Biological Propulsion for Water Exit: 3D Experimental Study of Archer Fish Jumping

by

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Abstract

Jumping for aerial prey from an aquatic environment requires both propulsive power and precise aim to succeed. Archer fish, better known for their spitting abilities, will jump multiple body lengths out of the water for prey capture, especially in competitive foraging scenarios. Prior to jumping, archer fish aim from a stationary position with the snout located directly below the water’s surface. Rapid acceleration to a ballistic velocity sufficient for reaching the prey height occurs with a mere body length to travel before the fish leaves the water completely and experiences a thousandfold drop in force-producing ability. In addition to speed, accuracy and stability are crucial for successful feeding by jumping. The combination of these factors in the archer fish’s unique jumping strategy may bring new insights to the design of underwater vehicles capable of spatially-constrained acceleration or water exit.

This thesis examines the hydrodynamic mechanisms underlying the archer fish’s jumping abilities. First, behavioral and kinematic trends from five specimens are presented to elucidate key jump attributes. Modulation of oscillatory body kinematics and use of multiple fins for force production are identified as methods through which the fish can meet requirements for both acceleration and stabilization in limited space. In addition, flow field measurements made using planar particle image velocimetry (PIV) reveal vortical wake structures originating from the caudal, dorsal, anal, and pectoral fins. Exact fin interactions cannot be identified from a single slice through the wake, suggesting a need for further three-dimensional study.

To address this limitation, a volumetric particle image velocimetry system meeting specific requirements for the study of jumping archer fish is developed. The multi-camera measurement system is based on the synthetic aperture particle image velocimetry (SAPIV) technique. The SAPIV system provides time-resolved measurements of both the fish’s wake and its aerial trajectory, working within the optical access constraint created by the fish jumping from directly below the water’s surface. Image processing improvements to measure fin-fin and fin-body interactions despite partially-occluded tracer particles are also implemented. The capabilities of the system to make time-resolved measurements of multiple fins during a single jump are
demonstrated. To utilize the 3D velocity field data provided by this technique, approaches to quantitative wake analysis suitable for isolated three-dimensional wake structures and interacting multi-vortex wakes are presented.

Finally, detailed 3D SAPIV measurements of flow from the archer fish’s dorsal, anal, and caudal fins at jump onset are obtained. Quantitative wake measurements reveal how variations in tail kinematics relate to thrust production throughout the course of a jumping maneuver and over a range of jump heights. Measurements also highlight momentum flux into the wake emanating from the upstream dorsal and anal fins. These flow structures augment the caudal fin wake during subsequent tailbeats. By performing measurements in 3D, the timing, interactions, and relative contributions to thrust and lateral forces from each fin can be evaluated, elucidating the complex hydrodynamics that enable archer fish water exit.

Thesis Supervisor: Alexandra H. Techet
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Chapter 1

Introduction

The ubiquitous phrase “swim like a fish” leaves little doubt over the prowess with which fishes move through aquatic environments. With over 24,000 species [110], fishes are also known for the wide range of evolutionary solutions they exhibit to meet unique survival challenges in multifaceted marine environments. This biodiversity has gained the attention of both organismal biologists, who seek to understand the complex evolutionary trade-offs and adaptations behind the wide variety of fish species, and engineers, who aim to apply elements of these adaptations to engineering problems with analogous operating requirements. This design framework of using swimming animals to develop underwater vehicles is a classic example of bioinspiration. Fish have provided inspiration for efficient vehicles such as the MIT RoboTuna developed by Barrett et al. [12] and maneuverable vehicles such as those described by Bandyopadhyay [11], Gordon et al. [63], and Fish et al. [49]. Novel actuation strategies and applications of such vehicles are summarized extensively in Du et al. [41].

The exchange of ideas between biology and engineering is not one-sided. Engineering advances in instrumentation, analysis, and modeling have also enhanced understanding of biological observations. The study of locomotive behaviors in their truest form (i.e., on a live fish) requires experimental investigation to simultaneously address biomechanics, fluid physics, and animal behavior. In many cases, especially when examining high-performance survival specializations, the behaviors of interest
are fast, unsteady, and highly three-dimensional. Experimental techniques that reduce assumptions and constraints on animal behavior are also desirable. In a recent review, instrumentation challenges to measure fins and wakes in three dimensions constitute many of the opportunities that Lauder [83] highlights as necessary work to advance the scientific community’s understanding of swimming hydrodynamics. In addition to instrumentation, engineering advances must include analysis and modeling efforts to overcome inevitable limitations such as noise and resolution in experimental measurements.

In particular, this thesis considers the case of one species, the smallscale archer fish (Toxotes microlepis), launching itself out of water to feed. Experimental difficulties associated with studying the jumping archer fish include interaction with multiple fluid media, hydrodynamic activities at multiple locations along the body, and the fish’s surprisingly complex cognitive capabilities. These measurement challenges are addressed using synthetic aperture particle image velocimetry, a time-resolved three-dimensional flow measurement technique based on light-field imaging. Flow fields resolved using this technique contribute new understanding to multi-fin swimming hydrodynamics and the complex interplay of feeding techniques exhibited by the archer fish. In an engineering context, these measurements also highlight multi-propulsor strategies with potential benefit to multiphase or tight-manuevering underwater vehicles.

1.1 Aquatic jumping as design inspiration?

With the increasing popularity of small, power-dense autonomous vehicles, it is becoming more feasible for a well-designed vehicle to travel in both air and water. The ability to operate in multiple fluid media is especially desirable in marine research and disaster investigation scenarios (e.g., [93, 139]). Many vehicles designed for these operating conditions draw inspiration from fish (e.g., [55]), sea-birds (e.g., [90, 94]) and insects (e.g., [28]), in addition to conventional aircraft and submarine form factors. Despite the extensive study and prototyping in this area, few vehicles have
attempted a transition from water to air. In one design, Siddall and Kovac [140] use a compressed carbon dioxide tank to create a water jet capable of launching a 100 gram aquatic Micro Air Vehicle (MAV) out of the water; for repeated operation the tank must be recharged between launches. Siddall et al. [141] further use combustion of calcium carbide to create the pressure needed for a similar water jet thruster. The efficiency and overall energetic cost of these water-exit strategies has not been quantified, and neither provides capacity for control of the vehicle trajectory during launch. A more efficient take-off for these multiphase vehicles would expand the range over which they could operate before recharging. A take-off with a localized and natural wake signature would also prevent disruption when these vehicles operate in sensitive marine environments. Nature presents many prospective solutions to this water-exit problem.

Jumping by any organism requires substantial energy and precise muscular coordination. Aquatic jumpers in particular must produce thrust in manners compatible with the transition in fluid media and thousandfold drop in density (and thus force-producing ability) between water and air. Organisms ranging in size from large marine mammals and sharks to small copepods have developed aquatic jumping strategies compatible with their size and survival goals (e.g., prey capture, escape, mating, or migration). The larger animals tend to employ burst swimming for short periods before water exit (e.g., [23, 31, 68, 73, 87]), while smaller swimming fish tend to use S-type or C-type acceleration maneuvers [37] to generate jump thrust, often from a near-stopping position (e.g., [95, 137, 143, 114]. Even smaller organisms such as copepods exhibit jumping behaviors using unique hydrodynamic mechanisms for impulsive vortical formation [58].

Marine mammals and other large aquatic species produce impressive jump speeds and aerial maneuvers. Spinner dolphins generate both the angular momentum for high rates of aerial spin and the ballistic velocity for large jump distances by building up momentum while underwater [50]. Once out of the water, the typical specimen can increase its spin speed since the drag forces in air are significantly lower than that in water. Re-entering the water with a high rotation rate is proposed as a
mechanism for detaching remoras. Subsurface acceleration is also utilized by jump-
ing sharks. Brunnschweiler [23] reports blacktip sharks accelerating from a depth of
approximately 10 m to reach vertical water-escape velocities up to 6.3 m/s, taking off
at angles between 30-45°. These strategies are even replicated by organisms without
evolutionary adaptations for aquatic jumping. Aided by a large monofin for propul-
sion, elite human swimmers jump to reach heights of 2 m out of the water [116],
slightly over the body length of the athlete, by starting from several body lengths
below the surface.

On the smaller size extreme, copepods can break the water’s surface to evade
predators and travel significantly further in air than they can underwater [58]. Using
a sphere as a model plankton, Kim et al. [78] find that the organism size and the
impact velocity of a plankton with the surface determine whether it will break the
surface or be repelled by surface tension. This result presents a survival trade-off
in plankton evolution: while smaller plankton are less visible to predators, larger
plankton possess the additional kinetic energy necessary to break the surface tension
by virtue of their increased mass.

The physical mechanisms that enable aquatic jumping are not always on the same
size scale as the jumping organism itself. Penguins tend to employ aquatic jumping
for both water-ice transitions after foraging and to elude capture (e.g., [172, 32]).
Yoda and Ropert-Coudert [172] suggest that Adélie penguins’ parabolic jumps up
onto ice floes are not driven by optimal efficiency, but instead to mitigate risk of
being captured as prey. Davenport et al. [32] present evidence that penguins use
air lubrication layers to reduce frictional and form drag in jumping maneuvers; these
penguins dive 15 to 20 m with air in their plumage. The compressed air releases upon
ascent to form a smooth layer over the body and generate a bubbly wake.

Among fishes specifically there is remarkable diversity in jumping strategies. In
some fish species, including trout and salmon, jumping is an oft-observed migra-
tory behavior (e.g., [79, 87, 88]), executed from depth in plunge pools at the base
of waterfalls. Kondratieff and Myrick [79] evaluate the maximum height a brook
tROUT can jump, finding maximum jump lengths of up to 4.7 bodylengths; these data
are used to inform fish ladder and waterway design. For predator evasion, African butterfly fish (*Pantodon buchholzi Peters*) and freshwater hatchetfish (*Gasteropelecidae*) jump upwards in a ballistic motion, aided by their pectoral fins in exiting the water [127, 165]. The average jump for the African butterfly fish is no more than twice the fish’s bodylength and the horizontal distance covered is about five times the standard length of the fish. Freshwater hatchetfish exhibit similar behaviors to the butterfly fish in their escape responses; high-speed video shows that hatchetfish follow projectile-like trajectories after their pectoral fins aid in escaping from the water [165]. The Trinidadian guppy (*Poecilia reticulata*) jumps spontaneously for population dispersal in waterfall-laden environments [143]. The guppy’s jumping behavior includes a preparatory phase of slow backward swimming using the pectoral fins, followed by forward acceleration with kinematics similar to C-start maneuvers and burst swimming.

Jumping to feed requires more precision than jumping for migration or escape (e.g., [99, 95, 114]). For feeding strikes in general, Weihs [162] surmises that when a fish was sufficiently motivated by hunger efficiency was secondary to short-term energy use. Ultimately, for long-term survival purposes, the overall energetic cost of feeding by jumping should not exceed the energetic gain provided by the targeted prey. The African tetras, *Brycinus nurse* and *Alestes baremoze*, can jump up to 1 m into the air to dislodge seeds from rice plants and then eat the seeds after they have fallen into the water [99]. Mangrove rivulus (*Kryptolebias marmoratus*) uses multiple kinematic modes, including jumping “launches” resembling S-type fast-starts, to travel up banks to feed on land [114]. Lowry et al. [95] reveals silver arawana fish (*Osteoglossum bicirrhosum*) jump using S-starts similar to those executed by ambush predators (e.g., [159, 112]) after a period of burst swimming. The arawana’s kinematics for aerial feeding were faster and included larger amplitude body motions than during in-water feeding. Lowry et al. [95], further emphasize that having more than one prey capture mode expands an organism’s “ecological niche” and gives it a “competitive advantage” in hunting and foraging. 

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Figure 1-1: Prey capture modes of the archer fish. (a) Archer fish spitting a jet of water at aerial prey suspended from a string. (b) Archer fish jumping greater than one body length for bait. The fish’s snout is positioned at the surface before initiating the jump. Images are taken at 1000 frames s$^{-1}$ and contrast has been linearly enhanced for clarity. Images taken by the thesis author.

1.2 Archer fish as model predators

Archer fish (genus *Toxotes*) are found in mangrove swamps, river mouths and upstream brackish and freshwater regions [97, 7]. *Toxotes* eats insects or small aquatic animals that live near the water’s surface. Archer fish employ several hunting strategies: spitting a water jet at an aerial target such that it falls into the water to be eaten, rapidly lunging in the water for fallen prey, or jumping to capture aerial prey [14]. Figure 1-1 shows photographs of the spitting and jumping prey capture modes. This wide range of foraging behaviors makes the archer fish a model predator and a unique fish for further hydrodynamic and biological investigation.

Previous studies of archer fish hunting use spitting, including control of jet hydrodynamics and aim, as an indicator of the fish’s cognitive capabilities (e.g., [157, 122, 152]). Schlegel et al. [133] find that archer fish fire larger masses of water as their prey grows in size (and thus attachment strength to leaves and branches) to avoid expending unnecessary energy on smaller, weaker prey. Vailati et al. [156] propose
that archer fish modulate the flow rate of the jet over time to maximize force on prey. Experiments have also suggested that jets are focused for specific prey heights [60] and hunting fish compensate for their distance to the prey [24]. Dewenter et al. [35] find that archer fish can spit to unearth buried prey underwater in addition to shooting down prey above the surface. The ability to modify the jet for this application suggests that archer fish spitting exhibits some behavioral hallmarks of tool use. This control over spitting is facilitated by sophisticated eyesight. Despite refraction of light at the surface and gravity effects on the water jet, spitting still hits prey with impressive accuracy [36, 153, 134]. Aiming studies have shown *Toxotes* can account for viewpoint dependency [134] and connect apparent size of the bait with relative position to the target [135]. Archer fish are also capable of pattern recognition, most dramatically exhibited by Newport et al. [108], who successfully trained archer fish to spit at printed human faces.

Successful prey capture following spitting requires advanced rapid maneuvering capabilities [166, 81, 117, 118]. For rapid maneuvering in water, archer fish execute C-starts, also known as escape responses when used for predator evasion, in which the body bends into a “C” shape before straightening and accelerating [37]. Wöhl and Schuster [166] find no difference between the maximum speeds of predictive feeding strikes and escape responses resulting from being startled. C-starts are reported to reach peak linear speeds above 20 body lengths s\(^{-1}\) and accelerations up to 12 times that of gravity [166]. Reinel and Schuster [117] further find that archer fish can control speed and trajectory following a C-start without performing any additional tail beats to accelerate.

Cognitively, the prey capture behaviors exhibited by archer fish are influenced by learning and competition. Rossel et al. [122] find when prey is dislodged, archer fish use the initial trajectory to predict the direction, speed and distance at which the prey will land. Fish then turn accordingly to pursue regardless of whether they are the shooter. Archer fish hunting is influenced by competition, and fish kept in schools have been observed to shoot more when competing for resources [62, 33]. Davis and Dill [33] observe a high degree of kleptoparasitism in captive archer fish,
with fish stealing prey shot down by another fish 43.6% of the time in captive groups of 3-7 fish and increasing probability of theft the more shots were required to bring down a particular prey. Additionally, Davis and Dill [33] find that the frequency of jumping is greater in larger groups of fish; jumping constituted 29% of the total prey capture behaviors observed in a group of seven fish compared to 17% of behaviors in a group of three fish. Based on field recordings, Rischawy et al. [119] suggest that competition is an evolutionary rationale for archer fish spitting, vision, and predictive starts because their habitats are also inhabited by other species of surface-feeding fish capable of fast responses to hydrodynamic stimuli such as prey hitting the water’s surface.

While jumping may compromise stealth or be less successful with moving targets, it presents a self-sufficient mode of prey capture where the jumping fish is the most likely one to capture the prey. This thesis builds on previous knowledge of archer fish aiming and maneuvering to provide detailed characterization of the jumping specializations in these fish. Study of this behavior will ultimately enable assessment of the role of jumping as a competitive foraging strategy, and of the archer fish as a possible role model for water-exit in an underwater vehicle.

1.3 Experimental analysis of fish locomotion

Imaging techniques are the backbone of experimental studies of fish locomotion. The contributions of high-speed imaging in particular to research in swimming hydrodynamics are summarized extensively by Lauder and Madden [85]. Kinematic studies of complex, unsteady maneuvers have utilized high-speed imaging to characterize body midline motions at high temporal resolution (e.g., [155]). Three-dimensional imaging techniques with multiple cameras also enable high-resolution motion tracking of fin surfaces (e.g., [86]). Kinematic observations can be used in conjunction with analytic models of swimming gaits (e.g., [92, 161, 170]) to predict swimming performance (e.g., [54]). The results of these kinematic imaging experiments can additionally be used to initialize computational fluid dynamics studies of the observed fin and body
motions (e.g., [38, 21, 20, 75]).

Assessment of locomotive performance requires coupled understanding of the relationship between swimming kinematics and their fluid environment. Qualitative flow visualizations can be obtained alongside the kinematics through modifications to the fluid a fish swims through. Rosen [121] swam a pearl danio (Brachydanio albolineatus) through a layer of milk to visualize the vortex patterns behind it. Hu et al. [70] similarly identify the wake envelope of a swimming tetra and observed activation of the pectoral fins during stopping by using polarized light shone through tobacco mosaic virus. Quantitative information from such methods is limited, though McCutchen [100] is able to estimate the Froude efficiency from the body speed of a fish and wake measurements using shadowgraphy. Ensuring natural behavior in a modified environment and the qualitative nature of the results are the main limitations when using such visualization techniques.

1.4 Quantitative measurements through particle image velocimetry

Particle Image Velocimetry (PIV) is a flow visualization and measurement technique that provides non-invasive, instantaneous snapshots of entire fluid velocity fields. PIV has been used to visualize and quantify flow fields in applications (and length scales) ranging from aerodynamic turbulence to microfluidic devices [4]. Tracer particles, illuminated by a laser for nearly-instantaneous lighting with minimal motion blur, are filmed over time using a camera. Each particle image is divided into windows; corresponding windows are cross-correlated between successive frames to determine the most probable displacement of particles between frames [76]. Windows typically overlap by 50-75% of their width to ensure smoothness of the resultant velocity field. With a known length scale and frame rate, the displacement can be converted to the flow velocity in each window. Extensive guides to the implementation of PIV measurement systems are presented by Raffel et al. [115] and Adrian and Westerweel [5].
PIV enables the relationship between kinematics and propulsion to be simultaneously evaluated with full-field quantitative measurements, providing another platform for comparisons in swimming performance. In one early application of PIV to fish swimming, Wolfgang et al. [167] employ PIV to compare wake vortices between forward swimming and turning in giant danio. Likewise, Müller et al. [105] compare wake measurements between larval and adult zebrafish to elucidate the increased significance of viscosity to the locomotive behaviors of the larvae. Using bluegill sunfish, Drucker and Lauder [40] observe changes in the orientation of pectoral fin wake momentum, and therefore variation in the direction of propulsive forces, by varying the freestream flow speed. PIV also enables increased understanding of the fish’s interaction with its surroundings, such as the kinematic and hydrodynamic response to upstream vortices in observed in Liao et al. [91].

1.4.1 Three-dimensional measurements

Brief aside on coordinate system. In this summary and the remainder of this thesis, the X-Y plane refers to the plane of a 2D PIV image (or images from a single camera within a multi-camera setup). Z is the out-of-plane dimension obtained during image processing to provide the particle volume information necessary for a three-dimensional measurement. Figure 1-2 provides a schematic of this coordinate system.

Particle image velocimetry traditionally provides velocity information in a single planar slice through a flow field, and the flow must be effectively two-dimensional in the measurement plane for results to be valid. Small amounts of out-of-plane motion will be projected onto the 2D measurements, altering results from their true values, while larger out-of-plane displacements result in a loss of signal completely. Several techniques incorporate multiple viewpoints to overcome this limitation and provide three-dimensional information. In order of increasing number of viewpoints, methods popular for studies specifically in biological propulsion include stereoscopic PIV, digital defocusing PIV/PTV, tomographic PIV, and synthetic aperture PIV. The fundamental differences between these techniques are applicable volume size
and tracer particle density, the reconstruction algorithm used to generate 3D particle volumes, and the trade-offs made between up-front equipment requirements and post-experiment data processing resources.

Stereoscopic PIV (stereo-PIV) uses two viewpoints, typically aligned horizontally with an angle between cameras, to resolve the three-dimensional motion of particles within a thin light sheet [113]. Focal planes for the angled cameras are matched to the light sheet orientation by using Scheimpflug adapters. The output is three velocity components on a 2D Cartesian (X-Y) grid. Stereo-PIV resolves both in-plane and out-of-plane motion, but does not generate a full volumetric flow measurement. To evaluate the three-dimensionality of fish wakes, Sakakibara et al. perform simultaneous stereo-PIV and kinematic measurements of a turning goldfish and measure substantial out-of-plane velocity [128]. Nauen and Lauder [107] use the ratio of streamwise velocity to velocity magnitude (derived from all three components as measured from stereo-PIV) to assess the swimming performance of trout.

Defocusing Digital PIV/PTV (DDPIV/PTV) films particles using a specialized aperture or pre-determined camera arrangement to create a coded blur pattern in
the resultant images. The spacing of corresponding particles within this pattern correlates with their depth in the Z-dimension [111]. Correspondence between the particle images must be clear to reconstruct the depth; the overall seeding density of the experiment is therefore limited. As a result of this sparsity, DDPIV is actually a particle tracking velocimetry (PTV) technique which generates 3D particle tracks that are then interpolated to gridded velocity fields. Using DDPTV, Flammang et al. [53], provide the first volumetric visualization of three-dimensional vortex rings shed by the caudal fins of bluegill sunfish and cichlids swimming in a flume. Results also show smaller vortices generated by the dorsal and anal fins being incorporated into the caudal fin wake of a successive tailbeat. Using the same 3D technique on a dogfish shark, Flammang et al. observe a linked wake structure from the shark’s asymmetric tail [51]; this topology is not sufficiently described by previous 2D measurements. In additional studies of biological propulsion, DDPIV/DDPTV has been used to study vortex formation in bioinspired drag-based paddling using plates of varying shape [77], simultaneous fin and jet propulsion in squids [13], and asymmetry in jellyfish wake vortices during maneuvering [59].

Elsinga et al. [43] introduced tomographic PIV (tomo-PIV) as another multi-view approach to 3D intensity field reconstruction. Tomo-PIV experiments typically use between 4-8 cameras, each with a high numerical aperture lens and a Scheimpflug adapter to align the plane of camera focus with the measurement volume. Particle volume reconstruction is performed using iterative algorithms, typically the Multiplicative Algebraic Reconstruction Technique (MART) or Simultaneous Multiplicative Algebraic Reconstruction Technique (SMART), to determine the 3D intensity distribution that best projects onto the individual camera views. An extensive review of reconstruction algorithms and implementation details is presented by Scarano [129]. Typically around five reconstruction iterations are required for convergence of the algorithm; determining the particle field for tomographic PIV requires substantial computational power and processing time. Once the reconstructions have been obtained, the volume is processed similarly to 2D PIV using 3D cross-correlations of interrogation windows. Henningsson et al. [65] report that 96 days of continuous data
processing were required to obtain the flow fields for a study of phase-averaged and instantaneous locust wakes using tomographic PIV. Adhikari and Longmire use tomographic PIV to study the non-planar, behavior-sensitive predator-prey dynamics of zebrafish feeding [2]. This application of tomo-PIV also required a visual hull method for object reconstruction and masking, enabling 3D PIV to be applied to near-body flows as well as wake features [1]. Murphy et al. [106] and Adhikari et al. [3] also use tomographic PIV to study the propulsive mechanisms used by swimming pteropods, finding similarities with insect flight despite very different Reynolds numbers.

1.4.2 Synthetic aperture particle image velocimetry

Synthetic aperture particle image velocimetry (SAPIV) applies concepts from light field imaging [89] to obtain 3D particle fields [17]. In general, SAPIV is similar to other 3D PIV techniques in that it uses an array of cameras, each with a different line of sight, to image a scene from multiple viewpoints. In SAPIV, images from each camera can be refocused into a volumetric stack of images over varying depth for processing with 3D cross-correlation algorithms. Figure 1-3 shows an example schematic of a SAPIV system used to resolve wake structures generated by giant danio during forward swimming and maneuvering.

Synthetic aperture (SA) refocusing simulates the effects of a camera with a narrow depth of field scanning through the light field. By spatially relating all cameras to a global coordinate system (divided into finely spaced focal planes throughout the measurement volume), combining images and determining where features are in focus, the 3D location of a particle can be determined. Equation 1.1 mathematically describes the refocusing of images at each focal plane as an averaging procedure:

\[
I_{SA_k} = \frac{1}{N} \sum_{i=1}^{N} I_{FP_{ki}},
\]  

(1.1)

where \( I_{SA_k} \) is the averaged image on the \( k^{th} \) focal plane, \( N \) is the number of cameras, and \( I_{FP_{ki}} \) is the transformed image from each camera. Following refocusing, an intensity threshold can be applied to remove particles that do not converge across
Figure 1-3: Experiment setup from a 30 Hz implementation of synthetic aperture PIV used to study giant danio swimming. Nine CCD cameras are arranged alongside a five gallon tank seeded with 50 µm particles. Illumination is provided by a volume-expanded 808 nm laser and reflected back into the tank by a first surface mirror. Figure reproduced from Mendelson and Techet [101].

all cameras at a given depth [17]. Variants on the refocusing algorithm to alter the signal-to-noise ratio include instead taking the product of all transformed images (equation 1.2, where $n$ is a parameter that exponentially alters the intensity scale of the source images):

$$I_{SA_k} = \prod_{i=1}^{N} (I_{FP_{ki}})^n,$$  \hspace{1cm} (1.2)

or applying a weighting function to penalize dimmer image regions [101]. The image mapping and reconstruction process for SAPIV is non-iterative and can be accelerated through the use of GPU parallel computing to be significantly faster than tomographic reconstruction [10], allowing for significant statistics to be compiled on complex problems in a feasible time frame for analysis.

Light field imaging of particles can also be performed with a single camera and a microlens array (instead of an individual lens); when used for velocimetry this method is known as plenoptic PIV [47]. With a microlens array instead of individual cameras,
there is a larger number of viewpoints, but the resolution of the final refocused image is limited by the size of the camera sensor split between all viewpoints. When light field imaging is performed instead with a camera array, the full resolution of the camera sensor is available for each viewpoint, but the number of viewpoints is more limited, especially when using costly high-speed cameras. However, Belden et al. [17] show that for particle fields, the quality of reconstruction plateaus beyond approximately ten viewpoints, and approximately 8-10 viewpoints are therefore typically used in a SAPIV camera system.

The SA refocusing technique is capable of resolving measurement volumes with Z-depths comparable to the X and Y dimensions (a feature missing in stereoscopic PIV). Due to the larger number of viewpoints, particles that would otherwise be occluded (at least partially) can in fact be seen using this method. Occlusions are inevitable when studying near-body flows, such as a fish tail blocking view of tracer particles in one row of cameras, making SAPIV an ideal technique for such applications. SA refocusing can be also performed in any reference frame through the definition of appropriate image transforms.

For flows interacting with bodies, the visual hull method of tomographic PIV [1] is also applicable to SAPIV and can be used to construct a 3D representation of the fish body [101]. Figure 1-4 shows the process of visual hull construction for images of the caudal fin of a giant danio. Binary images from each camera representing the fish body are refocused using equation 1.2 to determine the 3D regions where each source viewpoint contains the body, not the surrounding particle field.

Body kinematics are refined by tracking key points on the fish body, such as the eyes, fin-body junction points, and the tips of the caudal tail when available. Mendelson and Techet [101] track the caudal fin of a giant danio by constructing a local visual hull of the tip of each caudal fin at each time step; the centroid of each local hull is tracked over time in the volume to determine the time-resolved motion of each marker, as represented by the traces in figure 1-5. Using consistent camera positions and calibration techniques for kinematic measurements ensures the best agreement between the body reconstruction, the kinematics, and the wake hydrodynamics. The
Figure 1-4: Body reconstruction procedure for synthetic aperture particle image velocimetry. (a) Raw image of the caudal fin from the center camera of the array. (b) Binary mask images from all nine cameras (arranged the same as the physical camera array) show several different silhouettes of the caudal fin as the fish swims across the tank. (c) Three slices of the refocused mask. One tip of the caudal fin lies at $Z = -2.0 \text{ mm}$, the second tip at $Z = 6.0 \text{ mm}$, and the caudal peduncle at $Z = 14.0 \text{ mm}$. (d) Reconstructed caudal fin visual hull from the refocused mask planes. The mask is displayed at full resolution in Z with equivalent spatial resolution in X and Y. The elongation and tapering to a point in Z created by the discrete blur pattern of partial mask convergence are prominent. Figure reproduced from Mendelson and Techet [101].
Figure 1-5: Sample body, fin trajectories, and vortex ring measured behind a freely swimming fish using synthetic aperture PIV. A single vortex ring behind the fish during forward swimming at $U = 0.9$ BL/s. The single red arrow indicates the mean fish body velocity. The solid orange trace is the path of the upper tip of the caudal fin. The solid brown trace is the path of the lower caudal fin tip. The nodes on the traces indicate the position of the tail tips in the current frame and show agreement with the fish body mask. The isovorticity contour is drawn at $5 \text{s}^{-1}$. The peak velocity magnitude is 36 mm/s (0.6 BL/s). Every other vector along the Z-axis is plotted for clarity. Figure reproduced from Mendelson and Techet [101].

camera calibration functions for SAPIV also compensate for refractive effects [15], which has been shown to improve the localization of body features in underwater kinematic studies compared to a linear camera mapping [67].

1.4.3 Quantitative wake analysis from PIV

A major advantage of the quantitative flow field measurements yielded using PIV variants is that they can be used to assess swimming performance in different scenarios and between organisms. The exchange of momentum between fish and fluid during locomotion results in the formation of a vortical wake. In studies of biological propulsion, metrics for quantitative analysis of the vortex wake, including circulation, impulse, and their time derivatives, are a valuable indicator of performance. The hydrodynamic impulse of a vortical wake is a measure of the instantaneous force
that would be required to bring a fluid at rest to its current state [169]. Momentum and forces can be inferred with this quantity plus a corresponding pressure term to describe the inviscid, vorticity-free components of the flow field (e.g., [169]). In a general form for an infinite domain, the vortical impulse is:

$$\vec{I} = \frac{1}{2} \rho \int_V \vec{x} \times \vec{\omega} dV$$  \hspace{1cm} (1.3)

where $\rho$ is the fluid density, $\vec{x}$ is a position coordinate, and $\vec{\omega}$ is the vorticity vector. Through symmetry assumptions, the impulse for a toroidal vortex ring, a common model for a fish wake, can be simplified to:

$$I = \rho \Gamma \pi R^2,$$  \hspace{1cm} (1.4)

for a thin-cored vortex ring of radius R and:

$$I = \rho \Gamma \pi R^2 \left(1 + \frac{3}{4} \frac{r}{R}\right),$$  \hspace{1cm} (1.5)

for a ring with the previous dimensions plus a finite vortex core radius of $r$. The circulation $\Gamma$ is a measure of the vortex strength, defined from either velocity ($\vec{u}$) or vorticity measurements as:

$$\Gamma = \oint_C \vec{u} \cdot d\vec{l} = \int_A \vec{\omega} \cdot \hat{n} dA,$$  \hspace{1cm} (1.6)

where $d\vec{l}$ is a closed contour surrounding the vortex on a 2D plane and $dA$ is its enclosed area. For these axisymmetric vortex rings, the impulse vector acts exclusively in the direction of the axial jet at the center of the ring.

