How Bluegill Sunfish Maneuver: Analysis of Body and Fin Motion Under a Horizontal Obstacle

How Bluegill Sunfish Maneuver: Analysis of Body and Fin Motion under a Horizontal Obstacle

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Abstract

This study investigates how bluegill sunfish control fin motion to deal with the added locomotor complexity of swimming under a horizontal obstacle. While previous studies have focused on upright swimming in the forward and backward direction, in the current study blue gill sunfish rotate their bodies ninety degrees and swim on their sides in order to pass under a horizontal obstacle. The goal of this research is to develop an understanding of the orchestration of fin mechanics employed by bluegill sunfish that involve changes in speed and body rotation to navigate under a horizontal obstacle. This study analyzes how roll motion is produced and the interplay between pectoral, dorsal, anal, and caudal fins in complex maneuvering during rolling. Analysis of high-speed videography revealed a series of coordinated movements of all fins to achieve rolling, propulsion under the horizontal obstacle, and unrolling. While all fins were utilized to adjust pitch, roll, and yaw, pectoral fins were the primary locomotive fins in creating rolling and unrolling via a complex fin motion described as cupping. The fish switched from median and paired fin swimming during upright swimming to body and caudal fin swimming during sideways swimming, which drove propulsion under the horizontal obstacle. There are a variety of ways to maintain stability of the center of mass in non-linear, reverse, and sideways swimming, and these are accomplished via alterations in fin surface, beat frequency, and coordination with other fins. Beyond the application of these biomechanical principles to the field of robotics and underwater exploration, a deeper understanding of fish locomotion will help inform our knowledge of the evolutionary biology that has shaped these creatures.

Dedication

This effort is dedicated to my newborn baby, Āisha Nidar Suri. I love you more than anything else in this life and I cherish your authenticity. I wrote this while you slept in my arms inspired by your awe for this world. I pray you keep the awe and the curiosity for it is this awe and curiosity that will allow you to see the world for the magical place that it really is.

Acknowledgments

This work would not have been possible without the mentorship and help of Dr. George Lauder. I am grateful to Kara Feilich for many back and forth conversations, help with the experiments and much advice. I am grateful to Valentina Di Santo for encouragement throughout the experiments and much laughter during the process. I am also grateful to Kelsey Lucas and Dylan Wainwright for helping with the experiment set ups and fish care. I am grateful to Maggie Starvish for all the positive feedback she brought into my work. This work was supported by the Office of Naval Research MURI N000140310897.

Last, but certainly not least, I am deeply grateful to my husband who gave me the support without which this work would have not been possible.

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Chapter I

Introduction

For fish to be able to survive in complex environments, they must maneuver efficiently and be flexible. In this introduction, I will begin by demonstrating the importance of multifin control for fish species like the bluegill sunfish, the subject of investigation. I will then go on to explore aspects of blue gill sunfish locomotion, highlighting remaining areas of investigation. Finally, I will relate this work to the rising field of biorobotics, a key application of the knowledge gained from this investigation.

The Importance of Multifin Control in Swimming

Control of body orientation and multifin maneuvering is essential for stable swimming in these circumstances. Fish like bluegill sunfish (*Lepomis macrochirus*) use multifin control to manipulate roll, pitch and yaw in order to navigate such complex environments. Multifin control allows for high flexibility and maneuverability in order to swim through and around obstacles without having to compromise speed and efficiency. To swim under obstacles, precise timing of body and fin kinematics is needed in order to balance the torques produced by each fin's independent action and the body's orientation (Flammang and Lauder, 2013). In this study, I will investigate how bluegill sunfish control fin motion to deal with the added locomotor complexity of swimming under a horizontal obstacle that cannot be maneuvered around. When bluegill sunfish swim underneath obstacles, yaw, pitch and roll torques act on the body, along with hydrostatic forces, resulting in hydrodynamic instability. I hypothesize that having to swim under an obstacle will result in modified kinematics that reduce destabilization of the fish's center of mass, and at the same time allow the fish to reposition its body to fit under the obstacle.

Previous investigations of bluegill sunfish in the Lauder laboratory, Harvard University, have demonstrated the wide range of uses of multiple fins in fishes during aquatic locomotion. This study will focus on the biomechanics of the dorsal, caudal, anal, pelvic, and pectoral fins (See Figure 1). Previous studies have demonstrated how each fin serves a unique purpose depending on the nature of the movement, such as high vs. low speed swimming. For example, pectoral fins are considered high degree of freedom (DOF) propulsors, used to propel fish at lower speeds via a motion like a rowing oar, while also improving low-speed maneuverability (Gottlieb et. al., 2010). At higher speeds, these fins can serve as rudders to control pitch in fish like sturgeon and sharks (Wilga and Lauder 1999, 2000, 2001). Previous investigations have elucidated the function of multifin control in forward motion (Drucker and Jensen, 1996; Westneat, 1996; Lauder et. al., 2006), backward motion (Flammang and Lauder, 2009; Flammang and Lauder, 2016) and vertical obstacles (Flammang and Lauder, 2013; Kalionzes, et al., in preparation).

However, the biomechanics of multifin control in bluegill sunfish has never been studied when introducing a horizontal obstacle that requires the fish to manipulate yaw, pitch, and roll to move under the object. Unlike previous studies that focused on upright swimming in the forward and backward direction, the fish must rotate their bodies ninety degrees and swim on their sides in order to pass under horizontal obstacles. This opens a whole new set of questions unique to the current study. Questions I hope to answer during this experiment include: How is roll motion produced and what role do the pectoral fins have in assisting in such maneuvering? Do the dorsal and anal fins change motion with different roll speeds? How do the pelvic and caudal fins play a role in this complex maneuvering during rolling? How does the fish unroll, and recover normal posture after passing under the obstacle?

