x(t)$. The cell then performs different internal operations using so-called "gates" to produce two outcomes: the current memory state $C(t)$ and the current output $h(t)$. The gates performing the internal operation are the following:

- Selection gate: select the information to forget. This gate uses $x(t)$ and the previous cell's output $h(t-1)$ employing a sigmoid function, hence,

$f_t = \sigma(W_f[h(t-1), x_t] + b_f)$, where W_f and b_f are weight and bias coefficients;

- Input gate: select the information to remember. This step consists of two parts: first, a sigmoid function decides which values to update, $i_t = \sigma(W_i[h_{t-1}, x_t] + b_i)$. Next, a tanh function creates a vector of new candidate values, $\widetilde{C}(t)$, that will be added to the state; $\widetilde{C}(t) = \tanh(W_c[h_{t-1}, x_t] + b_c)$.

- Memory gate: update the previous memory state $C(t-1)$ into a new memory state $C(t)$ with the operation $C(t) = f_t C_{t-1} + i_t \widetilde{C}(t)$. The product $f_t C_{t-1}$ "forgets" information from the previous memory state $C(t-1)$. The product $i_t \widetilde{C}(t)$ selects new information to "remember."

- Update gate: finally the output cell is computed as $h(t) = o_t \tanh(C_t)$ where $o_t = \sigma(W_o[h_{t-1}, x_t] + b_o)$.

Appendix D. Bathymetry of the investigated site.

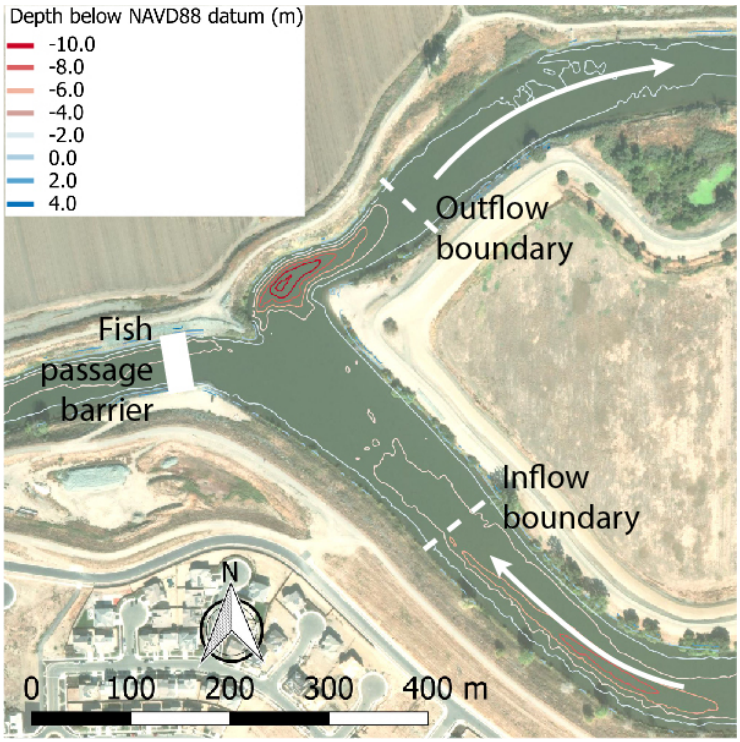

Figure 4: Bathymetry of the investigated site.