Forces can be inferred from the change in vortex wake impulse and additional terms describing inviscid/pressure and body force contributions [29]. Dabiri [29] cautions that instantaneous forces should be considered over stroke-averaged quantities when possible, since many different force histories and interactions can lead to the same average result. Rival and van Oudheusden [120] present an extensive review
of methods to predict forces from particle image velocimetry measurements, and insights on the challenges of doing so without direct pressure field measurements. In particular, the use of derivative-moment transformations (shown in equation 1.7 for an arbitrary vector quantity $\vec{F}$):

$$\int_V \vec{F}dV = \int_S \vec{x}(\vec{F} \cdot \hat{n})dS, \quad (1.7)$$

to convert volume ($dV$) to surface ($dS$) intervals is presented as both a convenient method of avoiding volume integrals of boundary-layer vorticity that typically cannot be measured alongside wake structures, and an unfortunate source of error amplification due to the sensitivity to choice of origin for the position vector $\vec{x}$.

Propulsive performance can also be assessed through the wake energetics, as energy lost to wake formation does not become usable kinetic energy possessed by the swimming fish.

The kinetic energy in a control volume can be calculated from the velocity magnitude field as:

$$KE = \rho \int_V \frac{1}{2} |\vec{u}|^2 dV \quad (1.8)$$

The kinetic energy of a vortical region in a three-dimensional domain can also be calculated from the velocity and vorticity fields as:

$$KE = \rho \int_V \vec{u} \cdot (\vec{x} \times \vec{\omega})dV - \rho \int_S [(\vec{u} \cdot \vec{x})(\hat{n} \cdot \vec{u}) - \frac{1}{2} |\vec{u}|^2 (\hat{n} \cdot \vec{x})]dS \quad (1.9)$$

The fundamental difference between the two approaches is the information density of different regions of the flow field [169] and the ability to address flow in a finite, as opposed to an infinite, domain.

The jumping archer fish is a unique application for these quantitative metrics because the aerial trajectory of the fish provides knowledge of the net force acting on the fish. The change in gravitational potential energy with jump height likewise presents a known quantity that the energetic cost of wake formation can be compared to.
1.5 Outline of thesis

This thesis aims to develop a mechanistic understanding of the multi-fin hydrodynamics involved in the aquatic jumping behavior of archer fish, and the role of jumping as an energetically viable feeding strategy for the fish. Key goals of this thesis are to understand the functions of multiple fins individually and in concert during a rapid burst jump maneuver (including propulsive and stabilizing roles), as well as the specific 3D wake vortex topology produced by multi-fin interactions. Experiments to measure the kinematics and flow field around a jumping archer fish are further used to observe the relationship between thrust production during a jump and maximum animal jump height. This analysis brings new understanding to the role of jumping as a foraging strategy for the archer fish, which is better known for its other hunting strategies (i.e., spitting at prey). This study is enabled by advances in experimental fluid mechanics, namely in the application of the synthetic aperture particle image velocimetry technique, near fast-moving fish bodies. Synergistic multi-propulsor relationships identified herein could be paradigm-shifting for the design of bioinspired aerial-aquatic vehicles. Beyond water-exit, the propulsive strategies explained herein have applications in aquatic maneuvering scenarios where space is the primary constraint.

Chapter 2 outlines methods for quantitative analysis of volumetric PIV data to assess jump propulsion. The chapter begins with an assessment of how two-dimensional models of wake hydrodynamics compare to the three-dimensional realities for the case of a turning giant danio. Next, a three-dimensional method of calculating wake impulse for isolated vortices of arbitrary geometry is presented. Shortcomings of this approach for wakes consisting of multiple, interacting flow structures are also assessed, and an alternate framework is presented for these cases. This chapter also discusses the challenges of assessing archer fish jumping performance from an energetic framework instead of a force/momentum balance. Limitations for quantitative analysis based on the resolution and assumptions of a given measurement system are ultimately assessed, making recommendations about best-practices for 3D quantitative
analysis of experimental flow field data.

Chapter 3 provides behavioral statistics and observations of archer fish jumping based on high-speed imaging and two-dimensional particle image velocimetry. These observations provide necessary background information, identify key aspects of the archer fish’s jumping behavior, and serve as motivation for three-dimensional experimental study. This chapter concludes with a preliminary three-dimensional study that expands on the hypotheses developed from 2D data. Limitations of this 3D study are used to define a set of measurement system requirements for further archer fish experiments.

Chapter 4 describes the technical challenges of performing synthetic aperture PIV on jumping archer fish, and the use of this technique to make time-resolved measurements at multiple locations on the fish body. The performance of particle reconstruction algorithms in the presence of body occlusions is characterized and improvements to the SAPIV technique for making near-body measurements are described. Experiment results obtained by applying these advances successfully resolve three-dimensional jets and vortex structures generated by the dorsal, anal, and caudal fins.

Chapter 5 brings together measurement and wake modeling advances to examine in detail the hydrodynamic interactions of the fish’s median fins (i.e., caudal, dorsal and anal). These experiments show mechanisms for interaction between these fins as well as variations in fin behavior with jump height and throughout a jump.

Chapter 6 summarizes the contributions of this work to both experimental fluid mechanics and fish biomechanics, and provides an outlook on other problems that would benefit from the same measurement strategies. Emerging approaches in fluid mechanics that would lend new insights to the jumping archer fish problem are also discussed.

The appendices include a list of additional energetic factors at play during a jump, comparison of archer fish specimens used in different chapters, and additional trajectory and kinematic measurements from the median fin SAPIV experiments.
Chapter 2

On analysis of circulation, impulse, and force in propulsive wakes using 3D PIV

2.1 Prologue

In studies of biological and bioinspired propulsion, the vortex circulation and hydrodynamic impulse are used to quantitatively assess performance. 2D PIV provides a single slice through a flow feature from which to derive measurements of vortex parameters describing strength and topology. The wake model described in this section is motivated by the statistical use of multiple slices through a wake structure to assess uncertainty of the approach used in 2D. A summary of those findings is first provided to motivate the wake model. Portions of the following introduction originally appeared in Mendelson L, Techet AH (2015). “Quantitative wake analysis of a freely swimming fish using 3D synthetic aperture PIV.” Experiments in Fluids 56(7).
2.1.1 Impulse measurement using planar cuts through vortex wakes

The axisymmetric vortex ring model (equations 1.4, 1.5) is a common approach to quantitative wake analysis from planar PIV measurements (e.g., [128, 145, 45]). Vortex circulation is determined from the positive and negative cores of a vortex pair or, for isolated vortices, from the line integral of velocity along the axial jet. The distance between positive and negative vortex cores is typically used as the vortex diameter. Sources of error using this approach include how close the wake topology is to an axisymmetric ring, misalignment of the light sheet and the vortex, and wake breakdown before circulation measurement.

Volumetric measurements of a turning giant danio obtained at 30 Hz using synthetic aperture PIV [101] are used to assess the uncertainty of this common 2D analysis procedure. The danio executes a 75° turn over 0.3 s. The fish enters the turn swimming steadily at 1.0 body lengths (BL)/s and exits the turn with velocity magnitude 1.3 BL/s; the wake structure resulting from this maneuver can be seen in figure 2-1a. The time t = 0 s corresponds to when the fish initiates the turn.

To obtain multiple circulation measurements using the full vortex geometry, it is first necessary to characterize that geometry without any assumption of symmetry. The vortex core line can be defined as a line representing the center of a vortex filament and is readily detected using algorithms to identify the local maxima of vorticity in a plane normal to the vorticity vector (e.g., [148]). At each point along the core line, a slice is taken through the point with the normal parallel to the vorticity vector at that location. The circulation and vortex core diameter are measured on each of these slice planes. Figure 2-1b shows the core line at t = 0.65 s and a sample slice through the vortex at one point along the core line.

Statistics from all circulation cuts can be used to better define a representative circulation for the entire vortex filament. To approximate impulse based off the results from the core line, the median circulation, which is less sensitive to outliers than the mean, is used in conjunction with the projected area of the vortex filament onto a
Figure 2-1: Giant danio wake, from SAPIV measurements, used to assess symmetry assumptions and circulation uncertainty in 2D wake analysis. (a) Vortex core line determined using the algorithm from Strawn et al. [148] at t = 0.65 s. The vortex loop extends beyond the measurement volume in the +Z direction, preventing complete determination of the wake geometry. (b) A rotated view of the vortex showing a sample slice through the vortex core. The slice normal vector is parallel to the core line at a given point. Figure modified from Mendelson and Techet [101].

plane normal to the axial jet, a better approximation of geometry than a circular ring. Upper and lower bounds on the impulse can be set by using the minimum and maximum circulation seen anywhere along the core instead of the median.

The circulation along the core line is analyzed at three timesteps spaced 0.20 s apart (figure 2-2). All three times at which analysis is performed fall after t = 0.3 s, the time at which the center of mass trajectory is no longer turning. At t = 0.45 s, the vortex loop is still attached to the fish body, and the vortex core line passes through the caudal fin as a result. The time t = 0.65 s is the first frame in which the isovorticity surface is observed to form a closed contour instead of connecting with the caudal fin, indicating that the vortex has been shed completely from the fish body. At t = 0.85 s, the caudal fin has performed an additional tailbeat, the effects of which may contribute to the circulation calculated in the slices nearest to the tail. The vortex cores at the edge of the filament have also begun to break down.

Circulation is plotted along the length of the core line at each time (figure 2-2b). The circulations at the two endpoints of the vortex core line are highest at t = 0.45 s, and drops by approximately 2 cm²/s in each time interval. The circulation calculated
Figure 2-2: Vortex core line identification and circulation measurements over time in the turning giant danio wake. (a) Vortex core lines at three instances in time relative to the vorticity isosurface at 8 s$^{-1}$. The green surface shows the location of the caudal fin from the visual hull. The marker points show the initial coordinate along the core line where the circulation profiles along the core line seen in (b) are computed. Marker points show individual circulation values, while the solid line shows a once-smoothed circulation profile. By $t = 0.85$ s the vortex decay at the start and endpoints and interactions with secondary flow features are prominent. Figure modified from Mendelson and Techet [101].
where the vortex is still attached to the caudal fin is much lower. At t = 0.65 s the circulation near the caudal fin (approximately 3 cm along the core line) is much higher and comparable with the circulation at the end points, but never reaches the maximum strength seen at t = 0.45 s. The caudal fin kinematics show a small oscillation of the tail as the fish emerges from the turn. Vorticity shed during this tailbeat and interactions with the primary turning vortex may be responsible for the local maxima in circulation seen at halfway along the core line at t = 0.65 s and t = 0.85 s. Sets of 2D PIV measurements obtained in either plane would present very different pictures of the vortex dynamics after the turn. SAPIV is able to capture that at different points along its length the vortex filament is simultaneously growing and decaying.

The projected area of the vortex core line in the direction of the axial jet has a maximum value of 3.4 cm$^2$, over 25% greater than the enclosed area of a ring with the diameter estimated from the X-Y plane (2.5 cm$^2$). Given the truncation of the vortex filament, the actual enclosed area will be even larger. Table 2.1 summarizes the impulse at each timestep as estimated from the median, maximum, and minimum circulation with the measured projected area ($I = \rho \Gamma A_{\text{proj}}$). The lower bound is not calculated for t = 0.45 s when the ring is still attached to the body. The lower circulation where the vortex is attached to the caudal fin at this time may be due to PIV masking and is not representative of the vortex filament itself. The bounds on the circulation at each time show significant range, and highlight the very different understandings of the wake that can occur if circulation is only taken at a single slice location.

Based on the limitations apparent from the analysis of the turning danio wake, an alternative to the axisymmetric vortex ring taking advantage of volumetric measurements is desirable. This chapter describes a method for characterizing circulation and impulse in 3D with the goals of facilitating cross-comparison to earlier 2D studies while utilizing the added information provided by volumetric techniques.

The following text originally appeared in Mendelson L, Techet AH “On analysis of circulation, impulse, and force in propulsive wakes using 3DPIV.” 11th International
Table 2.1: Impulse estimated from the median and maximum circulations of the vortex filament in figure 2-2 at three instances in time. Upper bound and lower bounds on the impulse are also set by the maximum circulation value determined along the core line. A lower bound is not provided at t = 0.45 s because the vortex filament is still attached to the body and the lower bound is therefore affected by PIV masking and not representative of the vortex filament.

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<th>$\Gamma_{\text{max}}$ (cm$^2$/s)</th>
<th>$\Gamma_{\text{min}}$ (cm$^2$/s)</th>
<th>A (cm$^2$)</th>
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</table>

*Symposium on Particle Image Velocimetry*, Santa Barbara, CA, USA (September 2015).

### 2.2 Introduction

Unsteady aquatic maneuvers, including the rapid starts and jumps performed by fish, are highly three-dimensional events. The interactions between multiple fins and the body generate complex vortical flow structures that need to be resolved simultaneously across varying time and length scales in order to gain a full picture of the resulting hydrodynamics. Characterizing the impulses and vortex forces in such wakes requires accurate calculation of vortex circulation, geometry, and their temporal derivatives. While deriving these quantities from planar PIV data may seem a straightforward operation, the simplicity in the procedure can be credited more to the limitations in available data than the trivial nature of the calculation. Volumetric measurements show the full geometry and orientation of a vortex structure; there is no need to assume symmetry based on the information in a single plane. 3D PIV additionally can provide full vectors for derived quantities instead of components. It is also possible to simultaneously image vortex formation in multiple locations, demonstrating a need for complex vortex identification and segmentation procedures to independently analyze each flow structure. When vortex structures link, interact,
and have inherent asymmetries, a single circulation measurement is ultimately insufficient to characterize the impulse of the vortex ring. Even for isolated symmetric vortex rings at short timescales after formation, a case where the circulation is constant everywhere, evaluating the circulation at multiple locations can prove valuable, as it can be used to directly assess the uncertainty in its calculation.

Circulation and impulse are two fundamental quantities describing the momentum of a vortical flow. Circulation $\Gamma$ about a vortex core can be determined as either the line integral of velocity $\vec{u}$ about a closed contour $\vec{l}$ or, by Stokes’ theorem, as the area integral of vorticity $\vec{\omega}$ normal to and within the closed contour with area $A$ and normal vector $\hat{n}$ (equation 2.1). Two sample integration regions are shown in figure 2-3.

$$\Gamma = \oint_C \vec{u} \cdot d\vec{l} = \int_A \vec{\omega} \cdot \hat{n} dA$$ (2.1)

The hydrodynamic impulse $\vec{I}$ in a control volume $V$ due to the presence of vortex regions is defined as:

$$\vec{I} = \frac{1}{2} \rho \int_V \vec{x} \times \vec{\omega} dV$$ (2.2)

where $\vec{x}$ is the distance from a point in the vorticity field to the origin and $\rho$ is the fluid density. In the case of a thin-cored axisymmetric vortex ring, the impulse can be simplified to $I = \rho \Gamma \pi R^2$, where $R$ is the radius of the ring. This impulse acts in the direction of the vortex ring centerline axis. Many formulations for the forces acting on a body in flow include the impulse derivative $\vec{F}_{vor} = -d\vec{I}/dt$. While this circulatory force is far from the only factor that must be considered in a propulsive force balance, as pressure changes and added mass must ultimately be included [29], it is a valuable framework for many propulsive studies nonetheless. Impulse can be directly compared to the change in momentum of a maneuvering organism (e.g., [45]), and the strength of a vortex as measured by its impulse can be used to compare the relative contribution of multiple propulsors to a locomotive behavior. With an arbitrary vortex filament, such as a fish wake, the symmetry assumption made during planar PIV analysis may significantly underestimate the overall impulse in the wake.
The assumption that the impulse acts exclusively in the direction of the vortex ring axis may also not hold depending on the vortex topology. In the case of a turning fish, the vortex impulse direction may change over the course of the maneuver.

Previous studies have developed vortex impulse models taking advantage of more than a single geometry and circulation measurement, but none have fully coupled volumetric determination of geometry and orientation with a 3D impulse vector. Henningsson et al. [66] compute the impulse in a long vortex tube behind a swift using discretized circulation measurements along the length and span of the wake. Using 2D PIV data, the authors approximate the geometry of the vortex as a rectangle using the wingspan and flapping amplitude of the swift. Considering asymmetric vortex rings using numerical simulations and synthetic flow fields, Falahatpisheh and Kheradvar [48] introduce an asymmetry parameter and an averaged impulse, both of which are determined from multiple slices though the vortex ring. While the authors take into account local geometry by using the radial centroid of vorticity on each slice to calculate impulse, they still consider only the impulse acting along the axis of the ring about which they parameterize the slices.

In this study, a framework based on slices through the vortex ring is used to derive the net impulse vector of an arbitrary vortex filament in three dimensions. Vortex rings and other filaments are parameterized by their core line, a streamline describing the center of the vortex core. The vortex core line can be derived using eigenvectors of the velocity field, local maxima of the vorticity field, extrema of a vortex identification criterion or geometrically [123]. Using the core line to discretize any arbitrary vortex filament, the vector impulse can be described using the circulation measured along its length:

\[
\vec{I} = \frac{1}{2} \rho \sum_{i=1}^{M} \Gamma_i |\vec{s}_i| (\vec{x}_i \times \hat{n}_i)
\]

where \( M \) is the number of discrete points along the core line, \( \vec{x}_i \) is the position vector from the origin to the core point and the arc length of the discretized core segment is approximated by midpoints as

\[
|\vec{s}_i| = |0.5(\vec{x}_{i+1} + \vec{x}_i) - 0.5(\vec{x}_i + \vec{x}_{i-1})|
\]
preserve directional independence regardless of the direction along the core line in which the integration is performed. The unit normal \( \hat{n} \) is defined by the direction of the vorticity vector at the current point on the core line. Figure 2-3 provides a schematic of this geometry. By definition, the vortex core is parallel to the vorticity vector, thus for fine enough discretization of the core line \( \vec{s}_i \cdot \hat{n}_i \approx \pm 1 \). An immediate practical concern using this framework is the number of points along the core line necessary to accurately parameterize the vortex filament. From a purely geometric perspective, approximating the enclosed area of a circle or 2:1 ellipse by \( \sum_{i=1}^{M} |\vec{s}_i| (\vec{x}_i \times \hat{n}_i) \), is greater than 95% accurate for a discretization of 12 equidistant points about its circumference, which is a reasonable number of unique measurement locations to be derived from a volumetric PIV dataset. Approximations of wake geometry using line segments have also been applied to the analysis of helical vortices, such as those generated by wind turbine blades. The self-induced velocity of each segment is used to predict the wake kinematics (e.g., [18, 168]).

Figure 2-3: Schematic of the vortex ring parameterization used in the 3D analysis framework (equation 2.3). The vortex core line (dotted) is discretized into points \((\vec{x}_i)\) and the circulation about a normal \( \hat{n} \) parallel to the vorticity vector is measured at each point. These circulations are integrated around the arc length of the ring, divided into segments \( s_i \), to derive a full vector impulse. Sample circulation integration domains for velocity (contour \( l \)) and vorticity (area \( A \)) are also shown for reference.
2.3 Analysis methods

The process of measuring vortex impulse for an arbitrary network of vortex filaments can be broken down into the following steps. While the 3D reconstruction and velocity field interrogation processes across different volumetric PIV methods vary, the steps below can all be considered regardless of the measurement technique that was used to obtain the volumetric data, so long as results are Eulerian and on a Cartesian grid. In order to apply this method, calculations must be performed in a manner that is robust to the limited spatial resolution and measurement noise that can be present in PIV data. PIV directly yields a velocity field, and as a result many vortex identification methods are several postprocessing steps removed from the actual experimental measurement. The framework proposed relies heavily on direct velocity data to characterize vortex dynamics (avoiding use of any quantity beyond a first derivative of velocity) instead of the classical vorticity-based definitions for many quantities.

2.3.1 Vortex region identification

The role of a vortex identification criterion in this study is to identify candidate regions for the core line identification algorithm. The presence of vortex structures within a measurement volume can be determined using the magnitude of vorticity or an identification criterion. Eulerian vortex identification criteria are often derived from the velocity gradient tensor (\( \nabla \vec{u} \)) and can be evaluated numerically from PIV data in the same manner as vorticity. The Q-criterion, the second invariant of the velocity gradient tensor, is derived as 
\[
Q = \frac{1}{2}(\Omega^2 + S^2),
\]
where \( \Omega = \frac{1}{2}(\nabla \vec{u} - (\nabla \vec{u})^T) \) and \( S = \frac{1}{2}(\nabla \vec{u} + (\nabla \vec{u})^T) \), and represents a comparison between swirl and shear in the flow. When \( Q > 0 \), swirl dominates, and the flow is in the vicinity of a vortex core. \( \lambda_2 \) is also derived from the eigenvalues of \( (\Omega^2 + S^2) \). Numerous studies have compared the results given by different identification criteria for analysis and visualization purposes (e.g., [27],[96]). Lu and Shen [96] show very similar results using three different vortex identification criteria in the case of a flapping wing, all of which reduce the vortex region further than a vorticity threshold alone. In this study,
the Q-criterion is used to reduce the search space for the vortex core lines, though similar results would be yielded using a different Eulerian criterion.

2.3.2 Core line identification

The main challenge in implementing the analysis framework of equation 2.3 is accurately determining the geometry of the vortex core line, which is not known a priori and must be determined from the PIV measurement. Fundamentally, core line identification is a search for local extrema in a fluid quantity: velocity, vorticity, or an identification criterion. Algorithms that specifically detect the vortex core line are reviewed extensively in Roth [123]. Many of these methods require high spatial resolution, mesh manipulation, or additional knowledge of the pressure field and are thus poorly suited for PIV. For working with PIV data, using a method based on critical points of the velocity field presents several advantages. With any other quantity, the search procedures for extrema and core line fitting are similar, plus the added cost to derive whatever quantity is being investigated.

The core line identification procedure is a modification of that described by Sujudi and Haimes [149]. To convert each original PIV vector location to serve as the center of a cell, the velocity field is interpolated by a factor of two in each dimension. The velocity gradient tensor \( \nabla \vec{u} \) is then calculated by second order central differences and its eigenvalues and eigenvectors determined at points within the search space identified by \( Q > 0 \). For each point, if there exists only one real eigenvalue, the reduced velocity \( \vec{v}_{\text{red}} \) at the point is computed as the velocity minus its component in the eigenvector direction. If there is a zero crossing in all three directions within the \( 3 \times 3 \times 3 \) interpolated neighborhood around an original grid point, that point is considered a vortex core location. Rather than interpolating the plane on which each reduced velocity field components in the cell is zero and solving for their intersection directly, which frequently yields solutions outside the original cell given PIV noise, the centroid of the search cell, weighted by a factor of \( 1/|\vec{v}_{\text{red}}| \), is used as a sub-cell estimate of the core line location. Core points with contiguous indices on the original measurement grid are then sorted using a nearest-neighbor procedure to produce preliminary core
lines and smoothed once using a smoothing spline. The final number of points on the core line is proportional to the number of points on the original PIV grid and therefore each point will contribute a unique measurement of the vortex circulation.

### 2.3.3 Calculation of the circulation

Once the core line has been determined, it can be used to define the normal and location for slices through the vortex loop. On each of these slices, circulation can be determined from the in-plane velocity or vorticity data. For slices where the normal does not align with the original PIV grid, the in-plane velocity field is interpolated with data point spacing at the resolution of the original measurement. Circulation around closed contours can be directly found from the velocity field by integrating the component tangential to the integration path (equation 2.1). The integration is performed either iteratively over varying enclosed area until a peak value has been found or around a contour satisfying an identification criterion. In practice, the integration contours are often rectangular boxes on the PIV grid or interpolated ellipses matching the shape of the identified region. While iterative approaches better ensure that the circulation is not underestimated, they can fail in situations where multiple vortex features interact or are in close proximity. Thus, identifying the best non-iterative alternatives is desirable for complex flow fields.

Circulation is also frequently computed numerically as the area integral of all vorticity in a connected region (equation 2.1). The integration region is determined by where the vorticity magnitude is greater than a threshold \(|\vec{\omega}_{\text{min}}|\). \(|\vec{\omega}_{\text{min}}|/|\vec{\omega}_{\text{max}}|\), the threshold normalized by the peak vorticity magnitude within a particular vortex core, is typically prescribed arbitrarily as a certain ratio (e.g., 20%). Spedding et al. [144] introduces a correction factor that can be applied to circulation calculations to compensate for the subjectivity of the threshold choice. The circulation \(\Gamma_{\text{thr}}\), calculated with a threshold, can be related to the true circulation \(\Gamma\) by equation 2.4. This correction factor accounts for the tails of an assumed Gaussian distribution of vorticity and can be used to approximate the full circulation magnitude despite a thresholded vorticity calculation.
\[ \Gamma_{\text{thr}} = \left( 1 - \frac{\left| \vec{\omega}_{\text{min}} \right|}{\left| \vec{\omega}_{\text{max}} \right|} \right) \Gamma \]  

(2.4)

This method is not widely used in PIV studies where vorticity-threshold approaches to circulation are implemented, and is applied inconsistently in other studies. For example, Muijres et al. [104] uses \[ \Gamma = \left( 1 + \frac{\left| \vec{\omega}_{\text{min}} \right|}{\left| \vec{\omega}_{\text{max}} \right|} \right) \Gamma_{\text{thr}}, \] which diverges from equation 2.4 as the threshold increases. By Stokes’ theorem, equation 2.4 can also be applied when velocity about a contour defined by a vorticity threshold is integrated instead of the vorticity itself. For velocity-based integration, the correction factor performs best when the integration contour is a close fit to the thresholded edge (e.g., an ellipse) and does not include additional enclosed area to fit onto a grid (e.g., a bounding box). The relationship between the threshold of another identification criterion to the output circulation cannot be as easily defined. Since metrics such as the Q-criterion seek to find strong vortices instead of all vorticity, they may also substantially underestimate the circulation. As a result, a threshold of vorticity is used to define the integration region for both velocity and vorticity-based circulation procedures.

2.4 Test cases

2.4.1 Synthetic data

The robustness of the impulse procedure is assessed using synthetic 3D velocity fields of toroidal vortex rings. These simulations sample a known analytic velocity field on Cartesian grid points and superimposed additive zero-mean Gaussian white noise scaled by the local velocity magnitude. The distribution of tangential velocity \( u_\theta \) around the circular core line of the vortex ring is modeled as a Lamb-Oseen vortex (equation 2.5), where \( r \) is the distance from a point in the flow field to the vortex core line and \( a \) is a parameter controlling the size of the vortex core.

\[ u_\theta(r) = \frac{\Gamma_0}{2\pi r} \left( 1 - e^{-\frac{r^2}{a^2}} \right) \]  

(2.5)
The true circulation $\Gamma_0$ is explicitly prescribed in the equation and set to $\Gamma_0 = 2\pi$ for a nondimensionalized study. Spatial resolution is measured as $r_{crit}/\Delta x$, where $r_{crit}$ is the radial distance from the vortex center above which numerical integration of $\Gamma$ is consistent. The spatial resolution is varied between between 2.25 and 9 to characterize its effect on the circulation measurement.

The simulations are used to assess the relative performance of different 2D integration methods for circulation and inform the choice of integration method used in the subsequent experimental cases. The synthetic data are also used to assess the geometric approximation of the vortex core line. To isolate the role of vortex core line identification to determine reliable vortex geometry, impulse integration is performed with a known circular vortex core line and with the detected core line.

### 2.4.2 Time-resolved SAPIV experiment

To extend the analysis method to an arbitrary network of vortex loops and real experimental data, impulse analysis is performed on time-resolved synthetic aperture PIV (SAPIV) of a turning giant danio. SAPIV uses an array of cameras and light field imaging reconstruction algorithms to generate a 3D particle field for interrogation. Fundamental working details of SAPIV are presented by Belden et al. [17]. The SAPIV system (figure 2-4) used in all experiments consists of nine Vision Research Miro 310 high-speed cameras equipped with 50 mm Nikon lenses set to $f\# = 8$. Illumination is provided by an Oxford Lasers Firefly 1000 W 808 nm volumetric laser running with pulse duration $\delta t = 20 \mu s$. Images are recorded at 500 frames s$^{-1}$ and the time interval for processing is $\Delta t = 0.01$ s.

The giant danio used in the experiment has a mass of 8 g and a body length $BL = 7.5$ cm. The fish eye and the caudal peduncle (where a convenient marker stripe on the fish body is located) are digitized in images from each camera using the DLTdv5 custom Matlab software package by Hedrick [64]. The digitized images are then used to construct small localized visual hulls for each body feature as in [101], the centroids of which are tracked over time for 0.6 s. PIV interrogation is performed for the middle 0.2 s of the sequence. The time $t = 0$ s refers to the first
Figure 2-4: Setup for the time-resolved maneuvering fish experiment. Nine high-speed cameras are used to image a freely swimming giant danio in a five gallon tank. A near-infrared volumetric laser is used to provide illumination without disturbing the fish’s natural swimming behavior. The coordinate system of the measurement volume is defined with X and Y parallel to the front tank wall and Z perpendicular to the front tank wall.

timestep analyzed using PIV and is arbitrarily chosen. PIV masking is performed using the visual hull method [1]. Binary images of the fish body at each timestep for mask reconstruction are generated by reducing the size of the image with a Gaussian pyramid, segmenting the image using the grabCut algorithm [124], and rescaling the resultant binary image to its original size. The image segmentation routine is written using the openCV library [22] and is used instead of a thresholding procedure or edge detection. To reduce the visual hull shadow, elongation in Z created by the refocusing process (e.g., the masks seen in [101]), edge masks are refocused separately from the filled binary images. Based on where the edges converge, the reconstructed hull is truncated beyond the minimum and maximum depths that the body could physically occupy based on the width of the fish.

Image preprocessing prior to refocusing consists of subtracting a median-filtered
version of the image (7 × 7 pixel windows), convolution with a Gaussian blur kernel (3 × 3 pixel windows, σ = 0.5), local intensity normalization (21 × 21 pixel windows), and application of weighted refocusing [101]. Fast 3D reconstruction through refractive media is performed using the homography-fit (HF) method described by Bajpayee and Techet [10]. PIV interrogation is performed using a multipass cross-correlation implemented in a custom 3D version of MatPIV [150] with a final interrogation window size of 64 × 64 × 64 voxels and 75% overlap. The final spacing between vectors in physical units is 1.66 × 1.66 × 1.60 mm. Data post-processing consists of universal outlier detection [164] and 4D spatiotemporal smoothing using the smoother described and implemented in Matlab by Garcia [56].