Bluegill Sunfish Locomotion: The Known and the Unknown

The explosion in the number of teleost fish species (now numbering over 35,000 species) coincided with the evolution of complex marine habitats such as coral reefs with their intricate three-dimensional structure (Flammang and Lauder, 2013). Most fishes live in complex structured environments, which provide a continuous food supply and help them avoid predation. However, structurally complex habitats present a challenge when it comes to maneuvering through confined spaces, and fish must be able to change direction quickly and efficiently. This can be applicable to reef fishes and other fishes that live in complex and confined ecosystems where maneuvering can be essential for survival. Deep-bodied fish, such as bluegill sunfish, are well adapted to maneuvering in tight spaces around vegetation, and amongst rocks and sticks; many coral reef fish are also deep-bodied to improve maneuvering. For bluegill sunfish, it has been shown that such structurally complex environments provide protection from predation and an abundant food supply, and are preferred to other less cluttered environments (Crowder and Cooper, 1982).

To be able to maneuver in such environments, most fish utilize rhythmic undulations of their bodies and fins. The more undulatory waves that a fish can generate to push against the surrounding water and the faster and more exaggerated the waves are, the more power the fish can generate (Moyle and Cech, 2000). Bluegill sunfish utilize multifin control to adeptly navigate these complex environments; however the biomechanics of how they do this needs further investigation. Multifin control in bluegill sunfish involves an orchestration of a number of fins in a unique pattern, depending on the context of the movement. Figure 1 illustrates the key fins of bluegill sunfish studied in this investigation and previous studies.

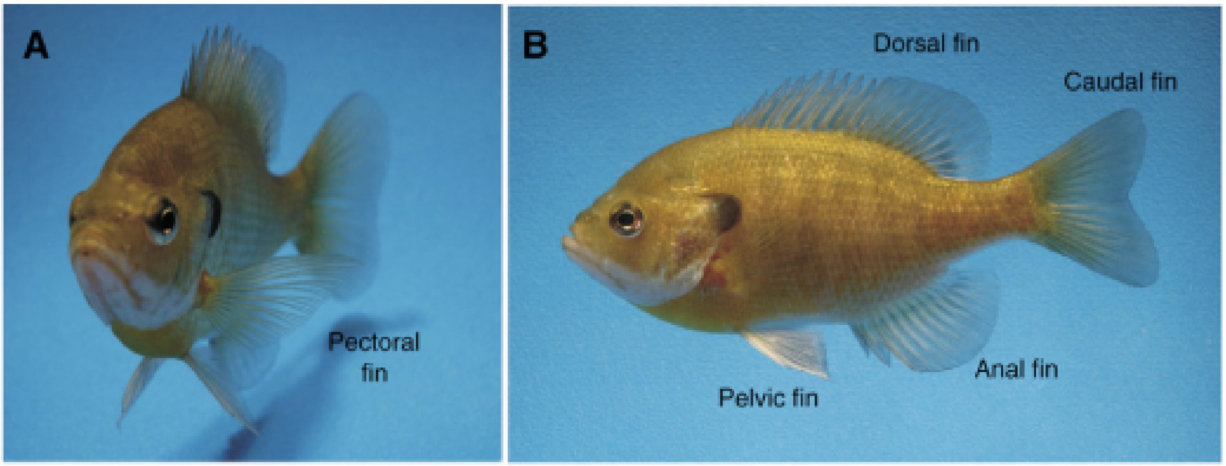

Figure 1. Bluegill sunfish *Lepomis macrochirus.* This figure displays all of the major fins involved in aquatic locomotion by G. V. Lauder et al., 2007, *Journal of Experimental Biology*, *210*, p.2767. (Copyright 2007 by Lauder et al.)

The bluegill sunfish is remarkable in its control of body position, and it is very effective at maneuvering in three dimensions in its native freshwater habitat. Bluegill sunfish have fine control over fin and body musculature, and approximately 50 intrinsic caudal muscles contribute to the movements involved in kick-and-glide, braking and backing up maneuvers, along with steady swimming (Flammang and Lauder, 2008). For this reason, there is great interest in understanding and eventually replicating the biomechanics of multifin control in fish, as such information could assist in the design of robotic underwater vehicles that are capable of enhanced maneuvering relative to current propeller-driven devices. In addition, bluegill sunfish make ideal research subjects because of their general cooperativity, steady swimming, and availability.

Despite the wide range of previous studies on bluegill sunfish fin function, there remains much to be understood regarding the role of pectoral fins in sunfish swimming and maneuverability, and especially for extreme maneuvers which have not yet been studied. Steady swimming with the paired pectoral fins involves two key motions: the propulsive stroke and the recovery stroke. In the propulsive stroke, the fin is retracted back in the perpendicular plane of orientation, while in the recovery stroke, the fin is rotated, or feathered, parallel to the flow of movement, so as to create net forward propulsion (Biewener, 2003). While it remains uncertain how exactly these fins generate force, the magnitude of thrust generated by the pectoral fins results from the change in fin velocity, shape, and stroke angle. This study will shed greater light on these details as they apply to the hydrodynamic changes involved with bluegill sunfish moving under a horizontal obstacle.

Considerable work has been done to study the function of pectoral fins in both forward propulsion and maneuverability of bluegill sunfish. Digital particle image velocimetry, a technique that allows the visualization of water flow patterns generated by individual fins, has demonstrated that bluegill sunfish create donut-shaped rings of vorticity from each pectoral fin, producing significant lateral hydrodynamic forces proposed to contribute to the species' maneuverability (Drucker and Lauder, 2000). Drucker and Lauder proposed a fundamental trade-off between speed and maneuverability that the sunfish must face in employing their pectoral fins. Maneuverability comes from being able to generate mediolateral force asymmetries between the right and left fins. While the sunfish were only able to swim half as fast as the black surfperch using their pectoral fins, Drucker and Lauder proposed that the orientation of vorticity allows for greater maneuverability. The question remains exactly how this reorientation takes place and specifically how vorticity mechanisms are utilized by bluegill sunfish in yawing, pitching, and rolling their bodies past obstacles. This study will further investigate the bluegill sunfish's ability to generate force asymmetries, particularly with pectoral fins, to swiftly rotate its bodies into a horizontal position and maneuver under a horizontal obstacle.

It is thought that individual fins in multifin control employ different biomechanical mechanisms during slow and fast swimming. For example, drag-based mechanisms employing simple rowing movements of pectoral fins are utilized at low speeds. On the other hand, lift-based mechanisms are used at high speeds when pectoral fins are used as hydrofoils to generate lift, which contains an anterior component that propels movement (Biewener, 2003). Another investigation that studied caudal fin muscles of bluegill sunfish with implanted electrodes demonstrated that intrinsic caudal muscles are recruited for high-speed swimming to stiffen the tail, while myotomal muscles are used to power undulatory body bending (Flammang and Lauder, 2008). My experiment involves the transition between slow and fast swimming as a bluegill sunfish faces an obstacle. This obstacle will require the fish to decelerate and accelerate while employing its pectoral fins to maintain stability. It is likely that these fins, in orchestration with body movements, as well as caudal, dorsal, and anal fin motion, utilize both drag-based and lift-based mechanisms in order to maximize speed and stability. Finally, the dorsal and anal fins undergo lateral undulations to create drag-based mechanisms for propulsion. How these fins contribute to pitch, yaw, and roll will be a key area of investigation in this study.

In our recent study of fish swimming backwards in a straight line, we concluded that control is important in maintaining reverse direction to generate thrust and balance torques (Kalionzes et al., in preparation). To be able to move backwards, fish shift from caudal fin propulsion when moving forward to paired fin propulsion. When backing through tight spaces in complex environments, the fins have to exert force on the surrounding water environment to be able to propel the fish backwards. When moving through the water backwards, bluegill sunfish often encounter obstacles and use both the body and fins to position themselves and move through a cluttered environment.

Given the importance of inhabiting complex environments, maneuverability is an important aspect of bluegill physiology and behavior. High maneuverability means low stability (Webb, 2002) because there is a tradeoff between the ability to rapidly generate maneuvering forces and the ability to maintain a stable body position. This tradeoff has been studied in previous experiments on backwards swimming, as well as maneuvering through obstacles during forward locomotion (Webb, 2002; Kalionzes et al., in preparation).

While our previous studies have employed vertical obstacles to study bluegill sunfish kinematics, horizontal obstacles (that fish have to squeeze under) have never been studied before, and this study offers unique insight into compensatory biomechanics required to navigate complex environments. Horizontal obstacles pose a unique challenge and represent the next frontier in our understanding of bluegill sunfish biomechanics. Our research thus far has focused on forwards and backwards swimming of bluegill sunfish in the upright position, but the sideways swimming required to pass under a horizontal obstacle has never been studied. This study further aims to understand how survival is possible in such challenging environments by elucidating the mechanisms by which bluegill sunfish achieve such high levels of maneuverability and efficiency in locomotion in sideways swimming. I hope to understand what aspects of body morphology have the most impact on stability and maneuverability under a horizontal obstacle.

A deeper understanding of fish locomotion will help inform our knowledge of the evolutionary biology that has shaped these creatures. Most fish devote a majority of their musculature to swimming. One of the major evolutionary pressures on fish is to improve swimming efficiency and performance (Moyle and Cech, 2000). Learning about how bluegill sunfish manipulate their bodies in unique and subtle ways in complex environments can help us understand how they have acquired prey, evaded predators, and adapted to ecological niches in their respective ecosystems over millions of years of evolution.

The Kinematics of Fish and its Biorobotic Applications

Kinematics is the study of movement and focuses on changes in position as a function of time. Historically, kinematic studies in fish have evaluated movement either based on the fish body, as in the current study where the motion of the fish’s body and fin can be analyzed with a fish-bound frame of reference, or using or an earth-bound position (Videler, 1993). Secondly, fish kinematic studies have involved inducing fish to swim against a water current at various speeds or recording voluntary movements in static environments, as is the case in our study. High-speed cameras with the ability to take high-resolution video of body positions of fish during movement have transformed the field of fish kinematics from the tedious pencil and paper hand calculations of Giovanni Borelli, the father of biomechanics, in 1680, to sophisticated analyses that can be employed for robotic design (Pope, 2005).

There are many important reasons to understand the biomechanics of living organisms. In the case of fish, much remains unknown about how they navigate the complex underwater environment, while maximizing speed, maneuverability, and efficiency. This knowledge can be applied to the development of manmade structures that utilize the principles perfected by over 35,000 species of fish over half a billion years of evolution. In the past 20 years, kinematic studies of fish have contributed to the construction of biomimetic fish robots (Figure 2). Based on studies such as this one, engineers have taken inspiration from living fishes to construct underwater robotic vehicles (URVs; Lauder and Madden, 2006).

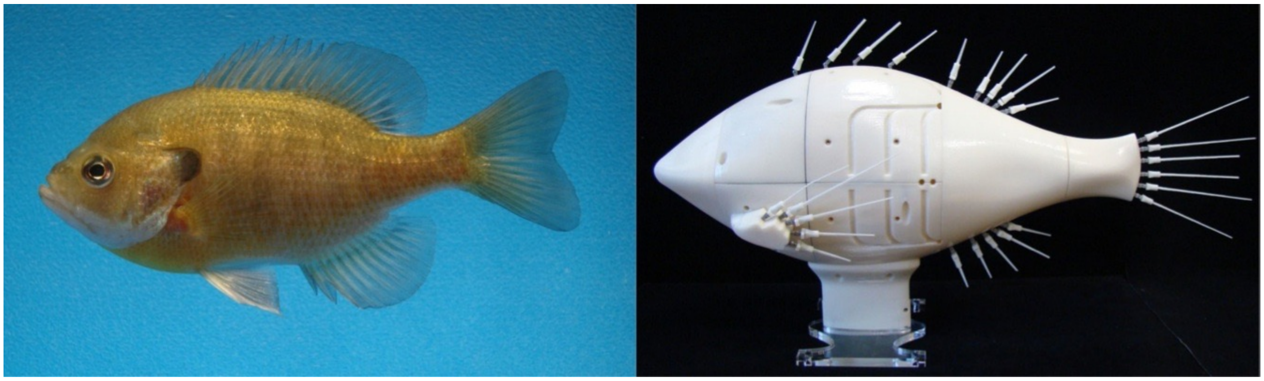

Figure 2. Bluegill sunfish and robo-mimetic fish. Robo-mimetic fish can be developed to closely mimic the complex orchestration of multifin control in bluegill sunfish. G. V. Lauder et al., 2007, *Journal of Experimental Biology*, *210*, p.2767. (Copyright 2007 by Lauder et al.)