2.5 Results

2.5.1 Synthetic vortex rings

Identification of the optimum method for calculating circulation is crucial to implementing the discretized impulse model. By testing several integration methods on 200 slices through the synthetic ring, their performance could be compared, and two methods are identified as yielding the best results. For a single 2D vortex core, both integrating vorticity within an area defined by a threshold (varied between 5 − 50% of the local maximum vorticity magnitude) and integrating velocity around an ellipse fit to the contour defined by the vorticity threshold yielded a normalized circulation Γ/Γ₀ ≈ 1 after applying equation 2.4. Integration contours defined as boxes on the original PIV grid could not be as easily corrected for the identification threshold because the area they enclose is less precise. The sensitivity of rectangular contour integration to the chosen threshold makes it less suitable for further implementation.

The synthetic data also shows that the core line points identified are a sufficient sampling of the original velocity field. Figure 2-5 shows normalized histograms of circulation taken on the 200 known core line points, and 41 detected points for the 3D synthetic vortex ring superimposed with additive zero-mean Gaussian noise scaled
by 50% of the local velocity magnitude. The circulations measured in both cases have a Gaussian distribution that is not substantially altered by using fewer detected core line points instead of the known locations. When vorticity is used to calculate the circulation, the peak in the histogram falls at a normalized circulation greater than unity. Since the noise adds additional velocity gradients to the flow field, these gradients propagate to the calculation of vorticity and contribute to the higher circulation values.

Figure 2-5: Histograms of the circulations calculated for the noisy synthetic vortex ring. Counts are normalized by the total number of circulation measurements. The blue histogram, determined with 200 known core line points, shows how the circulation varies from the true value due to the presence of noise. The red histogram shows 41 detected vortex core line locations and circulation taken normal to the vorticity at each location. The detected core line points do not significantly change the distribution of the calculated circulation values. Since noise introduces additional velocity gradients which are reflected in the calculation of vorticity, it follows that the circulation is overestimated using a vorticity-based integration method.

For validation purposes, it is important that variation in circulation around the ring is random, and not systematically underestimated in one region of the flow field. Figure 2-6 shows the distribution of circulation around the detected core line points in both the original and noisy datasets. The circulation shown is determined using velocity integration about an ellipse and the correction factor from equation 2.4. Since the noise is randomly distributed in the entire volume, the distribution does
not change substantially for vorticity-based integration, but the magnitude is higher due to the presence velocity gradients created by noise.

Figure 2-6: Azimuthal distributions of circulations calculated around the synthetic Lamb-Oseen vortex ring. (a) Circulation distribution on a synthetic Lamb-Oseen vortex ring (boundary visualized by $Q > 0$). The black line is the true analytic core line, while the points colored by dimensionless circulation are those detected by the core line identification algorithm. (b) Results of circulation analysis along the core line with additive Gaussian white noise scaled by 50% of the local velocity magnitude. The calculated magnitude of circulation varies around the ring, but is still between 0.9 and 1.1 times the true value.

Spatial resolution improves the results of the circulation calculation since the threshold for vortex region identification is enforced to greater precision. Increased resolution is most necessary for the in-plane integration step. In-plane resolution added artificially through interpolation immediately prior to contour identification yielded similar results to generating the synthetic flow field at a higher $r_{crit}/\Delta x$. In cases without noise or core line detection error, interpolating the velocity field in the 2D slice, re-calculating in-plane vorticity, and using a higher resolution threshold to define the integration area improved or did not alter the circulation measurement accuracy.

Table 2.2 shows the impulse calculated discretely from the circulation and core line measurements compared with the analytic thin-core impulse $I_0 = \rho \Gamma_0 \pi R^2$. All
results are shown for an original spatial resolution of $r_{crit}/\Delta x = 2.25$, the lowest spatial resolution tested, with interpolation to a factor of 1-10x spatial resolution once a slice through the volume has been taken. Interpolating the slice velocity field prior to taking circulation has a beneficial effect when the velocity field is not corrupted by noise and the core line points are known. When noise or core line detection error are added, any improvement from interpolation is inconsistent, likely due to propagation of noise during the interpolation process. These results also show that in some cases, error cancellation between the geometry and circulation can occur. When vorticity integration is performed on the noisy dataset with the detected core line points, the underestimated geometry and the overestimated circulation from noise in the vorticity field cancel almost perfectly. The presence of such error cancellations demonstrates one source of difficulty in performing uncertainty analysis of quantities derived from spatial integrals like circulation and impulse.

Table 2.2: Impulse calculated using different integration methods and a 20% threshold on vorticity magnitude to define the integration region. All results are shown with the correction factor from equation 2.4. The interpolation factors refer to the interpolation of the planar velocity field once a slice has been determined, but prior to evaluating the vorticity threshold.

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<td>0.961</td>
<td>0.962</td>
</tr>
<tr>
<td>Noisy</td>
<td>Vel Detected</td>
<td>41</td>
<td>0.966</td>
<td>0.950</td>
<td>0.948</td>
<td>0.947</td>
</tr>
<tr>
<td>Noisy</td>
<td>Vor Detected</td>
<td>41</td>
<td>0.966</td>
<td>0.985</td>
<td>0.997</td>
<td>1.000</td>
</tr>
</tbody>
</table>

The radial and tangential components of impulse, which are theoretically zero for a symmetric vortex ring, are never greater than 0.02% of the axial impulse when calculated using the core line approximation even in the case of noisy data. In the original dataset, the non-axial impulse components are several orders of magnitude
smaller. The radial and tangential components can also be used to demonstrate the advantages of using the discretized impulse model instead of calculating impulse directly from equation 2.2. If the noisy velocity field is integrated for impulse directly, the non-axial components reach magnitudes of 0.01 the axial impulse, two orders of magnitude larger than with the discretized impulse method. Even if the circulation is determined using vorticity, there is still more resilience to noise using equation 2.3 than if impulse is determined directly from the vorticity field. However, the error when impulse is determined using direct calculation from the vorticity field is still small in the synthetic test case.

2.5.2 Time-resolved fish wake

Biological flows are rarely a perfect symmetric vortex ring, and serve as a useful test case for the performance of the algorithm on actual experiment data. The features observed in the fish wake using SAPIV must be considered in the context of the danio’s kinematics. The trajectory of the fish eye shows two distinct bends during the image sequence. The fish enters the first bend swimming at a speed of 12 cm/s (1.6 BL/s) with unit tangent direction \( \langle 0.6, 0.3, -0.7 \rangle \) in the reference frame of the tank. Between the first and second bend the danio travels at a speed of 20 cm/s (2.7 BL/s) with direction \( \langle 0.8, 0.0, 0.5 \rangle \). The fish exits the second turn at a speed of 21 cm/s (2.8 BL/s) with direction \( \langle 0.9, 0.1, -0.3 \rangle \). The angle of the first bend is 80°, and the angle of the second bend is thus 50°. The fish accelerates during the first bend, but the second turn is primarily for direction change with little variation in the entrance and exit speeds of the fish.

The dominant wake structure during the second turn is seen in figure 2-7. While the second bend is the primary focus of the PIV image series, remaining vorticity from the first turn and secondary fins can be observed, especially shortly after \( t = 0 \) s in the \( Z > 10 \) mm region. Analysis focuses on the vortex tubes attached to the fish body at \( t = 0 \) s and their evolution into the vortex structure free of the fish seen at \( t = 0.18 \) s. The core line detection procedure captures additional small vortex features in addition to the main vortex filament, and proceeding to impulse analysis
Figure 2-7: Three timesteps of the giant danio’s vortex wake visualized by Q-criterion ($Q = 0.01 \max{Q}$) showing the initial vorticity attached to the caudal region of the fish body and the wake detachment over time. The solid line shows the path of the caudal peduncle over 0.6 s. The dotted line shows the trajectory of the fish’s right eye.

requires the use of a vortex core line filtering procedure not necessary in the simple synthetic test case.

Figure 2-8: Filtered and residual core lines detected over time in the danio wake. The filtered core lines detected over time show clearly the motion of the vortex structure as it is released by the fish. The residual excluded from impulse calculation consist of core lines entirely outside the region of interest and lines above a threshold from the centroid of all detected vortex core line points. For reference the black line shows the body trace of the caudal peduncle.

Once the core lines are detected for each timestep in the fish wake sequence, the
centroid of all detected points over all timesteps is used to filter the results geometrically, a step that removes many of the smaller, temporally-inconsistent features detected in the velocity field. Line segments outside a manually-defined region of interest, segments shorter than three points, and segments with centroids located outside a threshold from the global centroid are rejected prior to the impulse analysis. Figure 2-8 shows the results of vortex core line segmentation and the position of the core lines relative to the tail trajectory. The core lines detected after filtering show clear growth and motion over time, while the residual core lines do not show a clear temporal trend. Given the lack of consistency over time in the residual core lines, their contributions to the impulse are expected to be negligible, though physically they are likely responsible for ensuring that the vortex filaments in the wake form closed contours and that circulation is conserved in the entire fluid volume.

The valid core lines at each time step are each integrated independently to determine their contribution to the total impulse vector. Impulse over all timesteps is calculated using the centroid of the core points as the origin. Figure 2-9 shows the impulse components in the reference frame of the tank over time. The derived impulse is very noisy due to uncertainty in both the core line detection process and in the velocity data itself. Further investigation is needed to determine how much of the variation is due to core line detection and how much is due to underlying velocity uncertainty and noise propagating into the algorithm. Adding binning or temporal smoothing of the detected core line points would likely greatly reduce the noise in the impulse calculation. Despite the noise, it is clear that the magnitude and direction of the impulse vector changes substantially from t = 0.08 s to t = 0.15 s and trends can be examined by fitting a smoothing spline to the results. The smoothing parameter for the spline is chosen such that the smoothed impulse matches the number of inflection points in the corresponding tail kinematics. The impulse vector is most aligned with the eye velocity entering the second bend at t = 0 s and most aligned with the eye velocity after the second bend at t = 0.07 s, immediately before the drastic change in impulse magnitude created as the vortex is released from the fish tail. The extrema in the angle between impulse and body velocity are small; for both
the initial and final turn velocities, the dot product of the velocity unit direction and the impulse unit direction is between -0.75 and -0.95 at all times. A more interesting question is how the tail manipulates the impulse direction over time, which is best illustrated through examining the force.

![Figure 2-9: Impulse over time measured using both velocity and vorticity integrals for circulation in the reference frame of the tank. Both methods for deriving circulation yield very similar results when interpolated over time using a smoothing spline.](image)

By taking the time derivative of the smoothed impulse components, the circulatory force can be determined as \( \vec{F}_{vor} = -\frac{d\vec{I}}{dt} \). Figure 2-10 shows the results of differentiating the splines in figure 2-9 as force vectors. For a spatiotemporal reference, the forces are shown acting at the position of the caudal peduncle at each timestep.

The correspondence between the force vectors and the tail kinematics is clear, and the peak force magnitudes are observed as the fish emerges from the bend. While noise in the core line detection algorithm could be reduced significantly, the fact that a clear three-dimensional force vector that evolves in magnitude and direction over the course of a maneuver can be resolved from SAPIV data using the discretized impulse framework is a very promising result.
Figure 2-10: Force vectors and corresponding caudal peduncle position over time. The force is measured as the derivative of impulse using the curve fit to the velocity-based impulse in figure 2-9. Forces are shown as $\frac{d\vec{I}}{dt}$ (in the direction of the fish acting on the fluid), as opposed to $-\frac{d\vec{I}}{dt}$, the fluid force acting on the fish. Every other timestep is shown for clarity. Vectors do not change significantly for vorticity-based integration of $\Gamma$.

### 2.6 Conclusions

By coupling synthetic aperture imaging of both the giant danio’s kinematics and its wake, the method described in this study is able to capture the full hydrodynamic impulse vector in any reference frame. Using this analysis framework, it is clear that the impulse and vortex force vectors during a swimming maneuver may change dramatically in orientation as the fish manipulates vortices, and performing analysis that accounts for this three-dimensionality using planar PIV methods is often unfeasible.

While simple simulations show that the approximation used to discretize impulse does not significantly alter the derived impulse value, many challenges remain in robustly applying this framework to real experimental data. Improvements to the
process for detecting the vortex core line are necessary to reduce the measurement noise in the impulse. In synthetic aperture PIV in particular, particle reconstruction can be performed in any reference frame with appropriate definition of the refocusing transforms. As a result, it is necessary to determine if performing PIV interrogation in a frame closely aligned with the vortex core line yields improved performance of the core line identification algorithm or if the algorithm is frame invariant in its current implementation. Temporally filtering the detected core line points using Lagrangian predictions of the next core line location may also reduce the noise, and would facilitate the tracking of $\frac{d\Gamma}{dt}$ for material points in the vortex structure.

The current framework models the impulse using a thin vortex core assumption. In reality, the actual vortex impulse is larger due to the finite thickness of the vortex core [126]. For vortex structures where the core diameter varies substantially along the core line, the contribution of core thickness will be nontrivial to the impulse determined. Incorporating the geometry of the vortex core into the impulse discretization would further improve the fidelity of the model. A finite core formulation would be useful in cases where several vortex rings link together, such as forward swimming, since the core geometry changes during the linking process. In cases with minimal net change in speed but change in direction, such as the turning fish studied here, formulating the angular impulse in a similarly-discretized manner may yield additional insights.

2.7 Epilogue

2.7.1 Interacting wake features

The wake model developed in this section works best for isolated vortex filaments of arbitrary shape. As will be shown in chapter 3 (figure 3-19), the archer fish wake is composed instead of close-proximity, interacting vortices. Multiple interacting vortices present difficulties in applying the core line model. Wake segmentation is one major issue. Mendelson and Techet [101] show that the circulation calculated in the core shared between two linked vortex rings is stronger than elsewhere on the same
ring due to the interaction of multiple axial thrust jets from subsequent tailbeats. If the core line approach is applied to each vortex in this scenario, it will result in double-counting contributions of the interacting vortices to the predicted momentum, and the direction of the impulse vector will be biased.

The inability to characterize interactions between vortices using the core-line model is another limitation; such interactions can be crucial to obtaining accurate force predictions. Kriegseis and Rival [80] examine the breakdown of hydrodynamic terms contributing to the force measured on an accelerating thin plate using analogous kinematics in a quiescent tank and a flume with a freestream velocity. The motions are equivalent aside from reference frame, but have different measured force histories. In the flume, vortices shed and are advected out of the measurement volume instead of remaining attached as they do in the quiescent tank.

In complex flow scenarios, with non-trivial fin and wake interactions, the use of direct calculation methods (i.e., using equation 2.2) is inevitable. Some information about the influence of individual wake contributors can be inferred by calculating the impulse at multiple times and in reduced regions of the control volume. The latter is still limited, as drawing the boundaries around a wake feature too tightly is found by Mohebbian and Rival [103] to reduce the magnitude of the predicted force because high velocity gradients cross the control volume boundaries. Expanding beyond impulse, Rival and van Oudheusden [120] provide an overview of methods used for force estimation using Eulerian and Lagrangian experimental data. Estimating pressure from the velocity field, either by integrating the velocity gradients or solving a Poisson equation, is another class of approaches to predicting forces.

2.7.2 Wake kinetic energy

Propulsive performance can also be assessed quantitatively through a framework based on wake energetics instead of momentum transfer. This section examines whether an energetics-based approach can be used in the case of 3D measurements of a jumping archer fish. Appendix A examines additional considerations to using an energetics-based approach specific to the jumping archer fish problem.
The minimum energetic requirement for prey capture by jumping is the change in gravitational potential energy ($\Delta PE$) set by the vertical displacement ($h_{\text{max}}$) of the fish with mass $m_{\text{fish}}$.

$$\Delta PE = m_{\text{fish}}gh_{\text{max}} \quad (2.6)$$

A comparison between the energy in the flow field and the potential energy required to jump would be beneficial to assess the efficiency of jumping as a locomotive strategy. Since the archer fish generates all thrust in compact space and over a finite time, the duration of energy input can be captured in velocimetry experiments easier than with a species requiring a period of burst swimming for jumping acceleration.

Using velocity exclusively, the kinetic energy in a control volume is:

$$E_K = \rho \int_V \frac{1}{2} |\vec{u}|^2 dV \quad (2.7)$$

where $|\vec{u}|$ is the magnitude of the velocity vector. The kinetic energy of a vortical region in a three-dimensional domain can also be calculated from the velocity and vorticity fields as:

$$E_K = \rho \int_V \vec{u} \cdot (\vec{x} \times \vec{\omega}) dV - \rho \int_S [(\vec{u} \cdot \hat{n})(\hat{n} \cdot \vec{u}) - \frac{1}{2} |\vec{u}|^2 (\hat{n} \cdot \vec{x})] dS \quad (2.8)$$

where $|\vec{u}|^2$ is the velocity magnitude squared. Wu et al. [169] describe the term $\vec{u} \cdot (\vec{x} \times \vec{\omega})$ as the effective rate of work done by the impulse distribution. The surface integral terms describe work done on the boundaries of the control volume. In an infinite domain with the far-field at rest, the surface integral terms vanish, leaving

$$E_K = \rho \int_V \vec{u} \cdot (\vec{x} \times \vec{\omega}) dV \quad (2.9)$$

The expression in equation 2.7 is desirable for use with PIV data because it depends only on the velocity measurement provided by PIV interrogation. By definition, this quantity will also always be positive. However, equation 2.7 does not account for energy fluxes out of the PIV measurement volume, but instead assumes that energy
is contained within the control volume at all times.

Equations 2.8 and 2.9 require vorticity, a quantity that must be derived from the measured PIV data, and contain the position-dependent “moment arm” terms known to introduce sensitivity to choice of origin and domain boundaries [109, 34, 120]. The advantage of equations 2.8 and 2.9 is the information density of specific regions of the flow field varies between the two formulations. As emphasized by Rival and van Oudheusden [120] for force prediction, transforming volume integrals to surface integrals reduces the dependence of a calculation on resolution in near-body regions, and also enables calculations in finite-domains without quiescent far-fields. However, there is no mathematical guarantee that equations 2.8 and 2.9 will be positive, as there is with equation 2.7. The larger the domain over which equation 2.8 is applied, the greater terms at the surface of the control volume will be amplified by their position vector.

From an error propagation perspective, use of equation 2.7 is desirable because it utilizes the quantity directly measured during PIV processing. The vorticity-based energy formulations (equations 2.8 and 2.9) have more operations and terms, both error propagation sources, than their impulse counterpart (equation 2.2). With impulse, error in vorticity, determined by numerically differentiating the velocity field, is amplified by the position vector $\vec{x}$. In addition to that error contribution, with kinetic energy, the velocity error is introduced again by taking the product of $\vec{x} \times \vec{\omega}$ with the velocity vector. The surface integral terms in equation 2.8 also still include the velocity squared.

### 2.7.3 Effects of PIV processing on energy calculation

During the cross-correlation step of PIV processing, in 2D or in 3D, the peak of the correlation function is essentially an average displacement for all particles in that window. Velocity gradients within windows cannot be resolved; therefore processing PIV data is effectively a low-pass filter. These effects are particularly pronounced in 3D: information is smoothed over an additional dimension and the interrogation windows feasible for use are typically larger. For a valid cross-correlation peak, inter-
rogation windows ideally contain around ten particles [5]. In a 2D source image, all particles imaged lie within the thin light sheet. In 3D, an equivalent image density of particles is distributed across the depth of the entire light volume. The thicker the illumination, the fewer particles per 3D volume for the same number of particles per 2D pixel in source images. Interrogation window sizes of 48-64 voxels in all dimensions are common in 3D techniques, instead of windowing down to 16 pixels as with 2D measurements. Spatial resolution can be enhanced by using 75% overlap instead of 50% between windows, but the smoothing of velocities within a window is independent of the overlap. Examining equation 2.7, the kinetic energy scales with the velocity magnitude squared. Underestimating peak velocities within a window will therefore have a greater impact on kinetic energy than on vorticity or any other quantity that scales with $|\vec{u}|$ instead of $|\vec{u}|^2$.

The effects of windowing on kinetic energy calculation are assessed using a synthetic test case with an exact expression for the kinetic energy. The test case is a three-dimensional synthetic axisymmetric vortex ring with a velocity field of the form:

$$|\vec{u}| = \frac{8K r}{l} e^{-\frac{r}{l}}$$  \hspace{1cm} (2.10)

where K is a scale factor, r is the distance from any point in the flow field to the circular core line of the vortex ring (radius R), and l is a parameter controlling the vortex strength. Synthetic vortex ring flow fields of this form have previously been used to assess the accuracy of reconstruction and vector interrogation procedures in tomographic and synthetic aperture PIV [43, 17]. This vortex represents an extreme case where most energy and velocity gradients are located surrounding the vortex core. In contrast, the axial jet of a biological wake provides a region where more kinetic energy is contained with fewer spatial gradients than the flow field in equation 2.10.

The velocity gradients in the flow field vary with distance from the core line as:

$$\frac{d|\vec{u}|}{dr} = \frac{8K(l - r) e^{-\frac{r}{l}}}{l^2}.$$  \hspace{1cm} (2.11)
Figure 2-11: Deterioration in calculated kinetic energy with increasing 3D window size for two velocity gradient scales $(l = 0.1$ and $l = 0.05)$ and three spatial resolutions. Kinetic energy calculated decreases with increasing window size and with increasing spatial gradients.

At $r = 0$, the velocity gradients scale with $8K/l$. The strength parameter $l$ can therefore be varied to assess the dependence of energy calculations on the magnitude of velocity gradients within the flow field. There is additionally an exact expression for the kinetic energy from this flow field:

$$E_K = 48\pi RK^2l^2$$  \hspace{1cm} (2.12)

Synthetic flow fields of varying resolution are generated by varying the number of pixels per ring radius $R$. Windowing is simulated by convolving a flow field generated from equation 2.10 at voxel scale with a box filter. The width of the filter in each dimension is equal to the window size. After low-pass filtering, the flow fields are downsampled to PIV-scale resolution by dividing them into overlapping windows and taking the velocity values at the center of each window as representative of the entire window. Figure 2-11 shows kinetic energy calculations for three resolutions (25, 50, and 100 voxels per vortex ring radius $R$) and two velocity gradients $(l = 0.1$ and $l = 0.05)$.

The kinetic energy drops more rapidly for the case with higher spatial gradients.
Kinetic energy also drops with decreasing feature size, increasing gradient magnitude, or increasing window size. Using 32 voxel windows, the smallest that is typically feasible for volumetric PIV, the vortex with a radius of 100 voxels maintains 82% of its kinetic energy following windowing and downsampling. The case with twice the gradient magnitude only retains 53% of its energy. At 48 voxel windows, the lower-gradient case drops to 67% of its energy; the high-gradient case is down to 31%. With 64 voxel windows, common for thick-volume 3D PIV, the highest-resolution, lowest-gradient case falls to 52%. In an experimental setting, the magnitude of all velocity gradients is not known \textit{a priori}. Where the data falls within the wide-range of severities for kinetic energy approximation is likewise difficult to predict.

![Figure 2-12: Experiment setup for the turbulent vortex ring measurements used to assess kinetic energy calculations. (a) Diagram of the nozzle and measurement volume. (b) Photograph of camera array (left) and laser placement (bottom) relative to the experiment tank. An additional 2D survey camera (top left) is used to determine piston velocity profile and stroke length.](image)

Smoothing operations to remove spurious vectors in the velocity field after cross-
correlation will contribute further underestimation to the kinetic energy by lowering peak velocities. These effects are characterized using a second test case: three-dimensional SAPIV measurements of an axisymmetric vortex ring generated by a mechanical piston. Unlike the synthetic flow field, this case includes a strong axial jet. This case is used to assess the effects of smoothing in both space and time toward the kinetic energy calculation. The effects of smoothing are also compared between impulse (equation 2.2) and energy (equations 2.7 and 2.8) frameworks.

![Figure 2-13: One timestep of SAPIV results for the turbulent vortex ring test case. The vortex ring is visualized by an isosurface of the Q-criterion. Velocity vectors showing the fast-moving axial jet at two slices through the centerline of the ring are shown, color-coded by their magnitude.](image)

Figure 2-13: One timestep of SAPIV results for the turbulent vortex ring test case. The vortex ring is visualized by an isosurface of the Q-criterion. Velocity vectors showing the fast-moving axial jet at two slices through the centerline of the ring are shown, color-coded by their magnitude.

Figure 2-12 shows the experiment setup for the experiment. The vortex ring is generated by a mechanical piston moving upstream of a 12.7 mm diameter nozzle to displace a slug of fluid. The ratio of stroke length to orifice diameter (L/D_o) for the vortex ring is 3.7, within the range of formation numbers that produces an isolated vortex ring instead of a multi-vortex jet. The Reynolds number U_{piston}D_o/\nu = 20,000,
a highly-turbulent vortex ring. Synthetic aperture PIV is performed six diameters downstream of the nozzle. The SAPIV array consists of nine Miro 310 high-speed cameras running at 2000 frames s\(^{-1}\). The measurement volume is approximately 80 \(\times\) 70 \(\times\) 65 mm. Two perpendicular cylindrical lenses are used to volume-expand a Photonics Industries 527 nm laser, which also pulses at 2000 Hz. A first-surface mirror is used to reflect the laser volume upwards into the tank from below.

SAPIV processing is performed via multi-pass cross-correlation with a final window size of 64 \(\times\) 64 \(\times\) 48 voxels and 75\% window overlap. The final vector resolution following cross-correlation is 1.36 \(\times\) 1.36 \(\times\) 1.6 mm. Two velocity field smoothing operations in post-processing are considered: smoothing the velocity field in space using a 3 \(\times\) 3 \(\times\) 3 local averaging kernel and fitting of local second-order polynomials in space and time over a region of 5 \(\times\) 5 \(\times\) 5 vectors in space and five timesteps [130]. Figure 2-13 shows one timestep of the SAPIV flow field results from this experiment.

Kinetic energy and impulse are calculated for 21 timesteps where the ring is centered in the measurement volume. Figure 2-14a shows the kinetic energy calculated from equation 2.7 for all three cases and kinetic energy calculated from equation 2.8 for the original and most smoothed (space and time) cases. The downward (Y) and off-axis (X,Z) components of the impulse vector calculated using equation 2.2 are also shown. The maximum absolute value for X-impulse calculated at any time is 54 gcm s\(^{-1}\) and the maximum absolute value of the Z-impulse is 65 gcm s\(^{-1}\). The Y-impulse is approximately ten times larger than the X or Z impulses calculated at any time.

Most notably, the energy calculated using equation 2.8 is actually negative for the case with unsmoothed data, and the sign on the smoothed data switches around \(t = 0.008\) s. This formulation is therefore far more sensitive to measurement and choice of origin than calculating kinetic energy from velocity. Spatially-smoothing the velocity field reduces the kinetic energy calculated, as does smoothing in both space and time; peak energies calculated after smoothing are approximately 75\% of the peak values calculated without smoothing. Spatial smoothing with the 3 \(\times\) 3 averaging kernel, however, has minimal impact on the impulse calculated. The increased smoothing when filtered in both space and time reduces the impulse, and also
Figure 2-14: Quantitative analysis of the turbulent vortex ring. (a) Kinetic energies calculated using equations 2.7 and 2.8. (b) Hydrodynamic impulse calculated using equation 2.2 with the origin located at the center of the vortex ring in X and Z and the middle of the Y-range the ring travels through. Axial (Y) impulses are shown for all thee cases by the red, blue, and black lines. Off-axis (X,Z) impulse components for all datasets are shown in green.

The fluctuations in impulse over time, which suggests the smoothing may be beneficial if the impulse derivative is ultimately required for a force estimate.

The circulation estimated from 2D PIV measurements of the same vortex ring generator is 400 gcm s\(^{-1}\) with a ring diameter of 1.5 cm and a core diameter of 1.0 cm. The expected impulse using an axisymmetric, finite-cored vortex ring model (equation 1.5) is -1000 gcm s\(^{-1}\). The direct calculation of impulse is reasonably accurate in all data-filtering cases. Impulse is invariant in a viscous vortex ring; the circulation decreases as the diameter grows [125, 61]. Variations of the impulse over time can be used to assess uncertainty. The impulse of the raw case is \(-657 \pm 70\) gcm s\(^{-1}\) (mean ± s.d.), the impulse of the spatially smoothed case is \(-660 \pm 69\) gcm s\(^{-1}\), and the...
impulse error of the space/time smoothed case is $-558 \pm 52 \text{ gcm s}^{-1}$.

The results examining the turbulent vortex ring suggest that an analysis framework based on hydrodynamic impulse is the most robust to processing parameters. Kinetic energies are best calculated from the original PIV velocity data if an energy expenditure to evaluate efficiency is ultimately required. In general, however, energies calculated from 3D PIV measurements should not be taken as an accurate measurement of energy expenditure. These quantities can only truly be compared within a study where all data is subject to the same processing parameters.

2.8 Summary

This chapter presents several approaches to performing quantitative analysis of volumetric PIV measurements. Wake analysis performed using impulse, both through direct calculation (equation 2.2) and use of the core line and circulation slices, is less sensitive to processing parameters than wake analysis using a framework based on kinetic energy. Impulse derivatives can be estimated using a smoothing spline to determine one term of an instantaneous force balance. Kinetic energy calculations using the velocity field directly (equation 2.7) are sensitive to the PIV processing parameters, especially in 3D. These estimates should only be compared between wake measurements with the same processing, and not with energies calculated through other means. However, using velocity directly to evaluate kinetic energy is still preferable to calculating the kinetic energy from equation 2.8; amplification of noise and additional mathematical operations can both reduce the magnitude of the energy calculated and in some cases result in nonphysical negative values. Theses findings inform the choice of analysis methods used for the jumping archer fish problem in chapters 3 and 5.
Chapter 3

Archer fish jumping prey capture in two dimensions: kinematics and hydrodynamics

3.1 Prologue

This analysis originally appeared in Shih AM, Mendelson L, Techet AH (2017). “Archer Fish Jumping Prey Capture: Kinematics and Hydrodynamics.” Journal of Experimental Biology 220(8). Data discussed in this section was originally collected by Anna Shih [138] and was processed and analyzed as part of this thesis.

This chapter is an introduction to the jumping prey capture mode exhibited by archer fish. High-speed kinematic images from five fish are used to determine aiming and success statistics. Kinematic data are also used to observe fin activities and how aspects of the fish’s body and caudal fin (BCF) swimming gait (see review of locomotive modes in Sfakiotakis et al. [136]) are modulated during a jumping maneuver. Two-dimensional measurements of the wake structures using particle image velocimetry are also used to derive hypotheses in need of further examination in 3D.
3.2 Materials and methods

Before presenting new analysis, an overview of the experimental methods used by Shih [138] to originally film the archer fish jumps in 2D is first necessary to describe the origins of the dataset. This summary also includes the analysis methods for the kinematic and hydrodynamic data used as part of this thesis.

3.2.1 Fish

Ten smallscale archer fish (*Toxotes microlepis*) were imported from a local aquarium store and housed in a 75% full 55 gallon (122 cm × 33 cm × 51 cm) brackish water aquarium (25-28°C, salinity 9.5 mS cm⁻¹, 9:15 hour light:dark cycle). Since the fish were not bred in captivity, ages and sexes were unknown. Fish were fed freeze-dried brine shrimp or bloodworms at the water’s surface daily. Fish were trained to jump prior to experiments by replacing daily surface feeding with food suspended from a string above the tank. During training, food was temporarily removed if the fish spat instead of jumping. Training was performed at least twice weekly for at minimum one month prior to testing. Five fish jumped for greater than fifteen trials under the kinematic experimental conditions described in the next section. All experiment protocols were approved by the MIT Committee on Animal Care (protocol no. 0709-077-12).