The concept of building robotic structures based on fish-swimming behavior dates back to at least one century ago. Initial studies investigated forward propulsion, undulatory wave formation, and tail function in fishes (Houssay, 1912), and laid down the framework for subsequent hydrodynamic studies that have been performed with the advent of high-speed cameras and microchip computing. In our current era, we believe that the simultaneous investigation of biological phenomena with robotic design will further open this field with innumerable possibilities for innovation and discovery. Combining biology and engineering allows us to make direct comparisons of different biologic designs and test them with subtle alterations to optimize performance and develop new approaches.

Robotic devices are a means of understanding how locomotor forces can be manipulated in aquatic propulsion. These studies help inform our understanding of biophysical phenomena, such as how thrust is created by multifin coordination, hydrodynamic interactions between dorsal and caudal fins, and how the flexibility of the propulsive surface affects the speed and efficiency of locomotion. Previous studies have studied a robotic model of the pectoral fin and used a flapping foil robotic device that models dorsal–caudal fin interactions, allowing investigation of the propulsive properties of flexible foils (Lauder et al., 2007).

The bluegill sunfish has been of particular interest as a prototype for a number of robotic studies based at MIT (Bio-Instrumentation Systems Laboratory) and Harvard University (Lauder Laboratory). Ian Hunter and James Tangorra of MIT have been working with the Lauder laboratory to develop a protoype robotic fin based on the bluegill sunfish pectoral fin (See Figure 3).

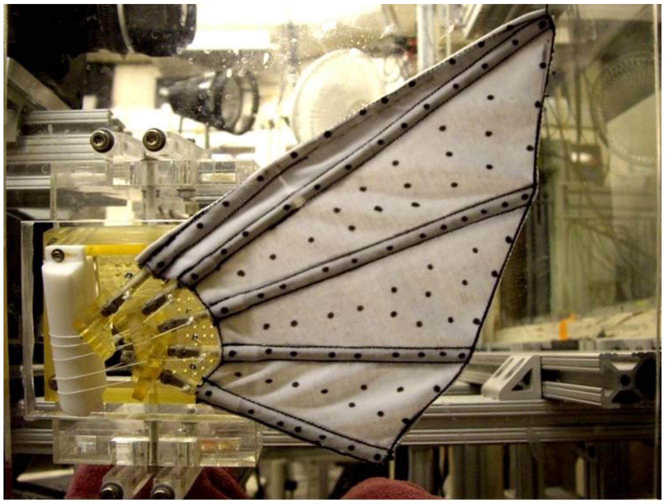

Figure 3. Robotic pectoral fin. A prototype fin developed in the Tangorra (Drexel University) and Lauder laboratories (Harvard University) based on the bluegill sunfish pectoral fin (Photograph taken in Lauder laboratory, Cambridge MA 2015).

One of the interesting potential applications of my thesis research is the ability to utilize our understanding of bluegill sunfish biomechanics to further improve Autonomous Undersea Vehicle (AUV) design in ways that exceed human-engineered systems and better mimic the performance of biological systems. A bio-inspired AUV with fish-like fins could also create fin movements that are biologically impossible, and hence generate swimming performance that is better than biological systems. For example, uncoupling the motion of the dorsal and anal fin from that of the caudal fin (Lauder et al., 2007) which fish cannot do, would allow new types of maneuvering performance. These types of innovations would allow AUV's to take lessons learned from the natural world and improve upon natural designs by optimizing the principles of biomechanics.

Chapter II

Materials and Methods

This section highlights the various aspects of my experimental design. I will begin by describing the fish used for this investigation. Next, I explain the horizontal obstacle construction. Thirdly, I will explain how I collect and analyze the data regarding fish biomechanics. And finally, I list the specifications by which each experiment was conducted.

Fish

For this experiment, bluegill sunfish, *Lepomis macrochirus,* Rafinesque (Fig. 1) were used. Fish were collected locally in Concord, MA and are maintained in lab settings at room temperature (~20C). Four fish (bluegill BG-A,BG-B,BG-C and BG-D) of similar size (17.5 ±0.08 cm total length, TL, mean ± s.e.m.), were used for kinematic study of maneuvering under horizontal obstacles. Each fish was maintained in its own individual aquarium containing 40L of fluid and fish were fed three times per week. The day before the experiment, fish were transported into a recirculating flow tank for acclimatization to the test environment. While in the flow tank, fish were fed daily throughout the experiment and were handled ethically according to the Harvard University Institutional Animal Care and Use Committee guidelines, protocol 20-03. Four fish were used for this experiment to account for individual variability. The length (tip of the nose to the center of the caudal fin) and body height (base of the dorsal fin to the base of the pelvic fin) of each fish was measured while fish were swimming in the tank.