Fish lengths and caudal fin surface areas were obtained by digitally photographing each fish in a narrow aquarium with a gridded background to provide scale and distortion correction. Images were taken with a Canon EOS 20D digital SLR camera equipped with an 18-55 mm zoom lens. Camera calibrations were verified by photographing an object of known length in the same tank. Standard length (6.8-11.1 cm range) was used as the characteristic body length (BL) scale to normalize data. The caudal fin surface area (1.7-5.3 cm²) was proportional to the length. Fish weight (7.9-28.3 g range) was obtained by weighing a beaker of water before and after adding the fish. Physical dimensions of each specimen are presented in table 3.1. Table 3.2 describes the number of kinematic trials for each fish, the maximum height, and the
prey capture success rate, which was determined as the percentage of trials in which the mouth closed on the bait. Failed jumps with bait heights below the maximum successful jump height of each fish were considered for analysis, but failed jumps with bait heights above the maximum successful jump height were not. Since the focus of this study was on the height attained, successful and failed capture kinematics were analyzed together.

Table 3.1: Standard length, tail area, and mass of each fish used in the 2D kinematic study.

<table>
<thead>
<tr>
<th>Specimen No.</th>
<th>Length [cm]</th>
<th>Tail Area [cm²]</th>
<th>Mass [g]</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>11.1</td>
<td>5.3</td>
<td>28.3</td>
</tr>
<tr>
<td>2</td>
<td>9.8</td>
<td>5.1</td>
<td>23.6</td>
</tr>
<tr>
<td>3</td>
<td>7.0</td>
<td>2.2</td>
<td>7.9</td>
</tr>
<tr>
<td>4</td>
<td>6.8</td>
<td>1.7</td>
<td>10.2</td>
</tr>
<tr>
<td>5</td>
<td>7.6</td>
<td>2.6</td>
<td>9.3</td>
</tr>
</tbody>
</table>

3.2.2 Kinematic analysis

Kinematic imaging was performed in the home tank. Custom plastic dividers were used to separate one fish for study while permitting it to swim freely and allowing water flow through the entire tank. A dried Gammarus shrimp (Tetra, Blacksburg, VA, USA) was suspended on a wire above the water’s surface for a range of heights from 0.25 - 2.5 BL to elicit jumping maneuvers. Bait position within the tank sufficiently prevented hydrodynamic wall effects on the jump flow field. Jumps were recorded at 700-900 frames s⁻¹ (0.0011-0.0014 s between frames) using an IDT Motion Pro X3 high-speed camera (1280 × 1024 pixels, 900-1008 µs exposure time). A Nikon Nikkor 50 mm lens (aperture f/4-5.6) yielded fields of view between 12 × 15 cm and 27 × 34 cm. The scene was back-illuminated by a bank of diffused fluorescent lights.

Kinematic image analysis was performed using Matlab R2014a (MathWorks, Natick, MA, USA). A total of 98 jumping sequences were analyzed (16-24 per specimen). To synchronize timescales, t = 0 s was defined as when the first jumping stroke was initiated by the fish’s caudal fin. Positions of the snout, caudal fin, bait and free
Table 3.2: The total number of jumps, maximum observed height and success rate of each fish used for 2D kinematic analysis.

<table>
<thead>
<tr>
<th>Specimen No.</th>
<th>Jumps (all views)</th>
<th>Jumps (tail kinematic views)</th>
<th>Max. Height [cm (BL)]</th>
<th>Success Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>16</td>
<td>10</td>
<td>11.0 (1.0)</td>
<td>94%</td>
</tr>
<tr>
<td>2</td>
<td>24</td>
<td>17</td>
<td>14.7 (1.5)</td>
<td>92%</td>
</tr>
<tr>
<td>3</td>
<td>18</td>
<td>8</td>
<td>13.7 (2.0)</td>
<td>94%</td>
</tr>
<tr>
<td>4</td>
<td>16</td>
<td>8</td>
<td>15.5 (2.3)</td>
<td>87%</td>
</tr>
<tr>
<td>5</td>
<td>24</td>
<td>11</td>
<td>20.0 (2.6)</td>
<td>71%</td>
</tr>
</tbody>
</table>

Surface were digitized using the custom Matlab software package DLTdv5 [64]. The snout was tracked automatically, while all other points were digitized manually. The vertical position of the snout was smoothed using a quintic smoothing spline to ensure a continuous second derivative [158]. Jump height ($h_{\text{max}}$) was defined as the maximum snout height above the free surface. Upward velocity ($v$) and acceleration ($a$) were calculated by analytically differentiating the snout position. Body midline traces were determined in Matlab by digitizing approximately ten points from the snout to the caudal fin along the fish’s centerline and fitting a cubic spline between the points. The midline spline was evaluated at every pixel along the length of the fish and converted to physical units for visualization.

Snout position was tracked to determine vertical trajectories since it had high contrast with the image background and could be easily detected for automatic tracking in the image data. Snout position also served as a better indicator of aim than center of mass (COM) position since the goal of a jump was for the fish’s mouth to reach the bait. The gravitational potential energy ($\text{PE} = m_{\text{fish}} g \Delta h$), kinetic energy ($\text{KE} = 0.5 m_{\text{fish}} v^2$) and total energy ($E = \text{PE} + \text{KE}$) were calculated over time for each run by assuming the COM was a fixed distance below the snout and followed a similar vertical trajectory. In the energy calculations, which treated the fish as a ballistic projectile, $m_{\text{fish}}$ was the overall mass of the fish, $g = -9.8 \text{ m s}^{-2}$ was gravitational acceleration and $\Delta h$ was the change from initial to maximum snout height. Given the nature of the jump kinematics, approximating the COM position from the snout position contributed minimal error to the energy estimates. The snout remained aimed
at the bait for the jump duration and there was not significant body bending until after bait capture. Direct tracking of a point at the stretched-straight COM in five validation runs (one per specimen) had a root mean squared error (RMSE) of 2-4% and a maximum of 8% disagreement with the estimate of COM position as a constant offset from the snout. Similarly, Tytell and Lauder [155] found small displacement of the COM of a bluegill sunfish during the extreme bending of a C-start maneuver, and Xiong and Lauder [171] estimated at maximum 5% error in COM tracking during forward swimming by assuming the COM was a fixed point on the fish body.

The digitized caudal fin trajectory was used to count peak-to-peak propulsive tail strokes. Strokes that ended or initiated at the body midline were considered half strokes. Stroke amplitudes and durations were measured for runs where the kinematic images provided a ventral view of the body and complete tail kinematics could be seen without occlusion from the anal fin. The peak-to-peak amplitude of each tail stroke was measured by plotting the lateral displacement of the tail from the body axis over time; durations were measured as the interval between successive peaks in the displacement curve. Mann-Whitney U-tests (Matlab function `ranksum`) with \( p < 0.05 \) considered significant were used to assess differences in stroke amplitude (in BL) and duration (in s). Comparisons were made using specimens and stroke numbers with \( n \geq 5 \) runs with visible tail trajectories. Specific factors considered were the specimen, the timing of a stroke in a jump sequence (e.g., first stroke versus third stroke) and the overall jump height.

### 3.2.3 Flow visualization

Wake features generated by a jumping archer fish were visualized using a high-speed, near-infrared implementation of 2D particle image velocimetry (PIV) [115]. A ten gallon tank (51 cm × 25 cm × 31 cm) filled halfway with water from the home tank was seeded with neutrally-buoyant, polyamid particles (average diameter 50 \( \mu m \), density 1.03 g cm\(^{-3}\)). Illumination was provided by a Lasiris Magnum diode continuous-wave laser with a maximum output of 2 W at 810 nm. Integrated laser optics produced a 10° fan light sheet. The laser was mounted below the tank with the light sheet parallel
Figure 3-1: Experiment setup for 2D PIV on jumping archer fish. Two cameras (one to film particle motion, one to monitor the aerial jump duration) running at 900 frames s$^{-1}$ viewed the ventral side of the fish as it jumped. The laser was positioned below the tank with the light sheet parallel to the tank wall and camera image plane (into/out of the page as shown here). Bait was placed between the tank wall and the near-infrared laser sheet. The tank was partially filled to provide space for the fish to jump above the free surface. Figure modified from [138].

to the front wall. Particles were imaged with an IDT Y-3 camera (900 frames s$^{-1}$; 1260 × 1024 pixels) equipped with a Nikon Nikkor 50 mm lens (12 × 10 cm field of view).

PIV was performed at bait heights of 0.5 and 1.0 BL. Bait was positioned between the front tank wall and the laser sheet. Positioning the bait 10 cm or less from the wall ensured that the fish jumped with its ventral side (as opposed to dorsal) facing the camera. A setup diagram is provided in figure 3-1. PIV analysis focused on the initial motions of the caudal, pectoral or anal fins, since alignment between the fish and the light sheet was not guaranteed at later times in a jump. DLTdv5 was used to manually digitize the trajectory of the in-plane fin (caudal or anal) in the PIV images to determine the kinematics corresponding to the observed wake structures.

PIV images were processed with LaVision DaVis 7 software (LaVision, Göttingen, Germany) using a multi-pass cross-correlation algorithm (32 × 32 pixel windows; 50% overlap), yielding approximately 45 vectors per body length. Velocity fields were post-processed in DaVis with median filtering, iterative interpolation to fill empty
vectors and a $3 \times 3$ averaging filter. Out-of-plane vorticity ($\omega$) was computed from the velocity fields using the Matlab function *curl*. To measure the strength of coherent wake vortices, circulation was calculated numerically as

$$\Gamma = \int_A \vec{\omega} \cdot \hat{n} dA = \sum_{i,j} \omega_{i,j} \delta A,$$  \tag{3.1}$$

where $\hat{n}$ is the normal vector of the PIV measurement plane, $i$ and $j$ were indices in the x and y directions and $\delta A = (16 \text{ pixels})^2 = 0.0225 \text{ cm}^2$ was the enclosed area between grid points. A threshold of $25 - 45\%$ of the local maximum vorticity in each vortex core was used to determine the integration region over which equation 3.1 was applied [45]. The vorticity threshold for each case was chosen as the lowest threshold at which close-proximity wake features did not merge. This calculation underestimated the circulation since vorticity below the threshold was excluded from summation. For a given vortex core, the circulation $\Gamma_{\text{thr}}$, calculated with a threshold $|\vec{\omega}_{\text{min}}|/|\vec{\omega}_{\text{max}}|$, was related to the true circulation $\Gamma$ as

$$\Gamma_{\text{thr}} = \left(1 - \frac{|\vec{\omega}_{\text{min}}|}{|\vec{\omega}_{\text{max}}|}\right) \Gamma.$$

The correction factor in equation 3.2 assumed a Gaussian distribution of vorticity [144] and was used to estimate the true strength of each vortex from the thresholded value, thus facilitating comparison of circulations calculated with different thresholds. Circulations were smoothed over time using a local averaging filter with a neighborhood of five time steps (0.0056 s).

The orientation of propulsive jets in the wake was measured as the median direction of the top 80% of velocity vectors in the vicinity of a velocity maximum. Angles were measured relative to vertical and were used to assess jet contributions to upward versus lateral forces.

The in-plane wake kinetic energy was calculated at each time step as

$$E_{K,2D} = \int_A \frac{1}{2} \rho |\vec{u}|^2 dA = \frac{1}{2} \rho \sum_{i,j} |\vec{u}_{i,j}|^2 \delta A,$$  \tag{3.3}$$
where $|\vec{u}|$ was the in-plane velocity magnitude and $\rho$ was the water density (1.00 g cm$^{-3}$ for experiment temperature and salinity). The control volume for kinetic energy calculations was identified manually to include all wake structures surrounding the fish body while limiting the inclusion of ambient flow structures and noise. For consistent filtering between kinematic and hydrodynamic energy data, the in-plane kinetic energy measurement was smoothed using a quintic spline.

### 3.3 Two-dimensional results

#### 3.3.1 Kinematics

Jumping kinematics followed the three stage framework for in-water fast starts [162, 37], with preparatory, propulsive and variable stages. The three phases of the jumping behavior were: (1) hovering, (2) thrust production and (3) gliding.

![Figure 3-2: Image sequence of specimen 5 jumping 2.3 BL above the surface. The aiming stage ended at time $t = 0$ ms. Frames from $t = 5.6-56.0$ ms showed a series of thrust-producing tailbeats. Abduction of the pectoral fins was also prominent from $t = 5.6-11.2$ ms. For $t > 56.0$ ms, the fish was above the water gliding toward the bait. Figure modified from Shih, Mendelson, and Techet [137].](image-url)
Before each jump the snout was positioned at the surface to sight prey (figure 3-2, t = 0.0 ms). Alternating motions by the left and right pectoral fins and an oscillatory wave in the caudal fin provided stabilizing forces that allowed the body to remain fixed in space. The vertical position of the snout measured from the surface during hovering was -0.01 ± 0.06 BL (mean ± s.d.). Starting snout position did not vary significantly by fish (Mann-Whitney U-test, p < 0.05 considered significant). The body was inclined at an angle below the surface (see also figure 3-1) and the caudal fin was deflected laterally toward one side of the body (figure 3-2, t = 0.0-5.6 ms). At the start of the thrust production stage, the pectoral and pelvic fins abduct (figure 3-2, t = 5.6-16.8 ms) and remain abducted until exiting the water.

Simultaneously, the fish initiated a series of propulsive tailbeats with an oscillatory
Figure 3-4: Relationships between bait and jump height, bait height and overshoot, peak velocity and jump height and peak acceleration and overshoot. Open markers correspond to trials where the fish does not capture the bait and closed markers correspond to trials with successful bait capture. (A) Maximum snout height was significantly correlated with bait height with a slope greater than a 1:1 relationship. (B) Overshoot, defined as jump height above the bait height, showed weak positive correlation with bait height but was greatest at intermediate bait heights. (C) Maximum velocity, non-dimensionalized by hydrodynamic Froude number ($V_{\text{max}}^2 \text{gBL}^{-1}$), correlated strongly with jump height. (D) Maximum acceleration, normalized by gravity, showed positive correlation with overshoot. Figure reproduced from Shih, Mendelson, and Techet [137].

wave traveling along the body. Figure 3-3 shows midline traces of the wave over time for a 2.3 BL jump. The snout trajectory was predominantly vertical. As more of the body left the water, the motion envelope of the tail decreased in amplitude. The thrust production phase was considered over when the fish ceased active tailbeats
or completely left the water (figure 3-2A, t = 56 ms). The gliding phase was when
the body accelerated only due to gravity or changes in posture (figure 3-2, t = 56.0-
140.0 ms). This phase was considered over when the fish reached maximum height.
The mouth closed on the bait during the gliding phase of a successful jump.

Bait height ($h_{bait}$) and jump height ($h_{max}$) were strongly correlated (figure 3-4A).
The maximum jump height observed was approximately 2.5 BL. Jump heights above
2 BL were realized in three specimens (specimens 3-5), while the two fish of greater
length and mass (specimens 1 and 2) had maximum observed jump heights of 1.0 BL
and 1.5 BL respectively. The minimum jump height observed in any of the trials was
approximately 0.5 BL, though bait was positioned as low as 0.25 BL.

The relationship between bait height and jump height was also quantified in terms
of the overshoot ($h_{max} - h_{bait}$). Overshoot was weakly correlated with bait height
(figure 3-4B). The median overshoot across all fish and jump heights was 0.16 BL.
Variation in overshoot range between specimens was observed (figure 3-5); specimens
1 and 2 had lower median and maximum overshoot than specimens 3-5. Undershoot,
with a jump height less than the bait height, was observed during early specimen
training but not during kinematic experiments.

Maximum body velocities ($V_{max}$) during each run ranged from 0.6-1.7 m s$^{-1}$ with
peak accelerations ($A_{max}$) from 10-103 m s$^{-2}$. The velocity, scaled by the hydrody-
namic Froude number ($V_{max}^2 (gBL)^{-1}$) to normalize for size effects, correlated strongly
with jump height (figure 3-4C). Acceleration, normalized by gravity, was strongly cor-
related with overshoot (figure 3-4D); higher accelerations were correlated with greater
overshoot. Peak acceleration varied among individual fish; two of the fish (specimens
3 and 4) typically achieved higher accelerations than the others across all jump heights
(figure 3-5).

Fish executed more peak-to-peak tail strokes ($N_{TB}$) to jump higher (figure 3-6A).
Tail strokes were not uniform; amplitudes varied across specimens and stroke number
(Figs. 3-6B-D, 3-7). Comparisons were made for groupings with greater than five
runs of available tail kinematic data. No significant differences between kinematics
and the total number of tail strokes (e.g., the first stroke of a two tailbeat jump versus
Figure 3-5: Box plots of overshoot and acceleration (for all jump heights) by specimen. Letters (i.e., a,b,c) denote statistically significant groupings using Mann-Whitney U tests with p < 0.05 considered significant. (A) The two larger fish (specimens 1 and 2) exhibited lower median and maximum overshoots than the three smaller fish (specimens 3-5). (B) Acceleration varied strongly by individual specimen. Specimens 1 and 2 exhibited the lowest accelerations. Specimens 3 and 4 reached the greatest accelerations.

the first stroke of a five tailbeat jump) were observed. For specimens 2 and 3, the third stroke was significantly narrower than the first two tail strokes. In the case of specimen 5, there was a significant decrease in amplitude between strokes 5 and 6 and earlier tail strokes (figure 3-6B-D). For the first two strokes, specimens 3 and 4 had the largest amplitudes (figure 3-7), though specimen 4’s first stroke was not significantly different from specimen 1’s.

Stroke duration differed between specimens. The two fish with the greatest lengths and tail areas (specimens 1 and 2) took the longest to complete a tail stroke. Duration was similar between all strokes by a single specimen (figure 3-7). Stroke durations did not vary significantly within data from specimens 2 and 3. Minimal variations were observed in stroke durations for specimen 5, though the time intervals were still very consistent between strokes.
Figure 3-6: Tail kinematics over increasing jump height and over the course of a single jump. (A) The number of peak-to-peak tail strokes executed by the fish increased linearly with jump height (in BL) with significant correlation ($p < 0.001$). (B-D) Amplitude variation with stroke number for specimens 2 (B), 3 (C) and 5 (D). Specimens 1 and 4 were excluded due to an insufficient number of runs showing full tail kinematics for greater than two tail strokes. Box plots show the median, upper and lower quartiles and whiskers to within 3 interquartile ranges of the upper and lower quartiles. Letters (i.e., a,b,c,d) above boxes denote statistically distinct groups within each specimen ($p < 0.05$) using Mann-Whitney U tests. Data was compared within but not between specimens. Additional tail kinematic statistics are shown in figure 3-7. Figure modified from Shih, Mendelson, and Techet [137].
Figure 3-7: Box plots of tail stroke amplitudes and durations. Letters (i.e., a,b,c) denote significant differences using Mann-Whitney U tests (p < 0.05). Outliers (o’s) are points greater than three interquartile ranges from the upper and lower quartiles. (A-C) Comparisons of tail stroke amplitude (normalized by BL) across specimens for the first three tail strokes. (D-F) Stroke durations compared by specimen for the first three strokes. (G-I) Stroke durations compared within each specimen for all stroke numbers.
Figure 3-8: Displacements for all trials and position, velocity, accelerations and energies for the 2.3 BL jump from figure 3-2. (A) Representative vertical trajectory from specimen 5 (thick black line) compared to displacement trajectories (relative to initial position) for all specimens (numeric legend) and jump heights. (B) Vertical position relative to the surface increased during thrust production and glide stages. (C) Velocity reached a maximum shortly before the tail left the water and the thrust production stage ended. (D) Acceleration was greatest at jump onset. The dashed line shows gravitational acceleration. (D) Kinetic, potential and total energy. Kinetic energy was greatest immediately before the tail left the water. The total energy increases during thrust production and plateaus during the glide stage. Figure reproduced from Shih, Mendelson, and Techet [137].

Time profiles of position, velocity, acceleration and energies (figure 3-8) highlighted three key times in the jump: \( t_{\text{glide}} \), when the tail left the water completely, \( t_{\text{bait}} \), when the snout reached the bait height and \( t_{\text{max}} \), when the snout reached maximum height. Peak velocity and thus ballistic kinetic energy always occurred while the tail was still in the water and before the fish reached its prey. Acceleration was greatest at jump onset. After the fish completely left the water and again after bait capture, continued tail oscillations caused changes in body posture reflected in the velocity, acceleration and energy traces; the magnitude of these fluctuations was small compared to the changes in velocity, acceleration and energy during thrust production. Despite fluctuations, the mean acceleration between \( t_{\text{glide}} \) and \( t_{\text{bait}} \) was \(-11.6 \text{ m s}^{-2}\), close to gravitational. Kinetic energy reached zero at the maximum height. Aside from the aforementioned posture oscillations, the total ballistic energy
plateaued during the glide stage.

![Energy comparison during the glide stage.](image)

Figure 3-9: Energy comparison during the glide stage. (A) Kinetic and potential energy balance during the glide stage for jumps above 1 BL. Kinetic energy was calculated at $t_{\text{glide}}$; potential energy was measured as the change in height between $t_{\text{glide}}$ and $t_{\text{max}}$. The dotted line denotes conservation of kinetic and potential energy. Energies were scaled by the mass of the fish for comparison across specimens. Figure modified from Shih, Mendelson, and Techet [137].

Energy balance was assessed during the glide stage for jumps greater than 1.0 BL. During thrust production and for jumps where the body was partially submerged at bait capture, hydrodynamic energy and the kinetic energies of individual fins would need to be considered along with the ballistic energies measured in this study. Maximum ballistic kinetic energies calculated during each jump ranged from 2.6-25.3 mJ. Changes in gravitational potential energy ranged from 2.8-33.7 mJ. During the glide stage, the kinetic energy when the caudal fin departed the water at $t_{\text{glide}}$ balanced the change in gravitational potential energy from $t_{\text{glide}}$ to $t_{\text{max}}$ (figure 3-9).

### 3.3.2 Hydrodynamics

Particle image velocimetry (PIV) revealed the wake structures produced by the fish during thrust production. The caudal fin and body wake during the first three tail strokes of a 1.0 BL jump consisted of coherent vortex structures shed by the caudal
Figure 3-10: Time series of PIV images for a 1.0 BL jump by specimen 5. Bright locations on the body mask show the position of the laser sheet. The pectoral, pelvic, and anal fins were located in front of the light sheet. The grey box shows the location of the free surface. Wake structures are labeled by the direction of their propulsive jets and the fin that created them. Jet angles are relative to vertical. The caudal fin shed a vortex during each tail stroke and propulsive jets were initiated along the body in the region between the pectoral fins and the caudal peduncle. A vortex wake structure from the dorsal fin was also present in the PIV plane at $t = 0.030$ s. Figure reproduced from Shih, Mendelson, and Techet [137].

fin and jets initiated by the body wave between the pectoral fins and the caudal peduncle (figure 3-10). The caudal fin wake resembled the classic reverse Kármán street of forward fish locomotion with a single vortex core shed per peak-to-peak tail stroke. The first two tail strokes produced a strong vortex pair between $t = 0.007-0.023$ s. At $t = 0.030$ s, multiple positive vortex cores were observed: one from the
caudal fin and one from the dorsal fin, which raw images showed was also present in the light sheet at this time. A patch of negative vorticity between the two caudal fin vortices appeared to pinch off from the negative vortex core of the second tail stroke.

The appearance of wake structures from fins other than the tail (figure 3-10, t = 0.030 s) and simultaneous motion of median and paired fins at the onset of a jump (figure 3-2A), motivated PIV focused on locations beyond the caudal fin. The wakes of the pectoral and anal fins for an 0.5 BL jump are seen in figure 3-11. Propulsive jets of downward orientation (± 15-18° from vertical) appeared near both pectoral fins at t = 0.010 s. The pectoral fin vortex pair on the viewer’s left side advected out of the measurement plane by t = 0.038 s, while the pair on the viewer’s right side remained in-plane. The anal fin also shed a vortex pair with predominantly lateral jet (76-80° from vertical). The same wake structures were observed for PIV performed on specimen 4 at the same jump height (figure 3-12). In both cases, one side of the pectoral fin wake is visible over a longer duration due to better alignment between the fin and the 2D PIV light sheet.

Energy transfer between the archer fish and the water was assessed quantitatively through the circulation of individual wake vortices and the total in-plane kinetic energy over time (equations 3.1 and 3.3). The in-plane kinetic energy was a lower bound on energy expenditure since dissipation and fluxes out of the measurement plane.

Figure 3-11: PIV time series for an 0.5 BL jump by specimen 5 with the light sheet initially aligned with the anal and pectoral fins. Propulsive jets and vortices were produced by the pectoral and anal fins during jump onset. The pelvic fin was in front of the PIV plane. Figure reproduced from Shih, Mendelson, and Techet [137].
Figure 3-12: Time series of PIV images of the anal fin for a 0.5 BL jump by specimen 4. The light sheet was positioned toward the front of the anal fin. Qualitatively, wake structures were the same as those seen in figure 3-11, with propulsive jets originating on the pectoral and anal fins.

plane reduced the cumulative strength of early features at later times. Analysis considered the wake strengths of the anal and pectoral fins for an 0.5 BL jump (figure 3-11) and the caudal fin during 1.0 BL (figure 3-10) and 0.5 BL (figure 3-13) jumps. Figure 3-14 shows time histories of the circulation and energy. Kinematic parameters for the jumps are provided in Table 3.3.

Figure 3-13: Time series of PIV images of the caudal fin for a 0.5 BL jump by specimen 5. The caudal fin wake resembled the reverse Kármán street of forward locomotion. The fish executed three propulsive tail strokes before reaching the bait.

The in-plane kinetic energy for the 1.0 BL jump reached a maximum at t = 0.030 s, which corresponded to when three tail stroke vortices and one dorsal fin vortex were seen in the wake (figure 3-14A). The in-plane kinetic energy of the 0.5 BL case was greatest at t = 0.037 s, which corresponded to the third and final tail stroke before
Figure 3-14: In-plane kinetic energy (A) and vortex circulations (B-D) over time for three jumping cases. (B) shows the anal and pectoral fins for an 0.5 BL jump (figure 3-11). (C) shows three caudal tail strokes and the dorsal fin vortex for a 1.0 BL jump (figure 3-10). (D) shows three caudal fin strokes of an 0.5 BL jump (figure 3-13). Markers are plotted at every other PIV time step for clarity (time between markers 0.004 s). Figure reproduced from Shih, Mendelson, and Techet [137].

prey capture. While kinematic data showed that the acceleration was greatest at jump onset, the mechanical energy input during a jump was not as instantaneous.

PIV performed looking at the anal and pectoral fins had two energy peaks: one at $t = 0.020$ s when the first jumping motions by the anal fin and pectoral fins were completed, and one that remained relatively constant from $t = 0.040$ s to $t = 0.050$ s, after the second anal fin stroke had been completed. By $t = 0.060$ s the in-plane kinetic energy had dropped considerably, as the pectoral fin and anal fin vortices had advected out of the measurement plane. The contribution of the pectoral fins to the total energy in this case was also underestimated since only half of the pectoral fin wake was in-plane. The initial slopes ($t < 0.015$ s) of the two 0.5 BL energy cases were similar despite measurements being focused on different fins.
Table 3.3: Kinematic and vortex parameters for PIV runs imaging the caudal fin for 0.5 BL (figure 3-13) and 1.0 BL (figure 3-10) jump heights and the anal fin for an 0.5 BL jump (figure 3-15).

<table>
<thead>
<tr>
<th>Height [BL]</th>
<th>Fin</th>
<th>Stroke No.</th>
<th>Amplitude [BL]</th>
<th>Duration [s]</th>
<th>$\Gamma_{\text{max}}$ [cm$^2$s$^{-1}$]</th>
<th>Time to $\Gamma_{\text{max}}$ [s]</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>Caudal</td>
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<td>0.15</td>
<td>0.026</td>
<td>73</td>
<td>0.019</td>
</tr>
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<td>0.019</td>
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<td>72</td>
<td>0.039</td>
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<td>0.011</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
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<td>0.013</td>
<td>67</td>
<td>0.019</td>
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<tr>
<td>0.5</td>
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<td>0.013</td>
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<td>0.032</td>
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<tr>
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<td>0.048</td>
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<tr>
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<td>0.018</td>
<td>-51</td>
<td>0.022</td>
</tr>
<tr>
<td>0.5</td>
<td>Anal</td>
<td>2</td>
<td>0.14</td>
<td>0.022</td>
<td>58</td>
<td>0.031</td>
</tr>
</tbody>
</table>

The time required for the circulation of any individual fin vortex to reach peak strength was much shorter than the timescale for the kinetic energy to reach a maximum. No single kinematic stroke contributed a majority of the kinetic energy to the wake. Circulations for the caudal fin cases (figure 3-14C,D) had additional maxima after initial shedding, likely due to 3D motion affecting vortex alignment with the light sheet or interaction with out-of-plane flow features. For the 1.0 BL jump, the circulation of the second tail stroke (figure 3-10, $t = 0.017-0.023$ s) was the largest. This stroke has the largest amplitude and shortest duration of any stroke in the sequence.

Table 3.3 lists the kinematic tail stroke amplitudes and durations, as well as corresponding wake parameters, for the cases in figure 3-14. Some strokes were captured in kinematics but not in PIV due to their position in the light sheet. The time to peak circulation ($\Gamma_{\text{max}}$) was measured from $t = 0$ s (first jumping caudal fin motion). For the 1.0 BL jump, the first tail stroke took over twice as long as the following three and was smaller in amplitude than the following three strokes. The second stroke had the shortest duration and the highest circulation. For the 0.5 BL jump imaging the caudal fin, the first two strokes had comparable amplitude and duration while the third stroke was lower amplitude and produced a weaker vortex. For the two 0.5 BL cases, the wake structures reached maximum strength over similar time
intervals (0.019-0.022 s for the first vortex core and 0.031-0.032 s for the second vortex core).

3.4 Observations from 2D measurements

3.4.1 Use of oscillatory kinematics for jumping

Archer fish jump utilizing traveling body wave kinematics (figure 3-2B), an acceleration behavior with little kinematic similarity to their in-water C-starts. Velocities (0.6-1.7 m s\(^{-1}\)) and accelerations (10-103 m s\(^{-2}\)) measured in this study were comparable with those reported by Wöhl and Schuster [166] for C-start maneuvers by *Toxotes jaculatrix*, a closely-related species of similar morphology and size, in aquatic prey capture (0.45-2.10 m s\(^{-1}\), 17-118 m s\(^{-2}\)) and escape scenarios (0.39-1.68 m s\(^{-1}\), 20-90 m s\(^{-2}\)). If similar speeds and accelerations are achieved by two different sets of kinematics, the question is raised of why oscillatory acceleration kinematics are preferable for jumping, while C-type maneuvers are used for in-water feeding strikes. Precision alone does not rationalize this difference in kinematics; archer fish perform C-starts with sufficient control over speed and orientation to pursue fallen prey by controlling the body bending speed [166, 117].