Horizontal Obstacle

A single, dark opaque horizontal obstacle was used for the experiment (Figure 4). It was constructed from a 26 cm long black acrylic tube, 8.7 cm in diameter wide, and 34 cm in length (McMaster-Carr, Princeton, NJ, USA, part#8532#K17). The obstacle was designed in a way that when the obstacle was lowered vertically to the bottom of the flow tank, it separated the flow tank in half. I lowered the obstacle to two different heights: half-body height, approximately 2 cm above the bottom, and full-body height, approximately 4 cm above the bottom, and recorded how the fish moved underneath it with multiple high-speed video system. A paddle was used to coax the fish to swim under the obstacle. Full-body height was measured based on the height of the fish along the y-axis. Half-body height was calculated as one-half of this length along the y-axis. The obstacle was fixed once the fish had entered the tank. The area under the obstacle was sufficient to complete a single fin beat. This was the first study of its kind employing a horizontal obstacle.

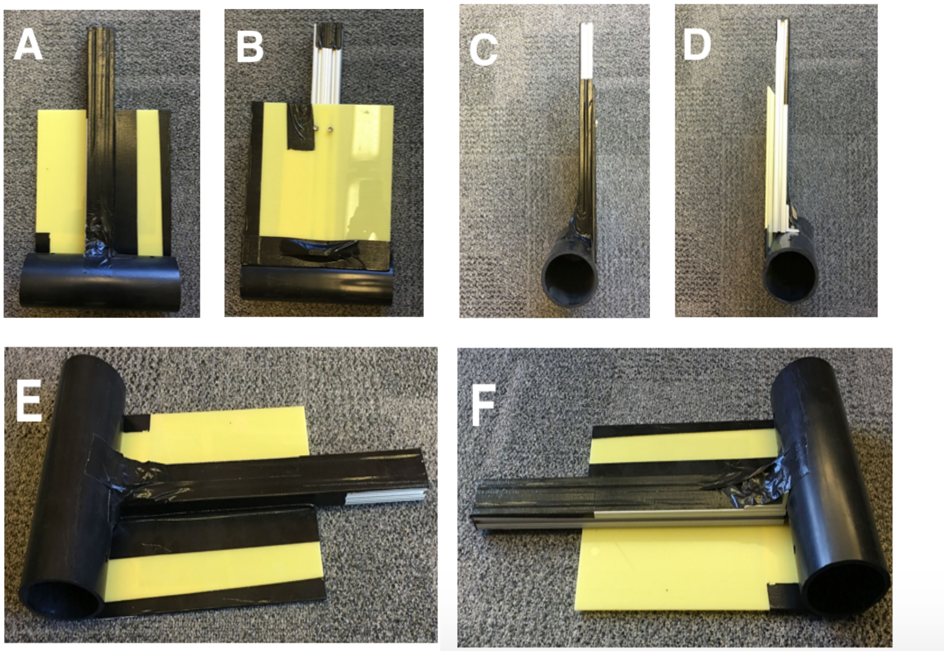

Figure 4. Horizontal obstacle assembly. A single, dark opaque horizontal obstacle constructed with a 26 cm long black acrylic tube, 8.7 cm in diameter wide, and 34 cm in length (McMaster-Carr, Princeton, NJ, USA, part#8532#K17). (A) and (B) represent front and back views of the obstacle. (C) and (D) represent upright vertical side views of the obstacle left and right respectively. (E) and (F) represent horizontal side views of the obstacle.

Kinematic Protocol

Fish were recorded while swimming in a 600 L flow tank with dimensions 26x26x80 cm. The lateral, posterior, and ventral views of the fish were recorded simultaneously using three high-speed digital video cameras (Photron, USA, San Diego, CA, USA, Figure 5).

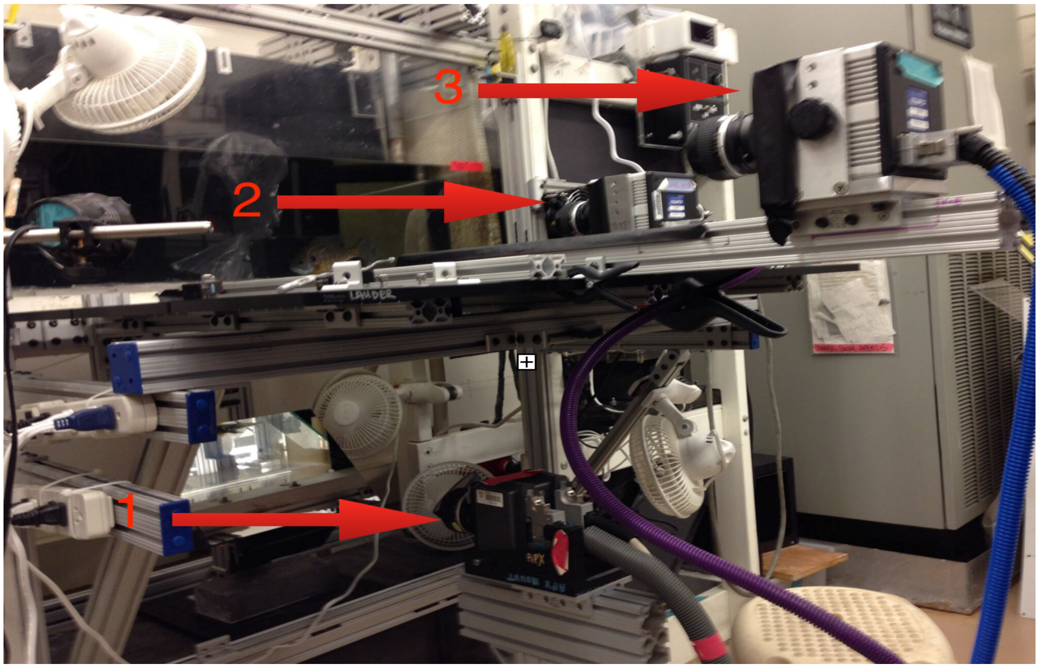

Figure 5. High speed cameras used during the experiment. Three high-speed digital video cameras (1), (2), and (3) (Photron, USA, San Diego, CA, USA) used to simultaneously to record fish when they swim under the obstacle. Posterior and ventral views were filmed through mirrors with camera (1) and (2). The side view was filmed with camera (3). Fish were filmed while swimming at 250 frames s-1 (with 1024x1024 pixel resolution)

The three different camera angles (posterior, lateral, and ventral views) used to capture these dimensions are displayed in Figure 6. Posterior and ventral views were filmed through mirrors. Fish were filmed while swimming under the vertical obstacle at 250 frames s-1 (with 1024x1024 pixel resolution). Each fish was recorded for 10-20 trials as it swam under the obstacle until adequate views were achieved with digital photography.