Posture and direction of motion provide some rationale for this kinematic dissimilarity. Timmermans and Souren [152] concluded that the fish do not use their mouths to aim during spitting but angle their bodies instead. Since the mouth is not used to aim, it is therefore feasible that aiming mechanisms are not spitting-specific and can be applied to other behaviors. Jumping and predictive feeding strikes are both initiated at the surface, allowing the fish to accurately sight prey located above the water. During a C-start, the archer fish body orientation transitions from the snout angled upward (for spitting or aiming) to level with the surface [166], whereas during a jump the body remains pointed vertically. Body posture also varied between aerial and in-water feeding in the silver arawana. During aerial feeding, the arawana was angled upwards, compared to level with the surface during aquatic feeding [95].
However, unlike the archer fish, S-type kinematics were seen at both postures.

Despite the presence of similar aiming mechanisms for jumping and spitting, the behaviors had different overshoot patterns. Timmermans and Vossen [153] found that spitting archer fish overshot and undershot in comparable frequency, and that specific aiming patterns varied substantially by individual. While individual variation in aim was also observed in the present study, undershoot was never observed during kinematic experiments, and specimens 3-5 had a much higher range of overshoots than specimens 1 and 2 (figure 3-5). The failure modes of spitting and jumping help explain this discrepancy. For spitting, overshoot, undershoot, and poor horizontal aim all result in failed prey capture. In contrast, during jumping only undershoot or poor aim result in failure, and prey can still be captured even with substantial overshoot. For jumping, a small amount of overshoot also ensures that the mouth closes securely on the prey. In this study, the median snout overshoot (0.16 BL), the constant term (0.13 BL) in the linear relationship between bait and jump height (figure 3-4A) and the snout length of the fish (0.15-0.17 BL) were all similar in length. These results suggest that there may be an advantage to the snout traveling approximately its length beyond the bait.

Overshoot was only weakly correlated with bait height (figure 3-4B), but bait height had influence on the aiming behaviors observed in specimens 3-5. The maximum overshots for specimens 3-5 were observed at intermediate bait heights (1-2 BL). In this range, the initial acceleration was insufficient to reach the bait but additional tail strokes may have provided more thrust than was needed. At bait heights greater than 2 BL, specimens overshot less because they were incapable of jumping higher. The two fish with the highest median and maximum overshoots (specimens 3 and 4) typically exhibited higher Froude-scaled velocities than the others (figure 3-4C). Acceleration, which was also greatest in these two fish (figure 3-5), was significantly correlated with overshoot (figure 3-4D). Specimens 3 and 4 also exhibited high initial stroke amplitudes and short initial stroke durations relative to other specimens (figure 3-7); the rapid acceleration of the tail necessary to achieve these kinematics corresponds to a large initial thrust force and likely less precise jump
The requirement of producing thrust even after partial water exit also influences jumping kinematics. Gazzola et al. [57] concluded that C-starts were the optimal kinematics for traveling distances because a large volume of fluid mass accelerates with the body to create a powerful added mass force. If half of the body is airborne, the added mass force of the C-start is reduced to utilize only the submerged volume. Substantial body bending for a C-type acceleration maneuver would also put the fish into an unstable posture with the COM offset from the vertical trajectory and the snout no longer aimed directly at the bait.

Oscillatory kinematics are more adaptable as the fish leaves the water. For specimens 2, 3 and 5, as the fish accelerated, the tail strokes decreased in amplitude with no significant change in duration (Figs. 3-6B-D, 3-7G-I). At jump onset, PIV showed jets formed along the body ahead of the tail (figure 3-10). As the body left the water, there was less propulsive benefit to a full body wave, as flow could only be generated by the submerged portion. Smaller tail strokes with a reduced motion envelope could contribute thrust while minimizing wasted energy or instability above water. The initial tail stroke and simultaneous additional fin motions produced the greatest acceleration of the body, but the smaller accelerations of later tail strokes ultimately yielded the velocity and thus ballistic kinetic energy necessary to reach higher prey heights. The correlation between acceleration and overshoot (figure 3-4D) suggests using multiple propulsive tail strokes gives the fish greater jump control and may be responsible for high prey capture success rates (table 3.2). While tail strokes can be considered a discrete unit of thrust production (figure 3-6A), kinematic differences between successive strokes (e.g., amplitude and tail speed) may be responsible for the highest jumps, speeds, or overshoot. The higher circulations in the caudal fin wake during a 1.0 BL jump than a 0.5 BL jump (figure 3-14) suggest this level of control may be possible, though statistical data at both jump heights is needed to confirm.

The unique vision capabilities of the archer fish, which create the constraint of jumping from the surface, have facilitated the development of a compatible jumping strategy. Archer fish exhibit a unique set of behaviors among similarly-sized fish: pre-
dominantly vertical jumping of multiple body lengths, considerable accuracy (>70% for all specimens in this study) and a stationary start at the surface. The Trinidadian guppy jumped vertically to comparable heights (in body lengths), but with minimal aim. The guppy also started from a depth sufficient to execute multiple C-start accelerations and transition to burst swimming before exiting the water [143]. The silver arawana also accelerated before aerial feeding strikes by using burst swimming followed by an S-start [95]. In both cases, fish were able to build momentum by traveling significantly farther than a body length in the water before exiting. Considering fish water exit maneuvers initiated from the surface, Mangrove rivulus initiated launches with S-type kinematics, but took off at an angle closer to 45° to maximize horizontal distance traveled rather than height [114]. Mangrove rivulus also used S-type kinematics during aimed prey capture pounces on a simulated bank, but the body was level with the surface and traveled no further than approximately 0.5 BL [114].

3.4.2 Energetic rationale for jumping

The ballistic velocities from this study were used to compare the mechanical energy requirements of spitting, jumping and in-water pursuit. Using maximal values reported by Vailati et al. [156] (velocity 4.5 m s\(^{-1}\), volume 0.1 cm\(^3\), height 0.14 m) and the density of fresh water (1 g cm\(^{-3}\)), an upper bound on the ballistic kinetic energy of spitting was estimated as approximately 2 mJ per shot. A rigid-body approximation of the kinetic energy required for in-water pursuit was estimated using the velocities reported by Wöhl and Schuster [166] at 2.5-40 mJ for a 10 g fish, similar to the jumping kinetic energy estimated in this study (2.7-46.9 mJ). These mechanical energy estimates suggest that in-water pursuit dominates energy consumption during hunting by spitting. In competitive scenarios where the fastest pursuit is required, mechanical estimates suggest jumping may be of energetic parity. However, these rigid-body mechanical estimates of prey capture energy requirements do not take into account the efficiency of each behavior, including energy transferred from the fish to the water. A ballistic energy balance was only applicable once the fish completely left the water (figure 3-9). The PIV kinetic energy time history (figure
3-14A) showed energy lost by the fish to wake formation occurred during the entire thrust production stage and was not dominated by the initial acceleration. Energetic wakes were also formed by the anal and pectoral fins in addition to the caudal fin.

Size effects may play a role in motivating jumping. Larger prey provide more energy to the fish upon consumption, but are also more energetically costly to hunt using spitting. Schlegel et al. [133] found that since the adhesion strength of prey attached to leaves or branches increases with size; a larger, higher-momentum jet and more shooting attempts were needed to capture larger prey by spitting. Jumping energetic costs depend solely on the prey height, not on its size. In this study, two larger archer fish (specimens 1 and 2) had lower peak jump height than three smaller specimens (specimens 3-5). One possible explanation is diminishing returns between the energy required to jump and the energetic gains of a particular prey. A larger sample size than the current study is needed to fully characterize size effects on jumping behavior.

3.4.3 Fin function at jump onset

Particle image velocimetry showed that the wakes of the initial fin motions by the caudal fin, pectoral fins, and anal fin were all of nontrivial strength. The force produced by a fin is proportional to its size, speed and the circulation of its wake. Therefore, the comparable circulations (figure 3-14B-D) between the wakes of caudal, anal and pectoral fins suggest that despite the correlation between tail strokes and jump height, the caudal fin was not the only fin contributing to the upward thrust. The energy measurements (figure 3-14A) likewise suggest these fins were partially responsible for the energetic costs of forming a coherent wake.

The functions of the anal and dorsal fins during locomotion have been widely studied, with suggested roles including thrust augmentation and stabilization [146, 154, 155, 26, 20]. These fins were also found to be active during specialized behaviors such as backwards swimming [52]. In a rapid-acceleration context, Tytell and Lauder [155] found that the dorsal and anal fins contributed momentum to the three primary propulsive jets generated by the body and tail during a bluegill sunfish C-start. In
the present study, the PIV measurements showed the orientation of the anal fin and caudal fin jets could differ substantially during jumping (76-80° from vertical for the anal fin versus 36-53° for caudal fin jets). This variation suggests that the anal fin may be producing independent wake structures. In measurement planes toward the front of the anal fin, the anal fin wake appeared as an isolated vortex pair and jet (figure 3-11), suggesting independent functionality. When the PIV light sheet was positioned toward the back of the fin (figure 3-15), the caudal fin’s third stroke was observed to pass through the wake of the first two anal fin strokes, suggesting that the aft portion of the anal fin also provides momentum that the caudal fin utilizes during a later tail stroke. The force producing ability of secondary fins may be limited to key times in the jumping sequence; Borazjani [20] found that anal and dorsal fins produced less than 5% of the thrust in a C-start except for one instance right before the start of the propulsive stage. The lateral orientation of the anal fin jet also suggests a stabilization role. The body and caudal fin produced lateral force in addition to upward thrust since propulsive jets were at a nonzero angle relative to vertical; lateral forces produced by the anal fin could counteract caudal fin forces to keep the fish’s snout upright.

PIV of the pectoral fins during their abduction at jump onset revealed jets acting close to vertically (10-18°). By momentum conservation, these wake structures indicate that the pectoral fins contribute upward thrust. Abduction of the pectoral and pelvic fins also increases the projected area of the fish in multiple planes and resultantly the added mass of surrounding fluid that must accelerate with the body. Paired fin abduction may also change the moment of inertia of the fish enough to have a stabilizing role. Given the limited space the archer fish has to accelerate before leaving the water, it is likely that the rapid, simultaneous motion of paired and median fins at jump onset generates the initial spike in acceleration (figure 3-8) before the fish performs subsequent tail strokes. Pectoral fin use during jump onset differs from the silver arawana and Trinidadian guppy; these fish both sweep their pectoral fins back along the body to be more streamlined [95, 143]. Mangrove rivulus uses its pectoral fins near the ground for stabilization during water exit over sloped surfaces
Figure 3-15: Time series of PIV images of the anal fin for a 0.5 BL jump by specimen 5. The light sheet was initially positioned toward the back of the anal fin. At $t = 0.026$ s the caudal fin was observed to enter the measurement plane and interacted with the anal fin wake.

[114]. Fin use during jump onset may be morphology as well as space driven; the archer fish is less elongate and streamlined than the arawana or guppy and possesses proportionally larger pectoral fins capable of moving enough fluid mass to produce nontrivial thrust.

Volumetric measurements have recently emerged as a valuable tool for studies of biological propulsion (e.g., [53, 101, 13, 106]). These techniques provide the ability to simultaneously analyze all fins involved during jumping. The wake measurements from PIV presented here are a 2D view of a 3D flow with substantial ambiguity about the fish wake structure. Variability of fish position within the light sheet and wake
interactions between fins both limited statistical assessment of the wake strength and energy measured from 2D PIV in this study. Mendelson and Techet [101] showed that assumptions regarding symmetry and the alignment of a wake structure with the light sheet can lead to miscalculation of the momentum in a complex 3D fish wake with interacting flow structures. Volumetric calculation of wake energy as in Bartol et al. [13] could further be directly compared to the ballistic energy of the fish. The kinetic energy of individual fins during the thrust production stage, energy used to deform the free surface, and changes in the fluid pressure field surrounding the fish must also be considered to perform complete mechanical energy accounting during a jump.

3.5 Epilogue

3.5.1 Preliminary 3D measurements

Preliminary volumetric measurements using synthetic aperture particle image velocimetry (SAPIV) were performed to assess the three-dimensionality of the wake, a main hypothesis formed from the 2D analysis. The fish specimen used for these experiments had a standard length of 6.5 cm and an approximate mass of 10 g. All husbandry protocols for this set of experiments were approved by the Massachusetts Institute of Technology Committee on Animal Care under protocol numbers 0312-026-15 and 0315-026-18.

Experiments were performed in a five gallon aquarium filled halfway with water from the home tank (figure 3-16). The tank was seeded with 50 µm polyamid particles (Dantec Dynamics). The SAPIV system for these measurements consisted of nine high-speed Phantom Miro 310 cameras (Vision Research) running at 600 frames s\(^{-1}\) with 1280 × 800 pixel resolution. Each camera was equipped with a 105 mm Sigma lens (f/8). Cameras were arranged in a 3 × 3 array spaced approximately 150 mm apart. The distance from the camera array to the front tank wall was approximately 250 mm. A synchronized Phantom V341 high-speed camera (Vision Research) with 2560 × 1600 pixel resolution was equipped with a 50 mm Nikon lens (f/8) and used
Figure 3-16: Experiment setup for synthetic aperture PIV on archer fish. A nine-camera high-speed camera array images an $80 \times 50 \times 50$ mm volume surrounding the archer fish’s median fins. The measurement volume is illuminated by a volumetric near-infrared laser. A separate high-speed camera is used to film the aerial trajectory of the fish.

as an additional survey camera in the X-Y plane. Images from the survey camera were used to track the snout to determine the vertical fish body trajectory above the surface. The SAPIV camera array was calibrated (to determine the relationship between image and world coordinates) with a multi-camera optimization procedure that compensates for refraction through the water and tank wall [15].

Illumination was provided by an Oxford Lasers Firefly 1000 W volumetric laser with a wavelength of 808 nm. The laser was pulsed with a 1% duty cycle (pulse duration of 16 $\mu$s), preventing any motion blur. As with the 810 nm laser used in the 2D study, the archer fish did not react to the presence of laser illumination. The thickness of the illuminated region was 50 mm. The seeding density of the resultant images was 0.03 part. pixel$^{-1}$, or approximately 150 part. cm$^{-3}$.

Weighted refocusing and the 3D cross-correlation code (based on MatPIV [150]) used in Mendelson and Techet [101] were used to calculate the refocused particle im-
ages and the velocity field. Multi-pass cross-correlation was performed with initial windows of $96 \times 96 \times 64$ voxel windows and two passes using $64 \times 64 \times 48$ voxel windows, all with 50% overlap. The final velocity field resolution after cross-correlation was $2.03 \times 2.03 \times 1.92$ mm, providing approximately 35 vectors along the standard length of the fish. Binary images constructed using an adaptive thresholding method [142, 101] were used to construct the visual hull [1] of the archer fish to prevent the body from influencing velocity field calculation.

![Figure 3-17: Digitized points on the pelvic (green), anal (purple), and caudal (blue) fins shown on the center array camera during the initial 3D archer fish SAPIV experiment. Images are 0.012 s apart. Scale bar is 5 mm.](image_url)

In addition to tracer particle motion, images from the SAPIV system were used to reconstruct the trajectories of multiple fins and reference points on the fish body. Marker points on the fish body were first digitized using DLTdv5 [64] in the four outermost cameras of the array (top left, top right, bottom left, and bottom right). The specific points on the body tracked over time were the two extremal tips of the caudal fin, the dark spot on the body at the caudal peduncle, the two junctions of the anal fin and the body, and the eighth fin ray (fifth behind the three spines) of the anal fin. Figure 3-17 shows the locations of these marker points on the center camera of the array for six times during the jump sequence.

The camera calibration used for refocusing of the PIV images and visual hull
masks was also used during body tracking. Using this calibration ensured reference frame consistency between the PIV and kinematic measurements. The body tracking code ran a SciPy [74] optimization using the BFGS algorithm to determine the point in 3D space that minimizes the residual when projected into the four input cameras. The output position of each marker was smoothed over time using a cubic spline. The three-dimensional fin trajectories output from the tracking procedure are shown in figure 3-18. Tail oscillations and a smaller-amplitude, lower-frequency oscillation in the anal fin trajectory are visible. Aerial trajectories, velocities, and accelerations were determined by tracking the fish snout and fitting smoothing splines in the same manner as the 2D study discussed earlier in this chapter.

![Figure 3-18: Reconstructed fin trajectories for the pelvic, anal, and caudal fins using the four outermost cameras in the nine camera array. Gridline spacings are 20 mm.](image)

Combined results from SAPIV and body tracking are shown at four times during a 0.9 BL jump in figure 3-19. The vortices formed by successive tailbeats during a jumping maneuver vary in orientation. The vortex ring formed by the first peak-to-peak tail stroke at jump onset in particular has a significantly different orientation than the second and third tail stroke vortices. This observation explains the difficulty in determining the wake structure from the two-dimensional slices through the wake presented earlier (e.g. figures 3-10 and 3-15).

At t = 0.03 s, a vortex structure is visible directly below the anal fin that appear to originate from this fin. By t = 0.04 s, this wake structure has assimilated into
Figure 3-19: First volumetric PIV performed on a jumping archer fish. The fish jumps 0.9 BL towards aerial bait. Wake structures are visualized by the magnitude of the 3D vorticity vector and colored by the magnitude of the 3D velocity vector. Eight reference points are used in the configuration shown on the fish body to locate the fins and body within the visual hull. Silhouettes show the corresponding location of the fish in the measurement volume as viewed from the 2D survey camera.

A larger vortex loop formed by the caudal fin. At \( t = 0.06 \) s a third vortex loop has been formed following another peak-to-peak tail stroke. To quantify the results, the hydrodynamic impulse (equation 1.3) and kinetic energy (equation 1.8) in the measurement volume are compared to the measured momentum (\( p_{\text{fish}} = m_{\text{fish}}v \)) and ballistic energetics from the fish aerial trajectory (figure 3-20).

The rate of growth of the hydrodynamic impulse calculated from the PIV mea-
Figure 3-20: Quantitative analysis of the measured 3D wake and 2D aerial trajectory. (a-c) Aerial position, velocity, and acceleration of the fish body as determined by tracking the snout. (d) Comparison of fish vertical momentum ($p_{\text{fish}}$) as measured from its trajectory and the vertical component of the hydrodynamic impulse. (e) Comparison of wake kinetic energy (PIV) with ballistic potential (PE), kinetic (KE), and total energies determined from the trajectory.

measurements was slower than the rate of body momentum increase measured from the aerial trajectory of the fish. The wake kinetic energy exhibited the same delay in timing of increases as the impulse. The peak kinetic energies measured in the wake are on the order of 1 mJ, while the change in gravitational potential energy of the fish is approximately 6 mJ. Earlier wake structures also advect out of the measurement volume before later tailbeats occur; the peak kinetic energy as calculated is therefore a lower bound on the energy consumed by wake formation during a jump.

One reason for the delay between fish activity and flow observation is the extent of the visual hull masking. Wake features do not appear in the PIV measurement volume until the body is significantly clear of them. This delay contributes to the slower growth of the hydrodynamic impulse vector than the ballistic momentum in figure 3-20d. Figure 3-21 shows the position of the kinematic marker points within
the visual hull. An additional plausible reason for the reduced momentum and energy predictions is that the measurement volume does not include the pectoral fins, which 2D measurements (figures 3-11 and 3-12) suggested could contribute some propulsion on jump onset.

Figure 3-21: Visual hull used for PIV masking at the first two times from figure 3-19 and corresponding tracked body points. There is not a clear boundary between the caudal and anal fins in the visual hull at either time.

The quality of near-body measurements is one major limitation of the preliminary experiment. The automated masking routine used to segment the body from the particle field, a modification of the method used in Mendelson and Techet [101], frequently failed to detect body regions, including shadow on the dorsal side of the fish body and the tips of the tail, which were immersed in the particle field. In addition to the elongation in the Z-direction characteristic of the visual hull method [1], the automated segmentation method also overmasked the fluid region between the anal and caudal fins in many frames (figure 3-21). In addition to introducing a delay in the timing of wake appearance, the overmasking of the fish body contributes to the difficulty in discerning the exact kinematics that led to the formation of the wake structure seen below the anal fin markers at $t = 0.03$ s in figure 3-19. An additional kinematic consideration for future experiments is that fish fins are not rigid, and additional markers along the lengths of the caudal and anal fins may be required to discern the curvature of the fins.


3.5.2 Requirements for further volumetric study

Based on the results of the preliminary study shown in this section, the following requirements for a modified SAPIV system to study archer fish jumping were determined:

- Synchronized aerial trajectories must be measured in 3D instead of 2D.
- The image processing routine used to create binary images of the fish for the visual hull must be able to identify the entire body without filling in gaps between fins.
- Optical access for the camera array must provide vertical fields of view from the initial position of the caudal fin up to the free surface.
- Kinematic markers must provide curvature information about caudal and anal fin kinematics in addition to rigid position estimates.
Chapter 4

Multi-camera volumetric PIV for the study of jumping archer fish

4.1 Prologue

This chapter consists of a manuscript prepared for Experiments in Fluids describing modifications to the SAPIV technique necessary for a high-fidelity study on jumping archer fish to meet the requirements identified at the end of chapter 3.

4.2 Introduction

Archer fish (genus *Toxotes*) exhibit multiple sophisticated prey capture strategies. These fish combine spitting, rapid in-water pursuit, and jumping to feed in competitive environments [14, 33, 119]. Of particular hydrodynamic interest is the fish’s ability to jump multiple times its body length out of the water to capture prey [137]. Archer fish jumps are initiated from directly below the surface, leaving limited space to accelerate before the fish exits the water completely. In chapter 3, it is observed using high-speed imaging that jumping is achieved using oscillatory tailbeat kinematics, coupled with rapid activity of additional fins at jump onset. Chapter 3 furthers present 2D PIV measurements which suggest that multiple fins contribute upward thrust (e.g., figures 3-10, 3-11, 3-12, 3-15), but that some of these fins serve more to
Figure 4-1: Fin activity during archer fish jumping. Shaded and outlined regions show the activity of the caudal (blue dash-dotted), anal (purple dotted), dorsal (green solid) and pectoral (red dashed) fins. The black box shows the location of the free surface. Images are shown 0.01 s apart. Scale bar is 2.0 cm. Background subtraction and linear contrast enhancement have been applied to the images for visibility.

stabilize and steer the body. Such control is crucial to enabling the fish to accurately capture its aerial prey. To understand the biomechanics of this behavior, as well as any potential for engineers to replicate these aquatic launches, it is necessary to determine the relative importance of each fin and body behavior to propelling, steering, and stabilizing the fish. Any interactions between the fins beyond their independent functions must also be considered.

Fins of particular interest include the pair of pectoral fins, located midbody near the fish’s center of mass, and the dorsal, anal, and caudal fins (i.e., the median fins) located on the aft end of the fish body. Figure 4-1 shows four high-speed images of a jumping archer fish taken 0.01 s apart with the pectoral, dorsal, anal and caudal fins labeled. Lauder [84] summarizes extensive previous study of these fins in other species of fish, especially in forward swimming and rapid maneuvering contexts. These studies have shown that fin use and specific hydrodynamic functions depend heavily on both morphology and the particular swimming scenario. For instance, Standen and Lauder [146] find different amounts of dorsal and anal fin activity in bluegill sunfish depending on the swimming speed.

In the case of the jumping archer fish, the jump height and swimming speed are closely related. The archer fish is effectively ballistic once out of the water, and faster exit velocities are therefore needed to reach higher prey heights. The kinematic study
results in chapter 3 show that the number of tailbeats executed by the fish increases with jump height (figure 3-6). Differences in the force produced by each tailbeat could not be assessed in the 2D study; variation of the fish’s position within the 2D PIV light sheet limited assessment of fin wakes with respect to jump height or prey capture success.

Volumetric particle image velocimetry techniques can provide simultaneous measurements of multiple propulsors involved during locomotive behaviors. Previous studies have leveraged various 3D velocimetry techniques to study novel and complex swimming strategies, including DDPTV of fin and jet propulsion combinations in squid [13] and tomographic PIV of sea butterfly parapodia [106, 3]. In a 3D study of forward fish swimming, Flammang et al. [53] used DDPTV to observe assimilation of upstream vortices from the dorsal and anal fins of a bluegill sunfish into the caudal fin wake. Volumetric techniques also reduce experimental constraints on animal behavior, as was leveraged by Adhikaki and Longmire [2] for the study of zebrafish prey capture, and allow for analysis in reference frames other than the measurement plane, as shown for fish wakes by Mendelson and Techet [101].

Synthetic aperture particle image velocimetry (SAPIV) is a volumetric PIV technique that uses light field imaging to reconstruct fields of tracer particles in 3D. Multiple cameras are used to emulate the effects of a single camera with a wide aperture and narrow depth of field scanning through a volume; particles are localized by where they appear in focus. As originally developed, SAPIV uses a particle reconstruction procedure of warping images from multiple views using transformations that correspond to a finely-spaced range of depths [17]. The transformed images at each depth are then averaged according to

$$I_{SA_k} = \frac{1}{N} \sum_{i=1}^{N} I_{FP_{ki}},$$

(4.1)

where $I_{SA_k}$ is the combined image on the $k^{th}$ focal plane, $N$ is the number of cameras, and $I_{FP_{ki}}$ is the transformed image from each camera. Image averaging, also known as additive refocusing, is followed by intensity thresholding of each focal plane to remove
the dim, discrete ghosts of particles that do not converge across multiple cameras at that specific depth [17]. Belden et al. [17] use a threshold of three standard deviations above the mean image intensity on each focal plane as the minimum brightness of a valid particle. Intensity normalization of particles within and across all images during preprocessing is crucial to the success of this segmentation technique. The stack of all thresholded focal planes is the final 3D particle volume. This non-iterative and highly-parallelizable algorithm reconstructs particle volumes faster than the iterative MART variants commonly used in tomographic PIV [10]. Additive refocusing can also be accelerated in refractive media using the homography-fit method described by Bajpayee and Techet [10].

The reconstruction speed of SAPIV presents an advantage for animal studies where a significant number of trials from multiple specimens are ultimately desired. With the additive refocusing algorithm (equation 4.1), however, more viewpoints are required (typically eight to ten instead of four) for a sufficient signal-to-noise ratio on particle reconstruction, as assessed by the reconstruction quality factor Q [17]. Reconstruction quality is not a direct indicator of velocity accuracy, but is commonly used to isolate the effects of the 3D particle reconstruction step on measurements. Bajpayee and Techet [9] show that the accuracy of the final PIV velocity field decreases slower than the quality of the reconstructed particle field when the number of cameras is reduced. Specific types of reconstruction errors have well-characterized detrimental effects. For instance, ghost particles formed by the coincidental convergence of multiple viewpoints at a location other than a true particle can reduce measured velocity gradients when they reach a high enough density [44]. In general, performance of the refocusing reconstruction procedure (equation 4.1) must also be assessed for scenarios where a moving body is also present in the measurement volume, and images are therefore not comprised exclusively of particles.

While SAPIV has been successfully applied to resolve vortex structures in fish wakes [101], the behavior of the archer fish imposes unique experimental constraints on the measurement system. The wakes of upstream fins (i.e., dorsal, pectoral, and anal fins) must be resolved before and during any interactions with the caudal tail. Achiev-
ing these measurements therefore requires both high-speed, time-resolved imaging and sufficient particle field reconstruction in near-body regions. Measured wake structures must additionally be assessed in context of the fish’s kinematics and also the jump’s outcome. In chapter 3, the aerial trajectory of the fish is used to estimate the maximum velocity and acceleration during a jump. For coupled understanding of the kinematics and hydrodynamics, this process of determining trajectories must be applied in 3D simultaneously alongside new volumetric velocimetry measurements. A convenience over free-swimming experiments is that fish position can be controlled by bait placement. In addition to the image analysis procedure near the fins and body, the physical setup of the SAPIV system must be assessed for use specifically on the jumping archer fish problem. Specifically, it is desirable to reconfigure the typical $3 \times 3$ SAPIV camera array for simultaneous under- and above-water measurements.

4.3 SAPIV system design

4.3.1 Optical access

The coupled behavior of the archer fish in and out of the water drives unique visibility constraints when using SAPIV to study aquatic jumping. Since the snout of the fish is positioned directly at the surface when it begins to jump, the SAPIV measurement volume must be located directly below the free surface. At certain distances and angles, camera viewpoints looking downwards at the measurement volume (e.g., the top row of cameras in a $3 \times 3$ camera array like those used by Belden et al. [16] and Mendelson and Techet [101]) will be unable to view the below-water regions closest to the free surface. Extreme viewpoints looking upwards at the measurement volume will also image the reflections of particles on the free surface. While avoiding these viewpoints, sufficient camera spacing for depth resolution must still be provided among cameras in the array [17].

Design requirements for the aerial imaging camera layout are based on the finding that the peak jump acceleration occurs immediately after jump onset and not from
later tailbeats (figure 3-8). Aerial-viewing cameras must therefore begin to capture the fish trajectory as soon as the snout breaks the surface to capture this acceleration. Separate aerial and underwater cameras are desirable to avoid having multiple calibrations for a single camera and to have a full camera sensor of resolution in each fluid media.

From a practical standpoint, these constraints reduce the number of cameras feasible to position viewing the below-water measurement volume, especially when using high-speed cameras where the physical size of the camera further limits spacing options. SAPIV has also been successfully implemented using two rails of cameras in a $4 \times 2$ array [82]. However, a single central camera in the array is valuable for aligning the 3D coordinate system during camera calibration and locating the fish within the experiment field of view. The proposed solution is two rails of cameras, with three viewpoints on the top rail to provide a head-on center camera, and four viewpoints on the bottom row aimed slightly upward (figure 4-2). The top row of cameras are mounted directly on the rail; the above-water cameras and the bottom row are attached by ball-head camera mounts. A photograph of the camera configuration is shown in figure 4-2b. By placing three cameras on the top rail, two additional aerial cameras can be positioned at a slight vertical offset on the same rail. This imaging configuration also avoids adding additional cameras (beyond the typical nine camera array) to an already hardware-intensive measurement technique. The number of cameras is not targeted for further reduction to provide sufficient viewpoints for particle reconstruction even with body-driven partial occlusions.

4.3.2 Mapping partial occlusions

One advantage of the additive SAPIV particle reconstruction algorithm (equation 4.1) is that an object or particle can be localized through this refocusing without appearing in every camera. This “see-through” effect for partial occlusions in synthetic aperture imaging has also been used to study dense bubble and droplet distributions [16, 132]. In the case of SAPIV around a body, occlusions of particles can be created by either another particle or the fish body. When a particle is occluded by another particle
Figure 4-2: Camera configuration for simultaneous SAPIV and 3D jump trajectory tracking. (a) Schematic of the camera placements for the jumping archer fish experiment. The free surface is located at approximately half the height of the tank. The shaded regions show the fields of view for the seven PIV camera array (red dotted line) and the two aerial trajectory cameras (green dashed line). (b) Photograph of the camera setup shows the physical implementation of the design in (a) alongside a 38 l tank.

along the line of sight of one camera, the particle will still reconstruct when refocused. Additive refocusing does not segment the intensity contributions of multiple sources along the same line of sight.

The more detrimental category of occlusions is those where a region of particles is blocked by the body in a subset of cameras. If the body is masked (set to zero source intensity) in individual camera images before refocusing, the occluded particles will refocus using equation 4.1 at a weaker brightness in the final focal stack. If the body is left unmasked, bright patches of the body will influence the final position and brightness of the reconstructed particles.

The visual hull method [1] is commonly used for body masking in tomographic and synthetic aperture PIV; this method projects binary images of the body along each camera’s line of sight to determine regions where all cameras contain the body. These regions are then excluded during PIV processing, which prevents body artifacts from contaminating velocity field calculations. Individual 2D masks from each camera can also be used to remove the body from images prior to reconstruction. It is possible to identify subsets of cameras where a region of interest is visible by applying equation 4.1 to the binary images used to create the visual hull. The result is an image stack
Figure 4-3: Visual hull and regions of six focal planes partially obscured by the fish body for SAPIV measurements of a jumping archer fish. (a) Reference image of the fish body from the center camera of the array. (b) Visual hull from combining body images at each focal plane. (c) Partial occlusion locations at six depths in the measurement volume. Shading represents the number of cameras in which a given voxel coincides with the body at each focal plane. Regions occupied by the body in all seven cameras correspond to the visual hull necessary for PIV masking. All Z coordinates are relative to the bait position behind the tank wall.
showing how many cameras have their visibility impeded by the body at each location. Figure 4-3 shows the visual hull and number of occluded cameras at six focal planes for one timestep of an archer fish jump sequence imaged using the seven camera SAPIV array.

At depths toward the edges of the measurement volume (e.g., \(Z = -7\) mm and \(Z = 38\) mm), most obscured regions are along the line of sight of the body in one or two cameras. The elongation of the visual hull in the viewing direction described by Adhikari and Longmire [1] is also observed, and image regions toward the center of the body at the outer depths have worse visibility. In regions towards the center of the measurement volume, the visual hull (occluded in all seven cameras) is identifiable, including the pectoral fins around \(Z = 2\) mm and the caudal fin at \(Z = 20\) mm. The regions surrounding the visual hull are nearly fully occluded. However, regions where occlusion is due to body features not located at those focal planes are still only blocked in a minimal number of viewpoints. For this analysis, points in front of and behind the body are treated the same; it is common for a bright body to wash out particles located in front of it, leaving them effectively still occluded. If a particle is not directly in front of the body in other viewing angles, it can however, still be reconstructed using those cameras.

4.3.3 Additive refocusing with reduced cameras and partial occlusions

The experimental constraints on camera placement and partial visibility will alter the performance of the particle reconstruction algorithm, as compared to an experiment without a body and a full nine camera SAPIV array. Specifically, particle reconstruction must be performed with an algorithm that performs in occluded regions with an abbreviated number of viewpoints and in regions with full visibility, ideally in one processing routine. The reduced number of SAPIV cameras, chosen in response to limited optical access near the surface and the need for simultaneous aerial measurements, adds an additional constraint on the reconstruction procedure.
Figure 4-4: Reconstructed intensities of fully visible and partially-occluded particles shown using three sample particles of uniform initial intensity. At depth $Z_1$, particle 1 is in focus, while particles 2 (fully visible) and 3 (partially-occluded) form a discrete ghost blur pattern. At depth $Z_2$ ghosts from particles 1 and 2 overlap to form a brighter ghost, and particle 3 is in focus at reduced intensity due to its limited viewpoints.

With partial occlusions, intensity separation of true, but occluded, particles from defocused ghosts following additive refocusing becomes increasingly difficult. Figure 4-4 shows this challenge for a simplified set of three particles: two visible in all cameras of a nine camera SAPIV array (particles 1 and 2) and one visible in only three cameras of a nine camera array (particle 3). All particles are shown with inverted intensity (darker particles are brighter) for visibility. At depth $Z_1$ particle 1 is in focus, while particle 2 forms a discrete blur pattern with one ghost per camera in the shape of the array. Particle 3 also forms a discrete blur, but is only visible in three cameras. At depth $Z_2$ particle 3 is in focus, and the other two form the discrete ghost pattern. The coincidental overlap of the ghosts from the two nine camera particles at depth $Z_2$ is not significantly dimmer than the in-focus particle visible in only three cameras at the same depth.

Belden et al. [17] show that reducing the number of cameras, either by design or as a consequence of occlusion, reduces the reconstruction quality of a particle field, as there is less intensity contrast between true and ghost particles. Belden et al. [17] also report that reconstruction qualities are lower for higher seeding densities. For densely seeded images, the probability of two or greater individual camera images converging without being a true particle location increases. Since additive refocusing
is an averaging algorithm, the intensity of a ghost increases linearly with the number of cameras contributing to it. In some densely-seeded scenarios, most ghosts may not be dimmer than true particles.

To further understand the limitations of image averaging followed by thresholding as a particle reconstruction strategy, an approach based on the probabilities of images converging is employed. This analysis is similar to that employed by Elsinga et al. [44] for tomographic PIV ghost formation. The goal of this study is to determine how bright most false particles are in different imaging scenarios. This approach examines cases where cameras randomly converge (i.e., assuming no correlation between viewpoints) to create a ghost particle. Probabilities for different subsets of falsely-converging cameras in an array are compared for varying source density and number of array cameras. The source density ($N_s$) is the product of the seeding density in pixels (ppp) and the area in pixels of an individual particle ($A_p$). This quantity essentially describes the probability that a given pixel in an image is occupied by a particle. The inverse probability (1-$N_s$) is the likelihood the corresponding pixel in other cameras is not a particle. Binomial probabilities can be used to calculate the likelihood ($N_g$) of a quantity of cameras ($G_C$) in a $N$ camera array overlapping during refocusing:

$$N_g = \frac{N!}{G_C!(N - G_C)!} N_s^{G_C} (1 - N_s)^{N - G_C}.$$  \hspace{1cm} (4.2)

The distributions of ghost intensities for varying source density and 4-10 camera SAPIV systems are shown in figure 4-5. All ghost probabilities $N_g$ are normalized by the source density to compare the number of ghosts to the number of true particles.

Ghosts formed by an individual camera have a high probability of occurrence at low source density, and, unsurprisingly, increasing the number of cameras increases the number of these ghosts relative to the number of true particles. However, at higher source densities there is a nontrivial, and in many cases higher, likelihood of ghosts forming from multiple cameras instead of a single camera. Regardless of the number of cameras, intensity thresholding for particle segmentation is only effective at low source densities when a majority of the ghosts are actually dimmer than the true
Figure 4-5: Densities of ghost particles ($N_g$) from a combination of cameras, normalized by the source density $Ns$, for reconstruction through additive refocusing in 4, 6, 8 and 10 camera SAPIV systems. Color is cut off in locations where the number of ghosts from a given number of cameras is below 10% of the total number of particles.
particles. When the source density is high enough that many ghosts form from three or more cameras, these false particles become comparable in intensity to partially-occluded true particles, though in practice the number of viewpoints for an occluded region will additionally scale with the total number of viewpoints.

The intensity distribution within an individual particle must also be considered when assessing the effectiveness of additive refocusing and thresholding. The probabilities in figure 4-5 apply to cases in which thresholding will appropriately segment the maximum intensity values of true and ghost particles. To prevent single voxel particles and their resultant peak locking (e.g., [71]), thresholding should remove the brightest ghosts while preserving the dimmest regions of true particles. Even when artifacts are sufficiently dimmer than true particles, the minimum intensity of a true particle must additionally be greater than the maximum intensity of the ghosts. The appropriate threshold for separating particles from noise is therefore also a function of the intensity profile of the imaged particles. Particle size and brightness is controlled in an experiment by the illumination and lens f#, which in turn is driven by the required thickness of the measurement volume, but can also be modified through preprocessing operations.

This limitation can be demonstrated considering one focal plane of a refocused image stack (i.e., one 2D slice through the voxel volume). A true particle with perfect convergence between all cameras located on that plane post-refocusing is modeled as a $3 \times 3$ Gaussian kernel with variance $\sigma^2$ and intensity ranges from $I_{\text{min}}$ to $I_{\text{max}}$:

$$I_{\text{min}} = I_{\text{max}} e^{-\frac{1}{\sigma^2}}.$$  \hspace{1cm} (4.3)

If a higher intensity threshold than $I_{\text{min}}$ is applied, the number of single-voxel particles, and consequently the likelihood of peak locking, increases. The maximum intensity of an out-of-focus ghost particle created by a single image during refocusing is $\frac{I_{\text{max}}}{N}$, where $N$ is the total number of cameras in the array. Thresholding to remove individual camera ghosts from each particle image in a 3D focal stack will remove
Figure 4-6: Intensity relationships between true particles and ghost particles with varying Gaussian profile for additive refocusing (equation 4.1) with 1-15 cameras. Curves of the maximum intensity of a ghost formed by 1-4 cameras for varying total number of cameras are compared with dashed lines representing the minimum true particle intensity for five different possible Gaussian particle profiles of varying $\sigma$. In many scenarios ghosts are brighter than the minimum intensity of a true particle on one focal plane of the refocused volume.

Information regarding true particles unless

$$e^{-\frac{1}{\sigma^2}} > \frac{1}{N}.$$  \hspace{2cm} (4.4)

Figure 4-6 shows how the maximum intensity of the ghosts formed by one to four cameras ($\frac{I_{\text{max}_{GC}}}{N}$) compares to the minimum intensity in a 2D Gaussian particle as described by equation 4.3. Regions above the lines representing each $\sigma$ will be retained if the threshold is set such that it preserves all true particle values in the $3 \times 3$ kernel. At $\sigma = 0.5$, retained intensities include all ghosts, even with 15 cameras. With a 7 camera array, 3 or 4 camera ghosts will be retained for $\sigma = 1$, but even the maximum intensity of a 1 or 2 camera ghost will be eliminated.

This analysis has shown that in partially-occluded scenarios, and in many fully-visible situations, the ability to segment real and ghost particles on the basis of intensity is insufficient. The smaller a particle is (lower $\sigma$), the harder it is to segment,
even with a large number of cameras. Small particles are frequently a consequence of
the high f# required for depth of field in volumetric PIV experiments, though this
limitation can be mitigated by blurring and re-normalizing particle intensities during
image preprocessing. These limitations to threshold definition and ghost removal with
partial occlusions suggest that additive refocusing is not appropriate for studies with
bodies such as the jumping archer fish.

Weighted refocusing, where low intensities have a negative weight during aver-
ing to cancel out ghosts, improves the signal-to-noise ratio between true particles
and their discrete blur [101]. Partially occluded particles still reconstruct at reduced
brightness using this method. However, for asymmetric camera arrays (i.e., not 3 × 3
cameras) like that necessitated by the measurement volume position, 3D particles
reconstructed by weighted refocusing do not have a Gaussian intensity profile and ap-
propriate weights are difficult and arbitrary to define. Therefore, weighted refocusing
is not considered for this study.

### 4.3.4 Alternate non-iterative algorithms

Two alternative, non-iterative particle reconstruction algorithms are the multiplic-
tive line of sight (MLOS) [8], also known as multiplicative refocusing when used in
synthetic aperture imaging [16], and the minimum line of sight (minLOS) [98, 102].
These algorithms differ from additive refocusing (equation 4.1) at the step where
warped images from all cameras are combined. The MLOS algorithm takes the prod-
uct of all warped cameras as the value at a voxel:

\[ I_{SA_k} = \prod_{i=1}^{N} (I_{FP_{ki}})^n, \quad (4.5) \]

The exponent \( n = 1/N \) preserves the original intensity scale of a particle through the
multiplication operations, but \( n \) can also be chosen alternately to modify the size and
intensity profile of the refocused particles. The minLOS algorithm takes the minimum
Figure 4-7: Probability of ghost formation on one focal plane for increasing number of cameras using MLOS or minLOS reconstruction. Color is cut off for a ghost density less than 10% of the source density.

pixel value from all cameras mapping to a voxel:

\[ I_{SA_k} = \min_{i=1}^{N} I_{FP_ki}. \]  \hspace{1cm} (4.6)

Of these two algorithms, the minLOS is more punitive, as it requires a bright particle in all cameras for a high image intensity reconstruction, whereas particle brightness on a focal plane via the MLOS algorithm can be increased by bright regions in some cameras and any nonzero value in others. With both the MLOS and minLOS algorithms, ghost particle formation requires agreement between all cameras, and the likelihood of ghost formation \((N_g/N_s)\) drops with each additional camera added to the array (figure 4-7). If these algorithms are applied globally, agreement between all cameras is likewise required to reconstruct true particles, a limitation in the extensive partially occluded regions described above for the jumping archer fish (figure 4-3). This limitation is not unique to synthetic aperture imaging; Adhikari and Longmire [1] suggest that velocimetry accuracy of partially-obscured regions in tomographic PIV could also be improved by running MART reconstruction in subsets of cameras corresponding to visible viewpoints.

The minimum line of sight algorithm, when combined with binary images of the
Figure 4-8: Reconstruction steps using a minLOS particle reconstruction coupled with image averaging to determine occluded regions. (a) Raw image from the center camera of the array. (b) Binary mask corresponding to the body in (a). (c) Preprocessed 2D SAPIV image created by combining (a) and (b) and performing preprocessing operations to enhance particle visibility. (d,g) Two slices through the focal stack reconstructed using minLOS refocusing. (e,h) Occlusion maps from additive refocusing of binary masks corresponding to the slice locations in (d,g). Brightness is proportional to the number of occluded cameras. (f,i) Refocused images after masking regions occluded in greater than four cameras.
fish body from each camera, also enables easy implementation of camera subgroup handling for reconstruction with partial occlusions. If image regions corresponding to the body are flooded at maximum brightness, the minimum is obtained from only valid particle viewpoints. This process is shown for a set of images measuring flow generated by the dorsal, anal, and caudal fins in 2D and at two refocused depths (figure 4-8).

The raw images from each camera (figure 4-8a) are used to obtain binary masks of the fish body (figure 4-8b). During image preprocessing before refocusing, regions corresponding to the body can be set to the maximum intensity value using the binary masks used to generate the visual hull (figure 4-8c); the minLOS algorithm can then be applied globally. The value of the combined image at each focal plane will be the minimum of the valid viewpoints; regions occupied by the body in all cameras will have maximum intensity (4-8d,g). The additive body images (4-8e,h) can then be used to mask the focal stack in regions not visible in a defined minimum number of cameras (4-8f,i). Of non-iterative algorithms, minLOS is both the most punitive and easiest to implement with occlusions. Use of the MLOS algorithm (equation 4.5) instead would require the additional parameter $n$ be varied depending on the number of contributing viewpoints. This algorithm has the most performance potential in near-body scenarios and is used in the remainder of this study.

4.4 Implementation

The SAPIV system designed to provide near-surface optical access and occlusion-compensated processing using minLOS refocusing is implemented on a live archer fish. Experiments are performed in a 38 l aquarium (51 cm × 25 cm × 30 cm) filled halfway (15 cm from the bottom) with water from the separate archer fish home tank. Bait (dried plankton) is suspended from a thread positioned through a hole in the aquarium hood located 8 cm behind the front tank wall. All results are from a smallscale archer fish (Toxotes microlepis) with a standard length of 7.0 cm and weight of 7.5 g. All animal use protocols are approved by the Massachusetts Institute of
Table 4.1: Imaging and processing parameters for the SAPIV study of the archer fish median fins.

<table>
<thead>
<tr>
<th>Seeding Density (ppp)</th>
<th>Source Density Ns</th>
<th>Array Spacing (mm)</th>
<th>Array Meas. Vol. to Tank Size (mm)</th>
<th>Vector Spacing</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.04</td>
<td>0.4</td>
<td>$\Delta X_{upper} = 170, \Delta X_{lower} = 130, \Delta Y = 125$</td>
<td>390</td>
<td>$70 \times 40 \times 35 \times 1.8 \times 1.8 \times 1.9$</td>
</tr>
</tbody>
</table>

Technology Committee on Animal Care (protocol number 0315-026-18). Fish training procedures and husbandry details are also discussed in detail in chapter 3.

Nine high-speed cameras (Vision Research Miro 310), seven for SAPIV and two for 3D aerial body tracking, are configured to image above and below the free surface as shown in figure 4-2. For a zoomed view of the median (i.e., dorsal, anal, and caudal) fins, the SAPIV cameras use 105 mm Sigma macro lenses ($f/16$). The aerial cameras are equipped with 35 mm Nikon lenses with apertures set to $f/11$ for both experiments. All cameras are synchronized at 750 frames s$^{-1}$. Table 4.1 lists the camera spacing and PIV processing parameters for the experiment.

Near-infrared laser illumination is provided using an Oxford Lasers Firefly 1000W volumetric laser. This wavelength is invisible to archer fish and is used to mitigate influence of PIV illumination on the archer fish’s behavior and aiming strategy. As in Mendelson and Techet [101], a first surface mirror is used to reflect the laser volume back into the tank for additional light. Illumination for aerial imaging is provided exclusively by ambient room lighting and overhead LEDs in the aquarium hood.

SAPIV cameras are calibrated with a bundle adjustment model accounting for planar refractive interfaces [15]. The aerial cameras are calibrated by direct linear transformation using the custom MATLAB software DLTcal5 and DLTdv5 provided by Hedrick [64]. The DLT software is also used to automatically track the fish snout above the free surface in 3D using the aerial camera data. Snout trajectories are used to measure the jump height of the fish and fit quintic splines to evaluate velocity and acceleration as in chapter 3. Underwater fin kinematics are determined by manually using DLT to digitize marker points, including the tips of the caudal fin, in the top
center, bottom left, and bottom right cameras. These points are then triangulated in 3D space using the refractive SAPIV camera calibration.

The binary masks necessary to construct the visual hull and map partially-occluded regions are generated using a semi-automated method based on the grabCut algorithm available in the OpenCV library [124, 22]. The algorithm is initialized for each camera with a bounding box around the fish body at the first timestep for SAPIV processing. The user can identify any over or under-masked regions of the fish body between segmentation iterations. The mask from the previous timestep is used to initialize the mask for the next timestep. The semi-automated approach is able to adapt to changes in body lighting throughout the duration of a jump sequence; fully automated approaches based on edge detection or intensity variation frequently failed due to this variation. Once the binary body masks are identified for each camera, image regions outside the body are preprocessed by subtracting a $5 \times 5$ median-filtered background image, convolution with a $3 \times 3$ Gaussian blur kernel ($\sigma = 1$), local intensity normalization (sliding $5 \times 5$ windows), and applying a low-intensity threshold to the 2D source images to remove any noise amplified during intensity normalization. Body regions from the mask are set to the maximum image intensity for use with the minLOS algorithm (figure 4-8c).

The homography-fit method developed by Bajpayee and Techet [10] is used to warp particle images from each camera to each focal plane. A minimum of four non-occluded cameras is required for a refocused region to be considered valid. Image regions with fewer than the required four viewpoints are masked along with the full-camera visual hull during PIV processing. The particle fields are processed using a multi-pass cross-correlation implemented in a modified 3D version of the MatPIV code developed by Sveen [150]. This code is also used in Mendelson and Techet [101]. Velocity fields are post-processed using a signal-to-noise filter using the ratio between the first and second cross correlation peaks, a $3 \times 3$ local median filter with a validity threshold of two standard deviations from the median for data, and smoothed at each timestep using the routine developed by Garcia [56]. Vorticity is calculated from the smoothed data using a second-order centered difference.
4.5 Results and discussion

The zoomed measurements of the dorsal, caudal, and anal fins at jump onset aim to understand whether the median fins work as separate actuators or as a larger composite tail. Results from simultaneous aerial and underwater measurements are shown in figure 4-9. Figure 4-9a-c shows the 3D position, vertical velocity, and vertical acceleration of the jump over time during a 1.6 body length jump. The body position, as viewed from the center array camera, tail trajectory over time, and corresponding wake formed by the first three tail strokes at three times are shown in figure 4-9d-i. Measurements of the X,Y, and Z position (4-9a) obtained from aerial imaging show that the snout moves in the opposite direction as tail motion at jump onset (t = 0-0.03 s). After the initial tailbeats the snout does not move laterally; the next major snout motion occurs when the mouth opens (t = 0.1 s).

Previous 2D PIV measurements show that the caudal fin wake during jumping resembles the reverse Kármán street of steady forward fish locomotion. In 2D, one vortex core appears to shed per peak-to-peak tail motion (e.g., figure 3-10). The vorticity contours over time (figure 4-9d-i) show the vortex ring structure of the first three peak-to-peak tail strokes.

The orientation of jet velocities, an indicator of wake momentum, also serves to illuminate the interactions of these fins. Figure 4-10 shows contours of the X,Y, and Z velocity components at two times during the jump. In the X direction (figure 4-10a-b), flow towards the body on both the dorsal and ventral sides (near the dorsal and anal fins) keeps the fish upright in its jumping posture. Downward momentum in the flow field, indicated by strong downward velocities (Y-velocity component v), is observed nearby the dorsal, caudal, and anal fins (figure 4-10c-d). Examining the velocities in the Z-direction (figure 4-10e-f), nearly aligned with the fish’s tail oscillations, negative momentum from the tail is balanced by positive momentum from the dorsal and anal fins at t = 0.024 s. Once the tail has passed through these fin wakes (t = 0.039 s) regions of alternating lateral flow corresponding to each tail stroke are observed.

The volumetric measurements of the median fins augment the findings of both the
Figure 4-9: Trajectory and wake measurements obtained with the seven camera SAPIV system for a 1.6 body length jump. (a) X,Y, and Z positions of the snout until the fish reaches maximum height and begins to travel downward. Vertical velocity (b) and acceleration (c) are determined from smoothing splines fit to the position data. (d-f) Images of the body from the center cameras at three times. (g-i) Wake measurements at times corresponding to those shown in the photographs visualized by vorticity magnitude. The gray surface shows the location of the visual hull and the solid black lines show the tail trajectory.
Figure 4-10: Momentum distribution in the archer fish wake. Caudal fin oscillations are shown by the solid black line and are approximately parallel to the Z-axis. Colored arrows show the direction of flow in each isosurface. (a-b) Surfaces of positive and negative velocity in the X direction. (c-d) Surfaces of downward Y velocities (thrust direction during a jump). (e-f) Surfaces of positive and negative velocities in the direction of tail motion (Z).

2D and 3D measurements from chapter 3. Based on the wake orientation, the dorsal and anal fins exhibit both propulsion and stabilization, and the question of primary function (whether these additional fins serve to propel or to stabilize during a jumping maneuver) remains. The primary function of these fins may vary depending on the jump height, and the timing of propulsive contributions may also be of importance.

4.6 Conclusions

Multi-camera systems for synthetic aperture particle image velocimetry provide the flexibility to be reconfigured based on optical access constraints. Design considerations in both camera array configuration and particle reconstruction are applied to develop a 3D measurement system for the complex two-phase measurements of a fast-starting jumping fish. The limitations of additive refocusing and intensity thresh-
olding presented herein can further be used to design SAPIV experiments for other similarly complex velocimetry scenarios. Additionally, a method for reconstructing and ultimately analyzing flow in partially-visible regions with minimal processing hassle is realized through the use of binary body masks and the minLOS reconstruction algorithm.

These techniques are promising to elucidate the complex hydrodynamics of archer fish jumping. The procedures described in this chapter can enable assessment of how wake structures and fin interactions vary with jump heights. Since archer fish start from rest at the surface, it is also feasible to capture the entire wake generation process in a field of view appropriate for 3D PIV experiments. With coupled information about the aerial trajectory, methods for force and energy prediction can be compared between PIV and the kinematics of the fish.
Chapter 5

Multi-fin propulsion during rapid acceleration in jumping archer fish

5.1 Prologue

This chapter builds on the two-dimensional behavioral characterization and preliminary experiments from Chapter 3, using the velocimetry system from Chapter 4 and the wake analysis insights from Chapter 2, to provide detailed volumetric analysis of the wake of a jumping archer fish.

5.2 Introduction

Jumping for aerial prey in an aquatic environment demands both propulsive performance and accuracy, as energy expended to jump is ultimately wasted if prey capture is unsuccessful. Archer fish (*Toxotes microlepis*) are sophisticated predators capable of not only the spitting behavior from which they draw their name, but also rapid in-water and aerial pursuits of prey [14, 33, 137]. Jumps performed by the archer fish accurately reach heights greater than twice the fish’s body length, initiated from directly below the surface following an aiming period [137]. This jumping prey capture behavior requires significant thrust generation in limited space, as well as the ability to control the jump trajectory even when the fish is partially out of the water.
In general, morphological and behavioral specializations enable the archer fish’s multifaceted prey capture repertoire. Physical adaptations of the fish body for spitting are well-characterized, including the nozzle-like groove in the mouth cavity [42, 152] and eyes adapted for vision near refractive interfaces [151]. Likewise, the rapid escape kinematics of the C-start, an optimal acceleration behavior shared by many fishes [37, 155, 57], are utilized by the archer fish for fast, accurate pursuit of in-water prey [166]. The cognitive capabilities of the archer fish during predation are also of significant importance. During in-water pursuit, the fish rapidly assesses where prey will land and defines a trajectory towards it through control of body bending and maneuver timing [117, 118]. Similarly, jets produced during spitting are tuned for specific prey sizes [133] and relative position to prey [60, 24]. Spitting can also be performed underwater [35], suggesting the fish can adaptively modify the jet based on the media it travels in.

Archer fish jump using oscillatory traveling body wave kinematics, a behavior distinct from the C-start used for acceleration during in-water pursuit of prey [137]. Chapter 3 shows that the fish closely match bait heights with jump heights, with prey capture success rates upwards of 70% in a laboratory environment, but slightly overshoot the original bait height [137]. These preliminary two-dimensional kinematic experiments also yield a complex set of fin relationships: the number of tail beats executed by the fish correlates linearly with the height attained by the fish (figure 3-6), however tail beat amplitudes are not uniform. Flow structures are also observed originating from additional fins on the body (figures 3-11, 3-12, 3-15).

The jumping behavior of the archer fish combines the rapid timescale of acceleration maneuvers with oscillatory kinematics more similar to forward swimming, driven by a requirement for thrust production even as the body exits the water. The jump height, the current speed of the fish, and the amount of the body still submerged can all influence the tail kinematics. Hydrodynamic differences between when the fish starts from rest (after aiming) and when the fish is partially out of the water traveling with some velocity are likely. Studies of the optimal pattern of tail oscillation during fast accelerations from rest suggest that the timing of each tailbeat is crucial.
to optimizing the thrust produced; under ideal circumstances the vortex formed by the first tail stroke serves as a “stepping stone” for the second tail stroke [6]. The tail is additionally an indicator of whether any hydrodynamic variation with jump height exists, especially at jump onset, or if all control over jump height stems purely from the number of tail beats, effectively acting as a discrete unit of thrust.

The kinematics exhibited by the body and caudal fin have implications for additional fins on the body as well, in particular the dorsal and anal fins located immediately upstream of the tail. Weihs [163] suggests that a large, rearward dorso-ventral fin pair stabilizes and directs flow toward the caudal fin, enhancing the momentum flux over the tail and thus increasing thrust. The complex interactions of the median fins have been explored for numerous swimming scenarios and species; these studies have shown that the fin functions observed vary substantially with both. For instance, the dorsal fin of a trout becomes less important for propulsion the faster the fish swims [39], while the opposite trend is observed for the dorsal fin in bluegill sunfish [146]. Additionally, in trout, the dorsal and anal fins can act to balance body torques rather than to produce net thrust [147]. Despite these correlations with speed, a single fin does not necessarily have a uniform function. During a C-start, fin ray kinematics suggest the anterior regions of the dorsal and anal fins serve to generate stabilizing spanwise flow, while the posterior regions serve to direct momentum toward the caudal fin [25, 26]. Furthermore, fin importance may be most prominent at certain times in a jump. In a numerical study of bluegill sunfish C-starts, the dorsal and anal fins contribute trivial tail force production except for one instance between preparatory and propulsive stages [20].

The transition between maneuver stages is also when actuation of the dorsal and anal fins is observed during an archer fish C-start [166]. A similar behavior is observed the onset of a jump, with abduction of the spines on the dorsal and anal fins. The traveling wave kinematics of the body drive waves in the anal and dorsal fins as well (figure 5-1a). Morphologically, the anal fin is of larger surface area than the caudal fin, suggesting it can contribute nontrivial force, and both the dorsal and anal fins possess a large number of spines and fin rays to control their extension and curvature.
Figure 5-1: Median fin activity during a jump and underlying fin ray structure. (a) Time series of images showing activity in the caudal, dorsal and anal fins during jump onset for a 2.2 body length jump. Images are taken 0.005 s apart by a high-speed camera running at 1000 frame s$^{-1}$. Brightness and contrast have been linearly enhanced for visibility. Scale bar is 2 cm. (b) X-ray of the median fins showing the structure of spines and fin rays for each fin. Scale bar is 1 cm. X-ray courtesy of Dr. Mike Esmail, MIT Division of Comparative Medicine.

Variations of propulsion with height may be observed from these fins as well as the tail. During spitting, aiming posture varies with distance to prey to address constraints from visibility and the necessary spitting direction [152]; similar variation in body orientation during jumping could alter the interactions between fins.

This chapter aims to understand the archer fish’s control over its body and caudal fin oscillations during jumping, as well as the roles of the dorsal and anal fins throughout this jumping process. In 2D, the difficulty of achieving alignment of the fish body with a measurement plane limited analysis of how wake structures interacted or varied with the height of the jump [137]. Volumetric flow measurement capabilities are necessary to resolve fin wake structures and the three-dimensional fin trajectories that create them. The three-dimensional aerial trajectory is simultaneously measured to understand how forces produced by the fish correspond to the observed net forces acting on the fish body.
5.3 Materials and methods

5.3.1 Fish and facilities

Six archer fish imported from a local aquarium vendor are housed in a 75% full 208 l (122 cm × 33 cm × 51 cm) aquarium (26-28° C, 12:12 light:dark cycle, salinity 6.5-12 mS cm\(^{-1}\)). Fish are fed dried plankton (San Francisco Bay Brand, Newark, CA, USA) or bloodworms (Omega One, Painesville, OH, USA) daily. Fish are trained to jump by replacing surface feedings with bait (dried plankton) suspended from a string above the tank at least twice weekly for at minimum two weeks before experiments. The specimen in all data presented here has a standard length (BL) of 7.0 cm and mass \(m_{fish}\) of 7.5 g. The area of the caudal fin is 2.1 cm\(^2\), the area of the anal fin is 2.9 cm\(^2\), and the area of the dorsal fin is 1.3 cm\(^2\). All animal experiment and husbandry protocols are approved by the MIT Committee on Animal Care (protocol no. 0315-026-18).

All experiments are performed in a separate 38 l aquarium (51 cm × 25 cm × 30 cm) filled halfway with water from the home tank. Fish are acclimated to the experiment tank for at minimum 20 minutes before beginning experiments. The experiment tank is heated using a 50 W heater to match the home tank temperature. Between jumps, the tank is aerated with an aeration stone for one minute and allowed to settle for at minimum five minutes before resuming experiments. An aquarium hood with integrated LED lighting is placed over the tank during experiments to provide illumination for aerial trajectory imaging and to better replicate lighting conditions used during training in the home tank. Bait is positioned through a hole in the hood located 8 cm behind the front tank wall.