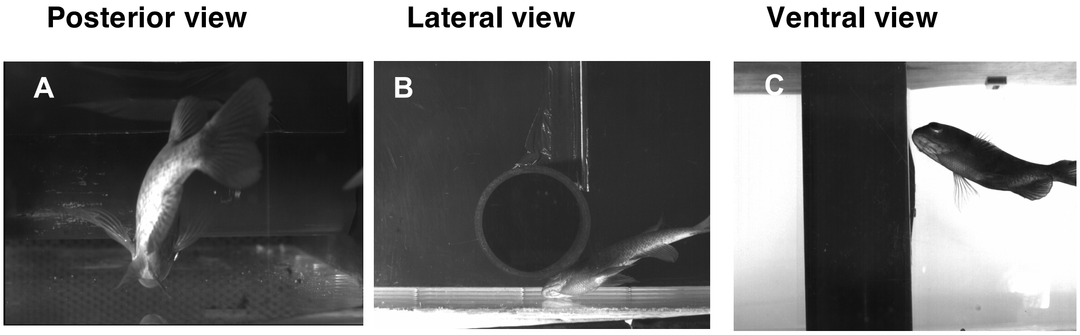

Figure 6. Posterior, lateral, and ventral images captured through high-speed digital photography. The photographs above represent images of the same fish from three different camera angles.

Data Analysis

Lateral, posterior and ventral recordings of the fish were analyzed. Videos were chosen such that swimming under the vertical obstacle was straight and in clear view of the caudal fin in all lateral, posterior and ventral views. The recording was stopped via trigger-signal attached to the cameras once the fish completed the full length of the obstacle. The videos were calibrated in lateral, posterior and ventral order and digitized using software written by Ty Hedrick (Hedrick, 2008) in MATLAB (MathWork, Natick, MA, USA). Lateral, posterior and ventral recordings of the fish were analyzed.

For the kinematic analysis, 30 points were digitized on the body of each fish as depicted in Figure 7: (1) dorsal fin at the base of the 1st ray from the beginning, (2) anal fin at the at the base of the 4th fin ray from the beginning, (3) tip of nose, (4) end of obstacle, (5) beginning of obstacle (6) right pectoral fin at the bottom lower base, (7) right pectoral fin at the tip of the 3rd fin ray (8) left pectoral fin at the bottom lower base, (9) left pectoral fin at the tip of the 3rd fin ray, (10) caudal fin at the tip of middle fin ray (fork), (11) dorsal fin at the tip of the 4th ray from the begging (12) anal fin at the tip of the 4th ray from the begging, (13) dorsal fin at the base of the 4th ray from the end, (14) dorsal fin at the tip of the 4th ray from the end, (15) caudal fin at the base of middle fin ray, (16) right base of the pelvic fin, (17) right tip of the pelvic fin (18) left base of pelvic fin, (19) left tip of pelvic fin, (20) anal fin at the base of the 4th ray from the end (21) anal fin at the tip of the 4th ray from the end, (22) caudal fin at the dorsal tip, (23) caudal fin at ventral tip, (24) center of mass, (25) left pectoral fin at the middle fin of the 6th fin ray, (26) left pectoral fin at the shortest tip of the last fin ray, (27) left pectoral fin at the base of the shortest fin, (28) right pectoral fin at the middle fin of the 6th fin ray, (29) right pectoral fin at the shortest tip of the last fin ray, (30) right pectoral fin at the base of the shortest fin. Four different bluegill sunfish were studied and each fish completed 10-20 trials of swimming under the horizontal obstacle. All trials in which the fish completed swimming under the obstacle were analyzed in the study.

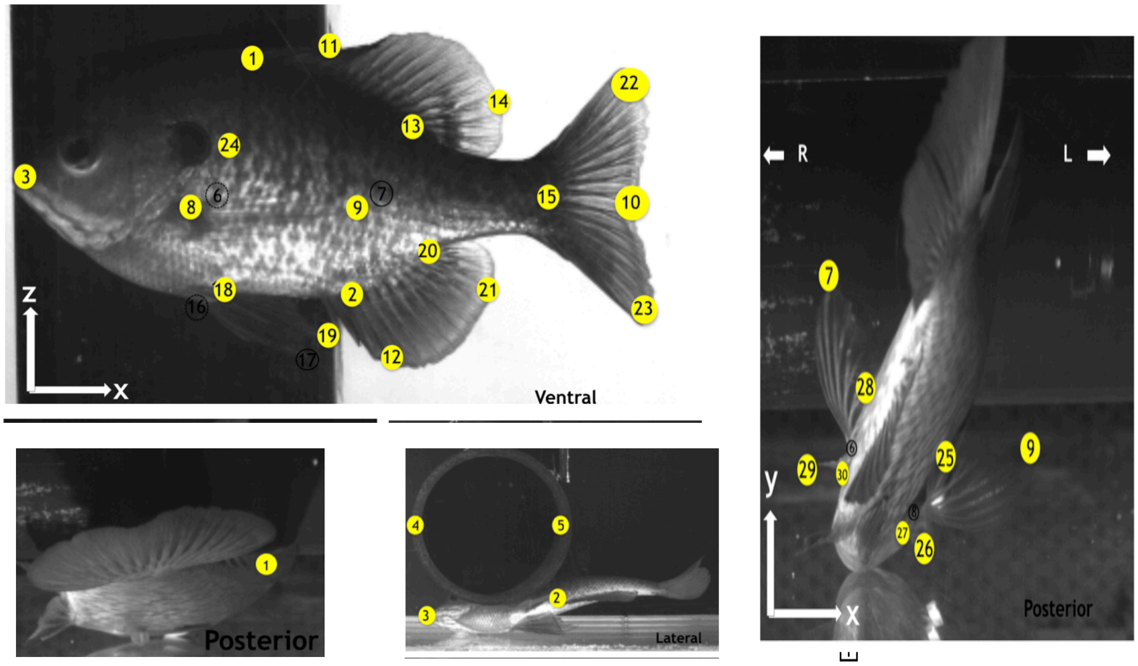

Figure. 7. Graphic representation of digitized points on the x, y, and z-axes. There are a total of 30 points, as listed in the text above.