5.3.2 Synthetic aperture particle image velocimetry

Synthetic aperture particle image velocimetry (SAPIV) \[17\] is used to elucidate the wake of the archer fish in 3D. For flow visualization, the tank is seeded with 50 µm polyamid particles (Dantec Dynamics, Skovlunde, Denmark). An array of seven Miro
310 cameras (Vision Research, Wayne, NJ, USA) with 105 mm lenses (Sigma Corporation, Ronkonkoma, NY, USA) is used to film the SAPIV measurement volume. For a thick measurement volume the lens aperture is $f/16$. Measurements of the fish’s aerial trajectory as it travels toward the bait are made by two additional Miro 310 cameras aimed above the free surface with Nikon 35 mm lenses with aperture set to $f/11$. Details on the design of the simultaneous aerial trajectory and flow field measurement system are presented in Chapter 4.

Images in the seven SAPIV cameras are refocused to obtain 3D particle fields using a minimum line of sight (minLOS) algorithm [98, 102]. This procedure is designed for near-body reconstruction performance, using non-iterative particle reconstruction algorithms for processing speed. The processing routine is described in detail in Chapter 4. Velocity fields are determined from the resultant particle volumes using a multi-pass cross correlation [101]. Velocity fields are post-processed using a filter based on the peak ratio of the cross-correlation function, a local median filter with a threshold of two standard deviations from the median of a $3 \times 3 \times 3$ vector neighborhood, and spatial smoothing [56].

The fish body is located and masked during PIV processing using the visual hull method [1], a commonly-used technique for multi-camera flow measurements around swimming organisms [2, 101, 106, 3]. Binary images of the fish body from each camera are combined to determine the region the body occupies in 3D space. The variation in body patterning on the archer fish body and variation in lighting throughout a jump maneuver prevented fully automated segmentation of the masks in the SAPIV images from this study. For each frame in each camera, the body is instead segmented using a semi-automatic routine using the “GrabCut” algorithm in openCV [22, 124]. Given an initial window in which the fish body is located (determined by drawing a bounding box around all image space occupied by the fish at any time during a jump sequence), the algorithm determines which regions are most likely particles or fish. The user can then approve the image, or manually identify under or overmasked regions and re-run the algorithm.
5.3.3 Kinematics and aerial trajectories

Aerial trajectories of the fish are obtained using the custom Matlab software package DLTdv5 [64]. The upper and lower jaws of the fish, along with any eyes visible in both aerial cameras, are tracked over time. Aerial tracking begins the first instance these features are visible above the surface. Velocity and acceleration in 3D are determined by differentiating a quintic spline fit to the position data [158, 137].

Kinematic markers describing each fin are also manually digitized over time in a subset of three cameras. Kinematic reconstruction uses the top center, bottom left, and bottom right cameras to provide the maximum spacing between kinematic cameras possible. Points tracked over time are the tips of the caudal fin, the three spines of the anal fin, the dark spot at the caudal peduncle, and the dark spot at the tip of the dorsal fin (figure 5-2). Eight additional points along the lengths of the caudal and anal fin are used to describe the curvature of these fins. These points correspond between cameras but not over time. Tracked points are then triangulated using the same camera calibration used for particle volume reconstruction. The trajectories are smoothed over time in X, Y, and Z using cubic splines. The fin edge outlines at each time are smoothed by fitting fourth-order polynomials to the ten tracked points. The standard length of the fish is used as the body length scale for normalizing jump heights and other kinematic variables.

Direction changes in the X or Z components of the tail trajectories (depending on the orientation of the body during a jump) are used to determine the duration $t_{stroke}$ of each peak-to-peak tail stroke; stroke amplitudes $A_{TB}$ are measured using the mean peak-to-peak amplitude of the dorsal and ventral tail tips in a best-fit plane parallel to the tail’s motion. Aerial and tail trajectories are then combined to determine the average acceleration of the fish over each tail stroke ($\bar{a}_{stroke}$) as

$$\bar{a}_{stroke} = \frac{\Delta v_{stroke}}{t_{stroke}},$$  

(5.1)

where $\Delta v_{stroke}$ is the difference in body velocity between the start and end of the tail stroke. The mean body velocity during a tail stroke $\bar{v}_{stroke}$ is also determined
from the vertical position at stroke onset an end as $\bar{v}_{\text{stroke}} = \frac{\Delta y_{\text{stroke}}}{t_{\text{stroke}}}$. The mean body velocity is used in comparisons of the tail speed ($\bar{V}_{TB}$) and the body speed during each tailbeat. The stroke-averaged net upward force ($F_{\text{net}}$) acting on the fish is estimated as

$$F_{\text{net}} = m_{\text{fish}} \bar{a}_{\text{stroke}},$$

(5.2)

In a force balance, the net force is the sum of all hydrodynamic forces ($F_{\text{fluid}}$) acting on the fish and the gravitational force ($F_{g}$) opposing the fish’s vertical motion ($F_{\text{net}} = F_{\text{fluid}} + F_{g}$). Based on the weight of the fish, the gravitation force is $F_{g} = -74$ mN.

### 5.3.4 Hydrodynamic analysis

The orientation of propulsive jets in the wake and fraction of the total momentum contributed to upward thrust $u_{y}/|\vec{u}|$ are used as metrics of propulsor effectiveness for each fin. Momentum transfer in the fish wake is also assessed through the hydrodynamic impulse, which is calculated from the vorticity field as

$$\bar{I} = \frac{1}{2} \rho \int_{V} \vec{x} \times \vec{\omega} dV,$$

(5.3)
As discussed in the epilogue of Chapter 2, this formulation for the impulse must be used because both fin interactions and close-proximity flow features are present in the wake. Using this approach, some individual wake features can still be isolated both spatially and over time for comparison. Specifically, the initial vortex formed by the first tail stroke during a jump (figure 3-19) is considered separately by calculating the impulse in a bounding box surrounding the vortex at times before other wake structures appear and begin to interact with it (e.g., up to $t = 0.03$ s in figure 3-19).

Impulse is calculated for the entire measured flow field over time, and also for the starting vortex produced by the first tail stroke. Figure 5-3 shows these two control volumes for a sample caudal fin wake. The origin for all full-field impulse calculations is the initial centroid of the visual hull representing the fish body. The origin for the starting vortex impulse calculations is the centroid of the bounding box surrounding the vortex. Calculated impulses are smoothed over time using a sliding average over five timesteps. Overall wake impulses are assessed at the conclusion of each tail stroke using values from the first frame where the entire vortex is visible separated from the body. These frames are identified manually. This measurement timing is a compromise between the entire vortex being visible (i.e., not in the visual hull region), and not including momentum from later propulsive motions in the assessment of each tail stroke. Changes in impulse in the thrust direction ($\Delta I_y$) are calculated between

Figure 5-3: Control volumes for hydrodynamic impulse calculation. Wake structures are visualized by vorticity magnitude ($100 \text{ s}^{-1}$). (a) The control volume surrounding the initial vortex ring from the first tail stroke. (b) Control volume for impulse calculation of the full wake using the entire measurement volume. The flow field in (a) is shown at twice the magnification of that in (b).
the start and end of each tail stroke. The average force for a tail stroke $F_y$ is then calculated as:

$$F_y = \frac{\Delta I_y}{t_{stroke}}$$

(5.4)

5.4 Results

5.4.1 Caudal fin wake structure

![Caudal fin wake structure](image)

Figure 5-4: Caudal fin wake structure for a 1.7 BL jump. (a) Slices located midplane along the span of the caudal fin reveal the orientation of the propulsive jets produced by each tail stroke. Tail motion, indicated by the black traces representing each tip, is approximately parallel to the X-Y plane. (b) Visualization of the three-dimensional wake by vorticity magnitude at times corresponding to the slices in (a). Each tail stroke produces a vortex ring that links with the wake of prior and successive tail strokes.

Time-resolved measurements of the caudal fin wake are used to assess how the wake varies between jump onset and later times during the jumping maneuver. Figure 5-4 shows three vortices formed from the first three tail strokes during a 1.7 body length jump. The first lateral excursion of the tail at jump onset produces a starting
vortex ring that is completely visible in the wake shortly after beginning the second tail stroke. During the second tail stroke, a jet forms along the body. At the end of the second tail stroke, the vortex associated with this jet is shed, producing a vortex structure that links with the starting vortex. Each subsequent peak-to-peak tail stroke contributes an additional propulsive jet that links with the previous wake structures. At $t = 0.017 \text{ s}$, the jet produced by the first stroke is more vertical than the jet formed by the second stroke seen at $t = 0.024 \text{ s}$. By $t = 0.039 \text{ s}$, the starting vortex has advected out of the measurement volume. The jets produced by tail strokes after jump onset have more lateral momentum than the initial jet when the tail starts from rest. All three rings are close to axisymmetric in shape.

Figure 5-5: Orientation of the caudal fin wake at three times during a 1.61 BL jump. Caudal fin motion is approximately parallel to the Y-Z plane. Slices through the velocity field are colored by the fraction of the overall velocity magnitude in the downward (thrust) direction. Wake vortices are visualized by vorticity magnitude as the transparent purple isosurfaces.

While the initial jet produced by the caudal fin at jump onset contains mostly downward momentum, the lateral momentum of this jet increases throughout the course of the first tail stroke. Figure 5-5 shows this progression through slices of the flow field at three times during a 1.61 BL jump. The initial flow during the first tail stroke is downward at $t = 0.012 \text{ s}$, but additional lateral momentum appears as the tail reverses direction around $t = 0.017 \text{ s}$. The axis of the resultant vortex ring is not oriented downward when it is free of the body, despite the initial downward momentum transferred at jump onset. At $t = 0.032 \text{ s}$, the alternating lateral orientation of
the first two jets is visible.

Figure 5-6: Hydrodynamic impulse over time for the caudal fin wake of the 1.7 BL jump seen in figure 5-4. Hydrodynamic impulse is calculated for both the volume surrounding the starting vortex and the entire measurement volume. Results from the starting vortex are only evaluated until the full wake from the first tail stroke is visible (shortly after the onset of the second tail stroke). Full-field impulse is plotted until the fish leaves the measurement volume. The square, triangle, and diamond markers denote the beginnings of the second, third, and fourth tail strokes respectively. *’s correspond to the times after each tail stroke where wake features were clear of the body and impulse could be evaluated.

The evolution of the caudal fin wake can be further understood by examining the momentum transfer and force production of each tail stroke. Figure 5-6 shows time histories of the hydrodynamic impulse calculated for both the starting vortex (control volume in figure 5-3a) and the entire flow field (control volume in figure 5-3b) for the 1.7 BL jump in figure 5-4. Of particular interest are the vertical (Y) impulse, which corresponds to an upward force on the fish, and the impulse in the direction of tail oscillations (X for this trial). At jump onset, the vertical (Y) impulse calculated for the reduced control volume surrounding the starting vortex closely follows the full-field impulse. The Z (dorso-ventral for this trial) impulses between the two control volumes also agree. The impulse in the direction of tail motion differs between the two, suggesting that the lateral (X) momentum in the full-field control volume originates elsewhere from the tail. The full-field impulse in the direction of tail motion switches signs during the second tail stroke. A corresponding decay in lateral (X) impulse is
not observed during the third tail stroke. By the third tail stroke, most of the body upstream of the tail is outside the measurement volume; lateral (X) force provided by the median fins or other upstream regions is therefore not reflected in the impulse of the third tail stroke. The Z (dorso-ventral) impulse hovers around zero, though a small sign change is observed during each tail stroke.

Figure 5-7 shows the vertical position, velocity, and acceleration of the fish during the trial in figures 5-4 and 5-6, allowing comparison of the hydrodynamic forces calculated from the impulse and the observed net force acting on the fish. The vertical component of the trajectory when measured in 3D resembles those measured in 2D for five jumping specimens (figure 3-8). The fish starts the first tail stroke from rest at the surface. The peak velocity (1.36 m s$^{-1}$) is reached slightly after the fourth tail stroke begins. Around t = 0.07 s, the height of the snout is greater than 0.07 m, the body length of the fish, and the fish is completely aerial. The acceleration peaks at jump onset and decreases with each subsequent tail stroke. The acceleration is approximately gravitational from t = 0.07 s until the fish opens its mouth and snout motion introduces small oscillation in the acceleration.

Figure 5-7: Height, velocity, and acceleration of the archer fish above the surface for the 1.7 BL jump seen in figure 5-4. The first tail stroke begins at t = 0 s. The beginning of each subsequent tail stroke is denoted by the square, triangle, and diamond markers.

Table 5.1 lists the kinematic, hydrodynamic, and aerial parameters for each of the tail strokes observed in figure 5-4. The tail moves slowest during the initial tail
stroke. The tail speed is always faster than the corresponding mean velocity of the body during each tail stroke. The change in hydrodynamic impulse between tail strokes is a lower bound on the wake momentum contributed by each tail stroke; wake structures dissipating and advecting out of the measurement volume will lower the total impulse measured in the flow field. The net force acting the fish is also a lower bound since the time-varying added mass and fluid entrained by the fish body upon water exit (see appendix A) are excluded.

Table 5.1: Tail kinematic (amplitudes, durations, and tail speeds), body trajectory (average velocities and accelerations during each tail stroke), and wake parameters (impulses and average forces) for the wake structures in figure 5-4.

<table>
<thead>
<tr>
<th>Stroke</th>
<th>$A_{TB}$ (BL)</th>
<th>$t_{stroke}$ (s)</th>
<th>$V_{TB}$ (m s$^{-1}$)</th>
<th>$ar{v}_{stroke}$ (m s$^{-1}$)</th>
<th>$a_{stroke}$ (m s$^{-2}$)</th>
<th>$\Delta I_y$ (gcm s$^{-1}$)</th>
<th>$F_y$ (mN)</th>
<th>$F_{net}$ (mN)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.21</td>
<td>0.013</td>
<td>1.14</td>
<td>0.33</td>
<td>49.9</td>
<td>-283</td>
<td>212</td>
<td>374</td>
</tr>
<tr>
<td>2</td>
<td>0.21</td>
<td>0.011</td>
<td>1.33</td>
<td>0.89</td>
<td>42.7</td>
<td>-260</td>
<td>244</td>
<td>320</td>
</tr>
<tr>
<td>3</td>
<td>0.25</td>
<td>0.013</td>
<td>1.32</td>
<td>1.23</td>
<td>16.9</td>
<td>-235</td>
<td>176</td>
<td>127</td>
</tr>
</tbody>
</table>

The force predicted from the first two tail strokes is less than the force required to provide the measured acceleration. Additional propulsive fins, such as the pectoral fins at jump onset, may be required to produce the requisite force. The forces come closer to matching for the last tail stroke. Additional fins are out of the water by this point; all propulsion must come from the still-submerged tail. Appendix C contains similar trajectory, kinematic, and impulse information for the jump in figure 5-5.

5.4.2 Dorsal and anal fin interactions

The caudal fin wake structures are not the only flow features visible in the measurements presented in figure 5-4. Additional vorticity alongside the anal fin is visible along with the wake of the first tail stroke (figure 5-4, $t = 0.017$ s). At $t = 0.024$ s, the caudal fin passes through this patch of vorticity, and a similar upstream vortex is once again observed on the posterior lobe of the anal fin. Vorticity is also present near the dorsal fin at this time. At $t = 0.039$ s, this second vortex region has again been incorporated into the main vortex ring wake of the caudal fin.
To investigate the hydrodynamic role of these wake structures, figure 5-8 shows the propulsive jets corresponding to the vorticity observed near the anal and dorsal fins for a 1.64 BL jump. In particular, these measurements show that the aft regions of the dorsal and anal fins contribute thrust at the end of the second tail stroke (figure 5-8b). The jets produced by the dorsal and anal fins contribute a lower fraction of their total momentum to vertical thrust, and have significant lateral momentum as well. Also of note in figure 5-8a-c is an upstream region of downward momentum that travels along the body on the ventral side.

The velocity profiles in figure 5-8d-f, taken along constant Y and Z, show that the
peak caudal fin wake velocities are in the Y (thrust) direction. The strong -Z velocity at $t = 0.020$ s (figure 5-8d) is in the direction of motion of the first tail stroke. At $t = 0.025$ s (figure 5-8e), the velocity profiles taken behind the tail at $Y = -57$ mm have not changed substantially from the earlier time in the axial (Y) or lateral (Z) directions. The downward velocities behind the dorsal and anal fins at $Y = -39$ mm are comparable in magnitude to the peak lateral velocities in these fin wakes. The lateral flow from these fins is directed opposite the tail jet in the $+Z$ direction. In the dorso-ventral (X) direction, the flow generated by the dorsal and anal fins is directed towards the body on both the dorsal and ventral sides. At $t = 0.035$ s (figure 5-8f), the lateral flow directly behind the tail is in the direction of motion ($+Z$) of the second tail stroke.

Fin kinematics provide rationale for the wake structures appearing at the posterior tips of the dorsal and anal fins. Figure 5-9 shows projections of the 3D edges of the dorsal, anal, and caudal fins over time using the kinematic markers shown in figure 5-2. The caudal fin is concave in the direction of its motion, an effect that allows the fin to interact with a larger volume of water than if it were flat. The tips of the caudal fin are therefore ahead in phase compared to the middle of the tail.

The X-Y view in figure 5-9 shows that the tail trajectory directly passes through
the posterior lobe of the anal fin, but that the path of a majority of the anal fin does not overlap with the tail at this jump height. The Y-Z view shows that the wave at the tip of the dorsal fin closely follows the waveform of the tail. This viewpoint also shows that the front of the anal fin remains more rigid, while the posterior lobe follows the waveform of the tail and dorsal fins. Based on these kinematics, momentum shed from the posterior of the dorsal and anal fins will intersect with the caudal fin trajectory, but momentum from the anterior of the anal fin will not. The phase between the dorsal, anal, and caudal fins is also examined to determine when upstream momentum is shed relative to the caudal fin. Figure 5-10 shows the lateral (Z) position of the posterior lobe of the anal fin, the tip of the dorsal fin, and the average caudal fin motion determined from the two tips of the tail (markers shown in figure 5-2).

After jump onset, the frequencies of oscillation for all fins match, but the phase differs. Both median fins reverse direction ahead of the caudal fin; the dorsal fin reverses first. The amplitudes of dorsal and anal fin excursion also increase as the jump progresses. Immediately following jump onset at \( t = 0 \) s, there is additional motion of the dorsal fin opposite the direction of the tail. The anal fin motion at jump onset is also slower than the tail; after this period (\( t \geq 0.01 \) s) its trajectory has the same slope as the caudal fin.

![Figure 5-10](image.png)

Figure 5-10: Lateral positions of the dorsal (spot on posterior lobe), anal (posterior lobe), and caudal (average of tail tips) fins over time for the first four peak-to-peak tail strokes of a 1.64 BL jump. Marker locations are shown in figure 5-2.
Appendix C contains, fin kinematic, trajectory, and hydrodynamic impulse information for the jump seen in figures 5-8, 5-9, and 5-10.

5.4.3 Summary of quantitative variations with jump height

The wake structures presented previously are for three cases with jump heights between 1.6 and 1.7 BL, a small fraction of the height range that the archer fish can reach. Summary plots for eight SAPIV jumps ranging from 1.0 to 2.0 BL and eleven 3D kinematic jumps ranging from 0.8 to 2.0 BL are evaluated to assess what factors vary with jump height. Figure 5-11 shows the durations of the first two tail strokes for eleven kinematic cases. The first tail stroke duration is significantly correlated with jump height (figure 5-11a, p=0.005); slower tail strokes are observed for lower jump heights. There is a trend of slower tail strokes at lower heights for the second tail stroke as well, but the correlation is not significant (figure 5-11b). There is not a strong correlation between the speed of the first tail stroke and the speed of the second tail stroke (figure 5-11c).

![Figure 5-11: Duration of the first two tail strokes as measured from 3D kinematics for eleven jumps. (a) The duration of the starting tail stroke correlates significantly with jump height. (b) The duration of the second tail stroke trends toward faster tail strokes at higher jump heights, but the relationship is not significant. (c) The durations of the first and second tail strokes are not strongly correlated.](image)

The hydrodynamic impulse of the starting vortex (control volume in figure 5-3a) at the conclusion of the first tail stroke is shown over varying height in figure 5-12. The overall magnitude of the starting vortex impulse vector (figure 5-12a) does not
vary significantly with jump height. The vertical component of the impulse (figure 5-12b), however, does increase for higher jumps ($h_{max} = -0.004I_y + 0.78$, $r^2 = 0.51$, $p = 0.045$). The ratio of the vertical impulse to the total impulse is also used as a metric of how much of the total force produced during the initial tail stroke is upward thrust. The highest ratios of vertical impulse to total impulse (figure 5-12c) are also observed at the higher jump heights ($h_{max} = -2.4I_y/|I| - 0.26$, $r^2 = 0.69$, $p = 0.011$).

Figure 5-12: Relationships between starting vortex impulse and jump height. (a) Impulse vector magnitude versus jump height for eight SAPIV measurements between 1 and 2 body lengths. (b) Vertical thrust ($Y$) component of the impulse vector for eight jumps between 1 and 2 body lengths. Overall jump height correlates with $Y$-impulse as $h_{max} = -0.004I_y + 0.78$, $r^2 = 0.51$, $p = 0.045$. (c) The fraction of the total impulse in the vertical direction versus the jump height. Jump height correlates with the fraction of total impulse oriented downward as $h_{max} = -2.4I_y/|I| - 0.26$, $r^2 = 0.69$, $p = 0.011$.

The overall impulse of the wake (control volume in figure 5-3b) also shows variation with jump height. Figure 5-13 shows the full measurement volume and starting vortex impulses in the $Y$-direction over time until the fish completely leaves the measurement volume. The slopes of the impulse curves over time in both control volumes are generally steeper at higher jump heights (i.e., greater $dI/dt$ forces), though some variation is seen for both individual tail strokes and overall trials.

By virtue of both decreased tail stroke duration (figure 5-11) and increased vertical impulse (figure 5-12), the upward force produced by the caudal fin during the first tail stroke, as determined by equation 5.4, also increases with jump height. Figure
Figure 5-13: The thrust (Y) component of hydrodynamic impulse over time in both overall and first tailbeat control volumes. Each trial is color-coded by jump height binned to the nearest tenth of a body length. Markers denote the beginnings of the second, third, and fourth tail strokes.

5-14 shows the stroke-averaged forces calculated for the first three tail strokes in eight jumps between 1 and 2 body lengths. The forces generated by the first and second tail strokes both correlated significantly with jump height (stroke 1: \( h_{\text{max}} = 0.0044F_{y,1} + 0.96, r^2 = 0.58, p = 0.027 \), stroke 2: \( h_{\text{max}} = 0.0037F_{y,2} + 0.62, r^2 = 0.63, p = 0.018 \)). The slopes of the correlations with height for the first two tail strokes do not vary significantly (i.e., forces vary the same amount with height for both tail strokes), but forces are typically higher for the second tail stroke. The forces calculated for the third tail stroke did not correlate significantly with jump height, but a third tail stroke only occurred for jumps above 1.5 BL. The forces calculated from the wake of the third tail stroke were lower than those calculated for the second tail stroke, but comparable with those from the first tailbeat.

5.4.4 Wake visualizations at low and high jump heights

To further understand how propulsion varies with jump height, trajectories, wakes, and fin kinematics are next compared in-depth for two example cases where the archer
Figure 5-14: Relationships between the average force produced by each tail stroke and jump height for the first three tail strokes. Force for the third tail stroke is only calculated for trials where the third tail stroke occurs within the measurement volume. The overall jump height correlated significantly with both the first and second tail strokes (stroke 1: $h_{\text{max}} = 0.0044F_{y,1} + 0.96$, $r^2 = 0.58$, $p = 0.027$, stroke 2: $h_{\text{max}} = 0.0037F_{y,2} + 0.62$, $r^2 = 0.63$, $p = 0.018$).

Figure 5-15: Photographs of the archer fish in the center array camera at jump onset, midway through tail stroke 1, and at the start of tail stroke 2 for two jump heights. (a) 1.08 BL jump. (b) 1.96 BL jump.

fish jumps 1.08 BL and 1.96 BL. Figure 5-15 shows time series of photographs from the center camera of the SAPIV array during the first tail stroke of each jump. The initial aiming posture of the fish is more vertical for the higher jump. The first tail stroke is also faster for the 1.96 BL case.
Figure 5-16 shows the aerial trajectories of the fish during the 1.08 and 1.96 BL jumps. For the 1.08 BL case, the peak velocity (1.0 m s\(^{-1}\)) is reached shortly after beginning the third tail stroke. With the 1.96 BL jump, the higher peak velocity (1.5 m s\(^{-1}\)) occurs shortly after the fourth tail stroke. The velocity at the conclusion of the second tail stroke is also greater during the 1.96 BL jump. The peak accelerations in the two cases, both observed at jump onset, are not substantially different (50 m s\(^{-2}\)). The acceleration curve of the 1.96 BL jump remains above the 1.08 BL jump until the conclusion of measured tail strokes, signifying greater overall acceleration throughout the jump duration.

Figure 5-17 shows the wake measured following the first and second tail strokes during the 1.08 BL jump. The starting vortex from the first tail stroke at t = 0.025 s is an axisymmetric ring similar to that seen in figure 5-4. At the same time, a vortex is also present below the anal fin. The orientation of the ring axis is less vertical than the starting vortex for the 1.7 BL jump shown earlier. The vortex from the second tail stroke has a more vertical axis than the first tailbeat, but a less toroidal shape. The orientation of these wake structures suggests that the body re-orient toward a more vertical posture between the first and second tail strokes.

Kinematic data from the dorsal, anal, and caudal fins shows this change in posture in figure 5-18. The traces of the fins also show that the tail kinematics are not as
well-approximated by planar motion as the previous jumps analyzed. Twisting of the body is also apparent in the anal fin traces. Compared to the 1.64 BL jump in figure 5-9, the tail passes through more of the anal fin’s path in this trial than what is seen at the higher jump height. The tail will therefore encounter wake structures from more anterior regions of the anal fin instead of just the posterior lobe.

Figure 5-18: 3D kinematics of the dorsal (dotted), anal (dashed), and caudal fins (solid) for the 1.08 jump in figure 5-17. Traces are colored by the time from jump onset.
Figure 5-19: Slices through the caudal (Z = -20 mm) and anal fin (Z = -14 mm) wakes during a 1.08 BL jump. The isovorticity surface shows the overall wake structure at this time. The black traces show the tail trajectory over the course of the jump.

Figure 5-19 examines the hydrodynamic implications of these kinematics through two slices through the vortex wake at t = 0.025 s. The first slice shows the axial jet of the caudal fin wake. The second slice, taken through the vortex below the anal fin, shows that the flow from this fin is not aimed at the tail (as it was with the 1.64 BL jump in figure 5-8). Instead, the anal fin jet is oriented downward. The peak velocities in the caudal fin wake are still much higher than those observed in the anal fin wake. The presence of this vertical jet below the anal fin likely causes the less-circular vortex structure seen at the onset of the third tail stroke in figure 5-17 (t = 0.037 s).

Figure 5-20 shows the hydrodynamic impulse over time for the 1.08 BL jump. The starting vortex contributes comparable dorso-ventral (X) and vertical momentum, suggesting that it also serves to re-orient the fish body posture. The downward
impulse exhibits a sharp decline during the second tail stroke. The full-field measurements of the Z impulse show that the second tail stroke also contributes significant lateral force.

Figure 5-20: Hydrodynamic impulse over time for the caudal and median fin wakes of the 1.08 BL jump seen in figures 5-17 and 5-19. Hydrodynamic impulse is calculated for both the volume surrounding the starting vortex and the entire measurement volume. Results from the starting vortex are only evaluated until the full wake from the first tail stroke is visible (shortly after the onset of the second tail stroke). Full-field impulse is plotted until the fish leaves the measurement volume. The square and triangle markers denote the beginnings of the second and third tail strokes respectively. *’s correspond to the times after each tail stroke where wake features were clear of the body and impulse could be evaluated.

The force predictions from the hydrodynamic impulse and from the aerial trajectory are compared in table 5.2. The force predicted from the starting caudal fin vortex alone (figure 5-17, t = 0.025 s) is again less than the force required to provide the initial acceleration of the fish measured from the trajectory. The force predicted from the second tail stroke wake comes closer to agreement with the force estimated from the aerial trajectory, but does not quite offset the gravitational force acting on the fish. The archer fish is still partially-submerged at this time, and buoyancy may also offset its weight.

Figure 5-21 shows the wake during the first three tail strokes of a 1.96 BL jump. The wake resembles the earlier case of the 1.7 BL jump in figure 5-4. The most notable difference is that from the end of the second tail stroke onward (t = 0.029-0.039 s), an
Table 5.2: Tail kinematic (stroke durations), wake (impulses and forces), and trajectory (velocities, accelerations, and net forces) parameters for the 1.08 BL jump in figure 5-17.

<table>
<thead>
<tr>
<th>Stroke</th>
<th>Duration (s)</th>
<th>( \bar{v}_{stroke} ) (m s(^{-1}))</th>
<th>( \bar{a}_{stroke} ) (m s(^{-2}))</th>
<th>( \Delta I_y ) (gcm s(^{-1}))</th>
<th>( F_y ) (mN)</th>
<th>( F_{net} ) (mN)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.016</td>
<td>0.32</td>
<td>42.4</td>
<td>-138</td>
<td>86</td>
<td>318</td>
</tr>
<tr>
<td>2</td>
<td>0.016</td>
<td>0.82</td>
<td>20.2</td>
<td>-262</td>
<td>164</td>
<td>151</td>
</tr>
</tbody>
</table>

additional vortex is visible attached to the main vortex ring chain. Figure 5-22 shows two slices through the vortex wake at \( t = 0.029 \) s to examine this flow feature in more detail. The slices through the wake show that there is an additional jet parallel to the main caudal fin wake, but of smaller size and lower peak velocity.

Three-dimensional fin tracking shows that this vortex originates from the anal fin. A similar anal fin jet can be seen at the conclusion of the second tail stroke of a 1.81 BL jump in figure 5-23. Unlike the 1.64 BL jump case in figure 5-8, these wake structures are not fully incorporated into the wake of the next tail stroke, as shown in figure 5-21 (\( t = 0.039 \) s) and figure 5-23 (\( t = 0.033 \) s).

As tail strokes become faster; the strength of the wake of the other median fins increases as well. The additional vortex momentum from all of these fins contributes to the steeper impulse curves seen for the 1.8-2.0 BL jumps in figure 5-13. Figure 5-24 shows the X and Z components of the impulse as well for the 1.96 BL jump; much more of the overall impulse is downward than in the 1.08 BL case in figure 5-20.

Table 5.3 summarizes the force production of each tail stroke for the 1.96 BL jump. As with the 1.7 and 1.08 BL jumps, the force predicted from the wake is insufficient for producing the initial acceleration measured from the aerial trajectory. Forces grow closer to matching the net force on the fish on the second and third tail strokes.