Experiments

Figure 8 offers a schematic representation of the experimental design. Bluegill sunfish A (BG-A) measured a body height of 6 cm and 5 video recordings were performed at obstacle height of 6 cm. The obstacle was then lowered to a half-body height of 3.5 cm and 5 additional trials were performed. Bluegill sunfish B (BG-B) measured a body height of 7.4 cm and 13 trials were performed at full body height of 7.4 cm. The horizontal obstacle was then lowered to a half-body height of 3.7 cm and 7 additional trials were performed. Bluegill sunfish C (BG-C) measured a body height of 6.3 cm and 6 trials were performed. The obstacle was then lowered to a half-body height of 3.15 cm and 8 additional trials were performed. Bluegill sunfish D (BG-D) measured a body height of 5 cm and 10 trials were performed at full length of 5 cm. The obstacle was then lowered to a half-body height of 2.5 cm and 5 additional trials were performed. All four blue gill sunfish went through both obstacle heights without difficulty.

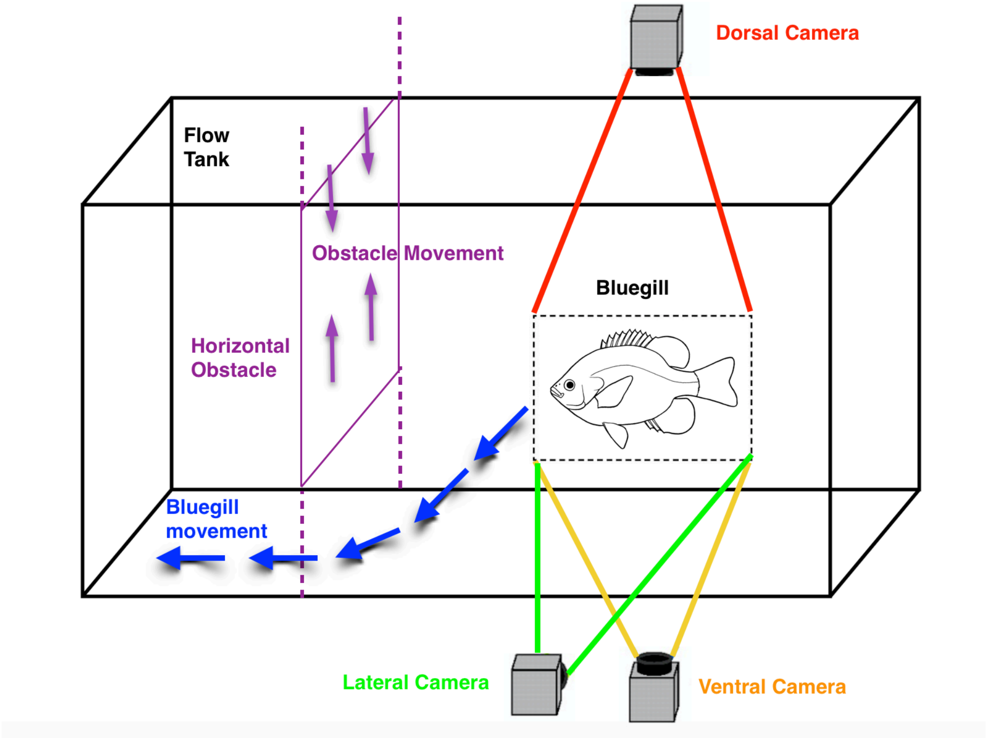

Figure 8. Schematic diagram of the experimental design. Flow tank with bluegill sunfish swimming in a static environment. A horizontal obstacle placed near the bottom of the flow tank forced fish to maneuver from one side of the tank to the other. Three synchronized high-speed digital cameras capture dorsal, lateral and ventral views of fish swimming under the obstacle.

Chapter III

Results

The first part of the results chapter describes the kinematics of blue gill sunfish based on body kinematics. The second part of the chapter focuses on fin kinematics including multifin control and complex fin movements like pectoral fin cupping.

Body Kinematics

Swimming under the obstacle involved three major phases of movement: rolling, propelling, and unrolling. I will first describe my observations of the blue gill sunfish's body movements and then discuss the kinematic analysis performed to analyze these movements.

Phases of Movement

Prior to the fish initiating its roll, the fish adjusted its pitch downwards until the nose or mouth of the fish made contact with the glass floor of the tank. As the fish tilted its pitch downwards, there were small adjustments in roll. Once the fish touched the tank floor with its body, this initiated a rapid rolling motion. Rolling involved multifin control, primarily driven by pectoral fin movements described as "cupping" in the section below. While the pectoral fins were symmetrically beating in a cupping movement, the dorsal and anal fins opposed each other, moving to opposite sides to create a torque along the long axis of the fish and further assisting in the rolling movement. The pelvic fins adopted a consistent kinematic pattern with an asymmetric shape that assisted in the rolling process. When rolling to the left, the right pelvic fin extended and the left pelvic folded. The opposite was observed when the fish was rolling to the right. The caudal fin also adopted an asymmetric "S" shape during this initial phase of rolling in coordination with the other fin movements to further contribute to the torque in the fish's body that assisted in rolling. There was a difference in the caudal fin asymmetry depending on the speed of the roll. During a slow roll, there was less asymmetry of the caudal fin. However, with faster rolls, there was greater asymmetry in the tail movements with increased trailing edge asymmetry to assist in rapid torque.