Appendix C contains similar trajectory and impulse information for the jump in figure 5-23.
Figure 5-21: Wake measurements at four times during the first three tail strokes of a 1.96 BL jump. The first peak-to-peak motion of the tail (seen through the solid black traces) occurs when the fish moves the tail toward one side during the preparatory aiming phase of the jump. Flow structures are visualized by vorticity isosurface and colored by velocity magnitude. Multiple vortices appear during the second tail stroke between $t = 0.029$ s and $t = 0.039$ s.
Figure 5-22: Slices through the caudal (Z = -20 mm) and anal fin (Z = -5 mm) wakes during a 1.96 BL jump. The isovorticity surface shows the overall wake structure at this time. The black traces show the tail trajectory over the course of the jump. At Z = -5 mm, an additional jet from the anal fin is visible parallel to the caudal fin wake of the second jumping tail stroke.
Figure 5-23: Propulsive jets from the caudal and anal fins during the second tail stroke of a 1.81 BL jump. The top row shows the wake structure at three timesteps, and the bottom row shows all velocity vectors with a magnitude of at least 300 mm s\(^{-1}\). The dotted purple and dash-dotted blue lines show the edges of the anal and caudal fins (legend in figure 5-2). Tracks of the caudal and anal fin edges show that this jet originates from the anal fin around \(t = 0.025\) s.

5.5 Discussion

5.5.1 Caudal fin contributions to jump thrust

The linked structure of the caudal fin wake resembles previous volumetric measurements of the chain of vortex rings observed during forward swimming in both flumes and quiescent tanks [53, 101]. The primary difference between jumping and regular forward swimming is the variation in the orientation of vortex ring axes throughout the course of a jump. At higher jump heights, the starting jet from the initial tail motion is predominantly vertical; lateral momentum first appears toward the end of the first tail stroke. Later vortices resemble the reverse Kármán street of forward fish swimming. At lower jump heights, the initial vortex is more horizontal, and later wake structures have more vertical momentum.

Three-dimensional tracks of simultaneous fin kinematics and aerial trajectories
Figure 5-24: Hydrodynamic impulse over time for the caudal fin wake of the 1.96 BL jump seen in figures 5-21 and 5-22. Hydrodynamic impulse is calculated for both the volume surrounding the starting vortex and the entire measurement volume. Results from the starting vortex are only evaluated until the full wake from the first tail stroke is visible (shortly after the onset of the second tail stroke). Full-field impulse is plotted until the fish leaves the measurement volume. The square, triangle, and diamond markers denote the beginnings of the second, third, and fourth tail strokes respectively. *’s correspond to the times after each tail stroke where wake features were clear of the body and impulse could be evaluated.

show that the vertical acceleration drops between successive tail strokes; the fish is therefore producing less force with each subsequent tail stroke. Peak acceleration is observed at jump onset, even in cases where the starting vortex contains less downward momentum (i.e., lower jump heights such as figure 5-17), and subsequent wake structures have more vertical thrust wakes.

The measurements of the caudal fin wake in tables 5.1, 5.2, and 5.3, as well as those presented in appendix C, underestimate the force required at jump onset. Force predictions are closer to those estimated from the aerial acceleration of the fish at later tail strokes during a jump. These findings further support the hypothesis from chapter 3 that additional propulsors are crucial to producing the initial acceleration at jump onset. The net force calculated from the fish trajectory is furthermore a lower bound on force requirements since the time-varying added mass of the archer fish is unknown over the jump. The added mass of the fish is likely greatest at jump onset when the body is entirely submerged and the pectoral and pelvic fins are abducted.
Table 5.3: Tail kinematic (stroke durations), wake (impulses and forces), and trajectory (velocities, accelerations, and net forces) parameters for the 1.96 BL jump in figures 5-21 and 5-22.

<table>
<thead>
<tr>
<th>Stroke</th>
<th>Duration (s)</th>
<th>( \bar{v}_{\text{stroke}} ) (m s(^{-1}))</th>
<th>( \bar{a}_{\text{stroke}} ) (m s(^{-2}))</th>
<th>( \Delta I_y ) (gcm s(^{-1}))</th>
<th>( F_y ) (mN)</th>
<th>( F_{\text{net}} ) (mN)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.012</td>
<td>0.32</td>
<td>54.4</td>
<td>-250</td>
<td>208</td>
<td>408</td>
</tr>
<tr>
<td>2</td>
<td>0.011</td>
<td>0.90</td>
<td>46.5</td>
<td>-325</td>
<td>305</td>
<td>349</td>
</tr>
<tr>
<td>3</td>
<td>0.011</td>
<td>1.28</td>
<td>24.7</td>
<td>-195</td>
<td>183</td>
<td>185</td>
</tr>
</tbody>
</table>

Thus, the force predictions from SAPIV for the initial tail stroke are likely even less of the actual required thrust.

The total impulse of the starting vortex (first tail stroke) does not vary significantly for jumps greater than one body length (figure 5-12a). The formation of optimal vortices, which are axisymmetric, is a governing principle of biological propulsion. There is a maximum amount of momentum that can be contained in a single vortex ring \([30]\). The muscular power of the fish may not be able to exceed this momentum transfer, or the fish may tune its kinematics to avoid higher-amplitude or faster tail motions. For the highest jump heights, additional vortices beyond the primary caudal fin wake are present during the second tail stroke (figures 5-21, 5-22, and 5-23). The overall impulse in the wake (figure 5-13) is increased (versus lower jumps) by the presence of these additional wake structures. Executing more extreme bending behavior than what is observed in a single tail stroke would also destabilize the fish by increasing the moment arm of gravitational force acting on the center of mass once it is aerial.

While the total amount of impulse in the starting tail stroke wake does not vary significantly with jump height, the orientation of wake momentum (figure 5-12b-c) and duration of the tail stroke (figure 5-11a) both do. The same amount of momentum distributed over a shorter time also corresponds to a higher average net force (and a correspondingly larger acceleration for the fish). The lack of a strong correlation between the duration of the first tail stroke and the second tail stroke (figure 5-11c) suggests some independence between tailbeats which the fish may be able to use to adjust its trajectory.
The orientation of the initial vortex formed by the first propulsive tail stroke varies substantially with jump height (figure 5-12c), as does the initial orientation of the fish body (figure 5-15). The first tail stroke contributes less upward thrust and more lateral force at lower jump heights. This increased later momentum may serve to generate torque that reorients the fish to a more vertical posture by the second tail stroke. An important question is whether the initial posture is driven by aim, or if the aiming posture used at this height is has hydrodynamic rationale. A trade-off with another prey capture mode may also exist; the fish posture may be less steep at lower jump heights to enable a subsequent maneuver or a split-second decision between prey capture modes. Energetic costs during the aiming stage may also be lower the less steep the angle is between the fish and the free surface. Posture variations are also observed during spitting; the angle between the archer fish and the surface decreases the farther the fish is from the target [152].

5.5.2 Median fin contributions vary with jump height

The curvature of the caudal fin into the direction of movement and the phase offset observed in the kinematics of the dorsal and anal fins (figure 5-10) resemble those observed during forward swimming in bluegill sunfish [154]. Upstream momentum from the anal and dorsal fins is also observed to interact with the caudal fin as the next tail stroke is executed (figure 5-8).

Interactions between the median fins vary with the height of the jump. Variations in initial posture between jump heights are shown by the fin kinematic data (figures 5-9 and 5-18). When the body angle is closer to horizontal, the entire span of the anal fin is oriented such that its undulation produces a downward jet (figure 5-19). As the body posture changes throughout the jump, the tail passes through more of the anal fin’s wake. The shape of the second vortex observed for the 1.08 BL jump (figure 5-17 and 5-18) suggests interaction between the anal fin wake seen at the end of the first tail stroke and the caudal fin wake from the second tail stroke. At higher jump heights, the tail only passes through the rear lobe of the anal fin, which faces downward, and a similar region behind the dorsal fin (figure 5-9). Strong wake
features from the anal fin are observed independently of the caudal fin wake at the highest jump heights as well (figures 5-21, 5-22, and 5-23).
Chapter 6

Conclusions and outlook

6.1 Thesis contributions

This thesis examines the fluid dynamics of the unique jumping behavior exhibited by archer fish using time-resolved three-dimensional measurements. To assess this propulsion, chapter 2 examines methods of performing quantitative analysis on volumetric measurements of fish wakes. This chapter presents approaches for both isolated, but arbitrarily-shaped wake structures and close-proximity, interacting wakes. Chapter 3 presents a characterization of the jumping prey capture mode, including analysis of a kinematic dataset from five specimens and preliminary PIV wake measurements in 2D and 3D. Chapter 4 addresses the limitations of the velocimetry seen in chapter 3 by developing a synthetic aperture PIV system specifically designed for near-surface water-exit flows such as the jumping archer fish problem. Chapter 5 combines volumetric PIV measurements with three-dimensional tracking of fins and the fish’s aerial trajectory to assess how propulsion varies with jump height and throughout the course of a jump. Interactions between the dorsal, anal, and caudal fins are also resolved through the use of volumetric techniques.

Specific contributions of this thesis to both the experimental fluid dynamics and organismal and evolutionary biology communities include:

- Analyzed uncertainty in calculating hydrodynamic impulse and vortex circula-
tion from 2D wake measurements by examining slices through volumetric data of arbitrarily-shaped isolated vortices (Chapter 2).

- Developed a model for parameterizing and calculating vortex impulse and its derivative for vortices of arbitrary shape resolved using volumetric PIV data (Chapter 2).

- Assessed limitations of analysis approaches based on vortex circulation calculations for wake slices in cases with linked vortex structures (Chapter 2).

- Evaluated the effects of PIV windowing, smoothing parameters, and measurement uncertainty on hydrodynamic impulse and kinetic energy calculations from 3D PIV data (Chapter 2).

- Identified that tail strokes executed by an archer fish during a jump are non-uniform, despite their linear correlation with the jump height (Chapter 3).

- Determined that the aerial stage of an archer fish jump is ballistic, and that the peak upward velocity is reached shortly before water-exit. (Chapter 3).

- Revealed variation in the orientation and position of propulsive vortices from the caudal fin throughout a jumping maneuver using synthetic aperture PIV (Chapter 3).

- Designed a camera configuration for synthetic aperture PIV near a free-surface with simultaneous 3D above-water imaging (Chapter 4).

- Evaluated the effectiveness of intensity thresholding as an artifact removal criterion during particle volume reconstruction for synthetic aperture PIV (Chapter 4).

- Improved 3D particle reconstruction in partially-occluded near-body regions using binary images identifying the body and the minLOS algorithm for synthetic aperture refocusing (Chapter 4).
• Compared the effectiveness of propulsive jets formed by the caudal, anal, and dorsal fins between fins, tailbeats, and with jump height (Chapter 5).

• Revealed additional wake structures generated by the anal fin at both low and high jump heights (Chapter 5).

• Identified a limit to the overall momentum transferred during a single tail stroke using the hydrodynamic impulse, and recognized that the orientation of this momentum varies with jump height (Chapter 5).

• Compared average force predictions for each tailbeat from PIV data to the average net force acting on the fish during each tail stroke of a jump, and determined additional propulsive forces must be present at jump onset. (Chapter 5).

6.2 Outlook and extensions of this work

This work continues the exchange of ideas between the engineering and biology scholarly communities by analyzing the complex hydrodynamics exhibited by a uniquely-evolved predatory fish. The behavior of the archer fish presents unique instrumentation challenges, which in turn drive advances in flow measurement capabilities around bodies and near the free-surface. This section describes additional applications of the instrumentation contributions of this thesis and questions raised by the findings of this work to further understand the archer fish’s propulsive capabilities.

6.2.1 SAPIV around bodies and interfaces

When coupled with body identification, the minimum line of sight algorithm demonstrates performance at resolving near-body flows despite the partial occlusion of tracer particles due to the presence of this body. The method for near-body particle reconstruction in 3D PIV can be applied to other problems in fluid-structure interaction. The occlusion mapping implemented in this thesis is an extension of the visual hull method [1], a technique most commonly used in studies of locomotion. However,
aside from swimming organisms, volumetric velocimetry techniques are desirable in applications including biomedical flows, turbomachinery, renewable energy, and vehicle design, all of which present potential for occluded measurement volumes and optical access constraints. The near-surface design of the SAPIV system in chapter 4 could potentially be used for additional studies of air-sea interaction, water entry, and water exit.

6.2.2 Wake analysis from experimental data

In studies of biological propulsion, it is ultimately desirable to be able to compare the performance metrics reported for one study (i.e., one species with one velocimetry technique), to another experiment studying related phenomena, but with a different species, scenario, or method. The lessons regarding the sensitivity of different analysis frameworks to processing parameters reported in chapter 2 help work towards the goal of cross-study comparison. Synthetic test cases show that velocity and vorticity-based approaches to calculating vortex circulation can be cross-compared provided differences in identification criterion can be accounted for. In addition, the axisymmetric vortex ring model is shown to be of limited applicability in some propulsive scenarios, The hydrodynamic impulse is shown to be robust to processing parameters and can be calculated from slices of the vortex circulation or the vorticity field itself. This approach is sensitive to origin choice, but more robust than estimates of energy expenditure, which are extremely sensitive to the processing parameters of the experiment. Impulse can be used to approximate force over a period of vortex shedding, though Dabiri [29] cautions that stroke-averaged quantities do not provide the entire force history of an organism and that vortex impulse does not describe inviscid contributions to the hydrodynamic forces.

6.2.3 Archer fish-inspired propulsion

Building a full mechanical, multipropulsor system to replicate the archer fish’s jumping prowess is not the most pragmatic way to apply the strategies for spatially-
constrained, accurate water exit revealed in this thesis. In particular, the hydrodynamic consequences of hypothesized aiming constraints do not need to be replicated in engineering contexts. Any archer fish inspired vehicle is also likely to reach limits in the power density of available actuators (e.g., [55]). Variation of effort based on the necessary height (inspired by the modulation of caudal fin kinematics), exploitation of earlier energy expenditures (as with the interactions of the median fins), and use of multiple actuators to meet space constraints (i.e., fast, multi-fin propulsion at jump onset) are all feasible design goals for implementing an archer fish-inspired water exit strategy in an engineering context.

6.2.4 Segmentation of fin interactions

The experimental methods used in this study are able to resolving complex multipropulsor interactions in jumping fish; segmentation of wake structures is done primarily through use of the coupled kinematic data or temporally. Additional methods of wake segmentation may provide additional information into how the tail exploits the momentum of the dorsal and anal fins. For example, Henningsson et al. [65] segments features in wake measurements behind a stationary flying locust using Proper Orthogonal Decomposition (POD) and are able to identify features of varying origins including both primary wing vortices and entrained Kelvin-Helmholtz vortices.

POD and related techniques also remove aperiodic measurement noise from the data, as shown by Epps and Techet [46] for a two-dimensional fish wake. In this 2D study, prior to performing decomposition on the fish wake, significant interpolation was required to place the wake measurements in a fish-centric reference frame at all times. With improved fish tracking, a suitable reference frame for 3D jumping may be determined. POD to segment wake features may improve applicability of the core-line discretized impulse model to the jumping archer fish, though the model’s lack of interaction between flow structures may still be a limitation.
6.2.5 Lagrangian methods

The windowed cross-correlation process underlying particle image velocimetry results in full-field measurements on a uniform Cartesian grid. However, the range of velocities that can be measured with particle volumes divided into a given window size is limited. The effective low-pass filtering of PIV processing, especially in 3D, is shown in this thesis to be detrimental to the calculation of quantities such as kinetic energy. The squaring of velocity is especially sensitive to the underestimation of peak velocities caused by spatial smoothing. Alternatively, Lagrangian methods that track individual particles have fewer limitations over the dynamic range of velocities that they can detect. These techniques are limited in the seeding density over which they can be applied. However, in thick 3D measurement volumes, large interrogation windows are needed to have a sufficient number of particles in each window. 3D cross-correlation operations for large windows also have increased computational costs compared to 2D. Recent advances in dense particle tracking such as the time-resolved shake-the-box method [131] may be better matched for the reconstructed volume’s seeding density than cross-correlation methods and provide greater dynamic range.

In addition to dynamic range, Lagrangian measurements may also enable new methods of wake analysis and segmentation. For instance, Huhn et al. [72] used elliptic Lagrangian Coherent Structures (LCS) to identify the upstream fluid that would ultimately become the wake vortices of a swimming fish. LCS may likewise bring new insights to the interaction between multiple fins observed during archer fish jumping and other swimming problems. Rival and van Oudheusden [120] also identify Lagrangian techniques as a promising tool for obtaining accurate load predictions from measured flow-field data by being able to utilize the trajectories of coherent wake structures, a method first described by Dabiri [29].

6.2.6 Surface effects on propulsion across the interface

The presence of a free surface during water-exit behaviors such as those exhibited by the archer fish introduces additional modeling considerations. Executing the same
jumping gait to accelerate when fully submerged would result in different net forces acting on the fish. The presence of the water-air surface has been considered for jumping problems at surface tension-dominated scales (e.g., [78]), but not at the scale where energy dissipation due to surface wave formation is the dominant surface effect. Previous analysis of basilisk lizards running on the water’s surface applied momentum models for a slug of fluid beneath the lizard’s foot and an axisymmetric vortex ring wake to assess how the lizard supports its weight [69].

Webb et al. [160] studied the performance of trout maneuvering in water of varying depth and found that decreasing depth also decreased the distance the fish traveled as a result of the maneuver. Energy dispersion in the shallowest case due to the free surface tested amounted to about 70% of the mechanical work performed when the trout was maneuvering in deep water. Depth effects were negligible only when the depth was greater than three times the width of the caudal fin. The energetic costs of locomotion near the surface have also been considered for locomotion along the surface, where the problem is analogous to the hull drag of a ship [19]. These scenarios are not a direct analog because the archer fish is moving through as opposed to below the surface. Organisms traveling along the surface such as penguins have been known to porpoise instead of constantly swimming below the surface [19], suggesting that the instantaneous energetic costs during water-exit are less substantial than constant ones during subsurface swimming.

### 6.2.7 Pectoral fins

Flow generated by the pectoral fins, located laterally midway along the fish body, is particularly difficult to measure during jumping. Flow structures generated by these fins must be measured in the short time window before the rest of the fish body passes through these locations. In a multi-camera setup, additional experimental challenges arise because these fins are frequently either occluded from one side or located directly in front of the body. This pair of fins exhibits some of the most complex behavior at jump onset (figures 3-11, 4-1). When the fish initiates its jump, the pectoral fins extend, sweep forward and pitch to direct flow downward, and then tuck partially but
not completely against the body. These fins are only completely retracted against the body when they leave the water. Based on the orientation of wake jets, the 2D PIV measurements in figures 3-11 and 3-12 suggest that the pectoral fins produced upward thrust. However, extension of these fins also increases the projected area of the fish in the direction of motion and therefore hydrodynamic drag forces acting on the fish. The extension of these fins may also be crucial for stability by modifying the fish’s moment of inertia. Zooming out far enough that the pectoral fins are visible in addition to the median fins is a spatial resolution challenge not resolvable with currently-available experiment hardware.

6.2.8 Coupling experiments and numerics

The spatial and temporal scales over which different fins act during jumping challenges the limits of dynamic range and spatial resolution possible in any PIV system, SAPIV included. Numerical modeling driven by high-fidelity 3D kinematics presents one possible solution to this limitation, and could resolve the difficulty in evaluating pectoral and median fins simultaneously. Numerical modeling also provides the opportunity to suppress the contributions of individual fins, as was demonstrated by Borazjani [20] for the median fins during a bluegill sunfish C-start. Optimization can further be coupled with numerical analysis to determine efficient swimming gaits (e.g., [57]); this approach could be used to determine if the archer fish’s pattern of tail kinematics is optimal for propulsion through the free surface.
Appendix A

Additional factors in energetic analysis of the archer fish jump

A.1 Motivation

Beyond the sensitivity to PIV processing and spatial resolution, several other factors contribute to the difficulty in assessing jump efficiency from PIV measurements. This appendix lists many of those factors and the magnitude to which they impact energy evaluations.

A.2 Viscous energy dissipation

Once kinetic energy has been transfered to the fluid by the fish, the contributions of that energy do not remain constant for all future times.

The viscous dissipation per unit volume $\mu \Phi$ describes the rate at which kinetic energy is dissipated into heat by viscosity. In Cartesian coordinates, dissipation can be calculated from the terms of the velocity gradient tensor as:

$$\Phi = 2 \left[ \left( \frac{\partial u_x}{\partial x} \right)^2 + \left( \frac{\partial u_y}{\partial y} \right)^2 + \left( \frac{\partial u_z}{\partial z} \right)^2 \right] + \left( \frac{\partial u_x}{\partial y} + \frac{\partial u_y}{\partial x} \right)^2 + \left( \frac{\partial u_y}{\partial z} + \frac{\partial u_z}{\partial y} \right)^2 + \left( \frac{\partial u_z}{\partial x} + \frac{\partial u_x}{\partial z} \right)^2 \quad (A.1)$$

The derivatives required to estimate large-scale viscous dissipation can be calcu-
lated directly from the SAPIV velocity field. However, the boundary layer surrounding the archer fish body cannot be resolved at the scale of the current measurements. Velocity gradients in the boundary layer are much larger than those in the vortex wake, especially during the initial acceleration of the fish from rest.

A.3 Free surface effects

The infinite domain assumption is contradicted more highly than usual in the case of the jumping archer fish since all propulsion takes place directly below the free surface. Energy required to deform the free surface is neither used by the fish or reflected in the SAPIV wake measurements.

A.4 Aerial projectile mass

When the archer fish leaves the water, it entrains a liquid sheet of water attached to and behind it (figure A-1). The projectile mass when the fish is airborne is therefore not simply the body mass. Subsequent tail beats after exiting the water provide the fish with one mechanism to remove the excess water, meaning that the mass of the projectile also varies with time throughout the gliding stage of the jump.

Image segmentation and binary image operations are used to evaluate to leading order the weight of water the fish shakes off during the gliding stage of a jump.

1. Crop images to above-water portion, invert images so background is dark and fish body is bright, and subtract first image to remove background and bait.

2. Binarize images via global intensity thresholding. Determine areas and shape of each blob in binary images (Matlab function regionprops).

3. Remove features smaller than 2 pixels or on the size scale of fish body, and features where the ratio of the major and minor axes for an ellipse of equivalent area is greater than 2.

4. Calculate radius using the mean of the major and minor axes.
5. Calculate volume of each droplet using the radius.

6. Filter total volume over time with a 9-point median filter.

This routine only considers entrained water once it has fragmented into individual droplets; the liquid sheet from the fish’s tail and any ligaments are not considered. Figure A-2 shows the mass of droplets measured using the image processing routine over time for six jump sequences by specimen 5 from chapter 3.

The weight of water in the initial sheet behind the fish is estimated to be on the order of 1 g, with a large amount of variation between runs, approximately 10% of the mass of the fish. Moreover, the mass of water attached to the fish is time-varying. The additional spikes in the droplet volume profiles are additional aerial tailbeats where the fish sheds excess water. A more sophisticated droplet tracking routine capable of tracking when drops appear and leave the field of view would provide the mass history of the fish over time for a better aerial energy balance.

A.5 Conclusions

Energy estimates made from 3D PIV measurements can be used to assess the rate of energy expenditure over time given a sufficiently large measurement volume. Peak
Figure A-2: Mass of droplets shaken off the fish during the glide stage of the jump over time for six jumps.

Wake energies can also be compared between trials with the same processing parameters, but energies calculated should be considered only as trends and not factual quantitative values. A direct measurement of jump efficiency considering the potential energy requirement of jumping and the hydrodynamic energy losses is infeasible due to the combination of PIV error sources and unmeasured quantities in the present study.
Appendix B

3D experiment specimen behavior

This appendix provides comparison between the specimen used in chapters 4 and 5 and the specimens characterized in 2D in chapter 3. Behaviors observed are consistent between the two sets of specimens.

The aiming behavior of the specimen used for 3D experiments is very similar to the specimens used in 2D. Figure B-1 shows the aiming relationships between bait height and jump height for the specimen, as well as its overshoot.

![Figure B-1: Relationships between bait height, jump height, and overshoot for the specimen used in the 3D experiments.](image)

The linear relationship for the five fish used in chapter 3 (figure 3-4) was $h_{max} = 1.06 h_{bait} + 0.13$ with $r^2 = 0.95$. The relationship between overshoot and bait height in Chapter 3 was $h_{max} - h_{bait} = 0.06 h_{bait} + 0.13$ with $r^2 = 0.07$ and $p = 0.011$. The cor-
The relation between overshoot and jump height is of similar likelihood for both datasets. The median overshoot over all jump heights for the specimen used in chapters 3 and 5 is $0.34 \pm 0.10$ (s.d.).

The snout trajectory is used to determine the height, velocity, and acceleration of the fish over time. When the mouth is closed; the lower mandible extends slightly beyond the upper lip, making the lower jaw the easiest point to automatically track in aerial images. When the mouth opens, both lips can be tracked independently. The eye is another marker that is easy to automatically track in DLT [64] that is located closer to the fish’s center of mass. Figure B-2 compares peak velocities determined by measuring the upper lip, lower lip, and eye over eight jumps with accompanying SAPIV data. Values calculated for the upper lip are lower because the mouth does not open until after peak velocity occurs. The eye matches closer to the lower lip, but is not yet above the water when peak accelerations occur, and is not visible in all body orientations.

![Figure B-2: Peak velocities calculated tracking the overall snout/lower lip, the upper lip, and the eye.](image)

The velocities, accelerations, and ballistic energies also agree with the five specimens analyzed in 2D in Chapter 2. Ballistic energies are again calculated for the glide stage of the jump when the fish is completely out of the water. There is not a statistically significant correlation between acceleration and jump height; the correlation
between acceleration and height is also weak in the 2D specimens.

\[
h_{\text{max}} = 0.42 \frac{v_{\text{max}}}{g} (gBL)^{1/2} + 0.48
\]

\[r^2 = 0.98\]

Figure B-3: Peak velocities, accelerations, and ballistic energies for the specimen used in Chapters 4 and 5.

The relationship between Froude number and jump height in Chapter 2 is \(h_{\text{max}} = 0.46Fr + 0.23\)
Appendix C

Additional kinematic and trajectory measurements

This appendix contains additional data used in the kinematic and hydrodynamic summary plots in chapter 5. Control volumes for the two impulse calculations are shown in figure 5-3.

C.1 0.89 body length jump

Figure C-1: Y position, velocity, and acceleration for a 0.89 body length jump.
Table C.1: Trajectory and tail kinematic parameters for the 0.89 BL jump in figure C-1.

<table>
<thead>
<tr>
<th>Stroke</th>
<th>Duration (s)</th>
<th>( \bar{v}_{stroke} ) (m s(^{-1}))</th>
<th>( \bar{a}_{stroke} ) (m s(^{-2}))</th>
<th>( F_{net} ) (mN)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
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<td>0.31</td>
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<td>2</td>
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C.2 1.51 body length jump

Figure C-2: Y position, velocity, and acceleration for a 1.51 body length jump.

Table C.2: Wake and trajectory parameters for the 1.51 BL jump in figure C-2.

<table>
<thead>
<tr>
<th>Stroke</th>
<th>Duration (s)</th>
<th>( \bar{v}_{stroke} ) (m s(^{-1}))</th>
<th>( \bar{a}_{stroke} ) (m s(^{-2}))</th>
<th>( F_{net} ) (mN)</th>
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</thead>
<tbody>
<tr>
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<tr>
<td>2</td>
<td>0.016</td>
<td>0.83</td>
<td>41.8</td>
<td>314</td>
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</table>
C.3 1.61 body length jump

Flow field data from this jumping trial can be seen in figure 5-5.

Figure C-3: Hydrodynamic impulse calculated for both full-field and starting vortex control volumes for the 1.61 body length jump seen in figure 5-5. *’s denote times representative of the impulse at the conclusion of each tail stroke.

Figure C-4: Y position, velocity, and acceleration for a 1.61 body length jump.
Table C.3: Wake and trajectory parameters for the 1.61 BL jump in figure C-4.

<table>
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<tr>
<th>Stroke</th>
<th>Duration (s)</th>
<th>$\bar{v}_{\text{stroke}}$ (m s$^{-1}$)</th>
<th>$\bar{a}_{\text{stroke}}$ (m s$^{-2}$)</th>
<th>$\Delta I_y$ (gcm s$^{-1}$)</th>
<th>$F_y$ (mN)</th>
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</tbody>
</table>

C.4 1.64 body length jump

Flow field data from this jumping trial can be seen in figure 5-8.

![Figure C-5: Hydrodynamic impulse calculated for both full-field and starting vortex control volumes for the 1.64 body length jump seen in figure 5-8. *’s denote times representative of the impulse at the conclusion of each tail stroke.]

Table C.4: Wake and trajectory parameters for the 1.64 BL jump in figure C-6.

<table>
<thead>
<tr>
<th>Stroke</th>
<th>Duration (s)</th>
<th>$\bar{v}_{\text{stroke}}$ (m s$^{-1}$)</th>
<th>$\bar{a}_{\text{stroke}}$ (m s$^{-2}$)</th>
<th>$\Delta I_y$ (gcm s$^{-1}$)</th>
<th>$F_y$ (mN)</th>
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</table>
Figure C-6: Y position, velocity, and acceleration for a 1.64 body length jump.

C.5 1.68 Bodylength Jump

Flow field data from this jumping trial can be seen in figures 4-9 and 4-10.

Figure C-7: Hydrodynamic impulse calculated for both full-field and starting vortex control volumes for the 1.64 body length jump seen in figures 4-9 and 4-10. *'s denote times representative of the impulse at the conclusion of each tail stroke.
Figure C-8: Y position, velocity, and acceleration for a 1.68 body length jump.

Table C.5: Wake and trajectory parameters for the 1.68 BL jump in figure C-8.

<table>
<thead>
<tr>
<th>Stroke</th>
<th>Duration (s)</th>
<th>$\bar{v}_{stroke}$ (m s$^{-1}$)</th>
<th>$\bar{a}_{stroke}$ (m s$^{-2}$)</th>
<th>$\Delta I_y$ (gcm s$^{-1}$)</th>
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C.6 1.81 body length jump

Flow field data from this jumping trial can be seen in figure 5-23.

Table C.6: Wake and trajectory parameters for the 1.81 BL jump in figure C-10.

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<th>Stroke</th>
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<th>$\bar{a}_{stroke}$ (m s$^{-2}$)</th>
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Figure C-9: Hydrodynamic impulse calculated for both full-field and starting vortex control volumes for the 1.81 body length jump seen in figure 5-23. *’s denote times representative of the impulse at the conclusion of each tail stroke.

Figure C-10: Y position, velocity, and acceleration for a 1.81 body length jump.
C.7 1.67 body length jump

Figure C-11: Hydrodynamic impulse calculated for both full-field and starting vortex control volumes for a 1.67 body length jump. *’s denote times representative of the impulse at the conclusion of each tail stroke.

Figure C-12: Y position, velocity, and acceleration for a 1.67 body length jump.
Table C.7: Wake and trajectory parameters for the 1.67 BL jump in figure C-12.

<table>
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<th>Stroke</th>
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Bibliography


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