Once the fish had sufficiently rolled to a position that it could fit underneath the obstacle, the fish entered the second phase of propelling under the obstacle. The pectoral fins contracted and tucked into the sides of the fish, minimizing drag forces. The propulsion of the fish through the obstacle was driven by coordinated undulation of the body, flapping of the caudal fin, along with low-amplitude flapping of the dorsal, anal, and pectoral fins. The pectoral fins and the body of the fish made numerous contacts with the obstacle and the glass floor of the tank as it traversed the horizontal slit.

Once the fish's body had crossed the horizontal obstacle, the fish began to unroll. Primarily driven by the pectoral fins, the cupping movement resumed in order to rotate the fish back to its original position. Dorsal and anal fins moved in opposite and coordinated directions to create a torque that drove this rotation, further assisted by the

"S" shape of the caudal fin. Analysis of the unrolling phase was limited by the camera views captured in this study.

Kinematic Analysis

Three-dimensional movements corresponding to adjustments in body pitch, roll, and yaw were analyzed as the fish swam under the horizontal obstacle. Each of these dimensions is depicted in a schematic diagram displayed in Figure 9.

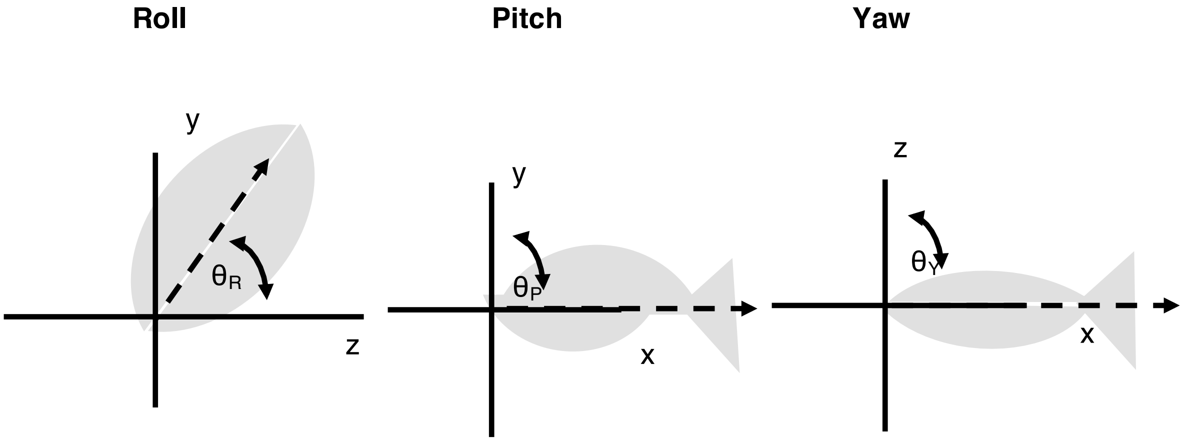

Figure 9. Schematic diagram of roll, pitch, and yaw. The diagrams depict the angles used to calculate A) roll (θ_R), B) pitch (θ_P), and C) yaw (θ_y) in two-dimensional space.

Body kinematics of fish were analyzed by following digitized points in space over a distinct series of points in time. Points in time were standardized across all fish and are as follows: T1 represents the point along the x axis at which the nose of the fish lines up with a set point at the beginning of the frame prior to the obstacle. T2 represents the point at which the nose of the fish lines up with the edge of the obstacle. T3 represents the point at which the base of the dorsal fin meets the edge of the obstacle. T4 represents the point at which the nose of the fish begins to exit the obstacle. T5 represents the point when the base of the dorsal fin leaves the obstacle. T6 represents the point when the base of the anal fin leaves the obstacle.

As the fish approached the obstacle, its body roll angle was adjusted to pass under the horizontal obstacle and swim sideways. After clearing the obstacle, the body roll angle returned to its upright position through a process called unrolling. Table 1 demonstrates the body roll angle of fish passing through the horizontal obstacle at discreet periods in time. Trials were conducted at full and half body heights.

Table 1. Body roll angle (in degrees) over a series of points in time.

	Points in Time					
Obstacle height	T1	T2	T3	T4	T5	T6
6 cm	85.4	79.2	-	-	55.4	60.8
	69.7	73	65.1	41.4	45.4	55.8
	54.7	44.1	32.3	29.5	33.1	36.8
	83.6	76.3	57	51.6	54	60.4
3.5 cm	64	71.6	45.3	15.7	30.8	41.6
	72.2	41.9	21.8	21	26.7	33.2
	72.5	43.1	21.6	16.3	26.2	42.1
	56.5	40.5	24.5	23.8	30.6	36.2
	82.6	52.9	20.8	21.6	34.5	49.0

Note. Obstacle height represents the distance to which the horizontal obstacle was raised. These angles were derived from the series of trials conducted with Fish BG-A at two obstacle heights.

At both obstacle heights, the body roll angle decreased from T1 to T4, the point at which the nose begins to exit this obstacle, corresponding to rolling motion (Table 1). The body roll angle increased from T5 to T6 during the unrolling motion. While the general trend of body rolling was comparable between fish swimming under the obstacle at the height of 6 cm vs. 3.5 cm, there were differences in the degree of rolling and unrolling observed. The initial body roll angle was comparable for all fish regardless of obstacle height, however the maximum roll angle seen at T4 differed significantly in the two groups.

The dynamic changes in body roll angle are depicted in Figure 10. Fish swimming under the full-body height obstacle maximally rotated at T4 to an average of 40 degrees from the glass tank floor. In comparison, fish swimming in the half-body height obstacle on average rotated to a position of 20 degrees from the glass tank floor at T4. Thus, as the obstacle height roughly doubled in size, the body roll angle required to pass under the obstacle also doubled.

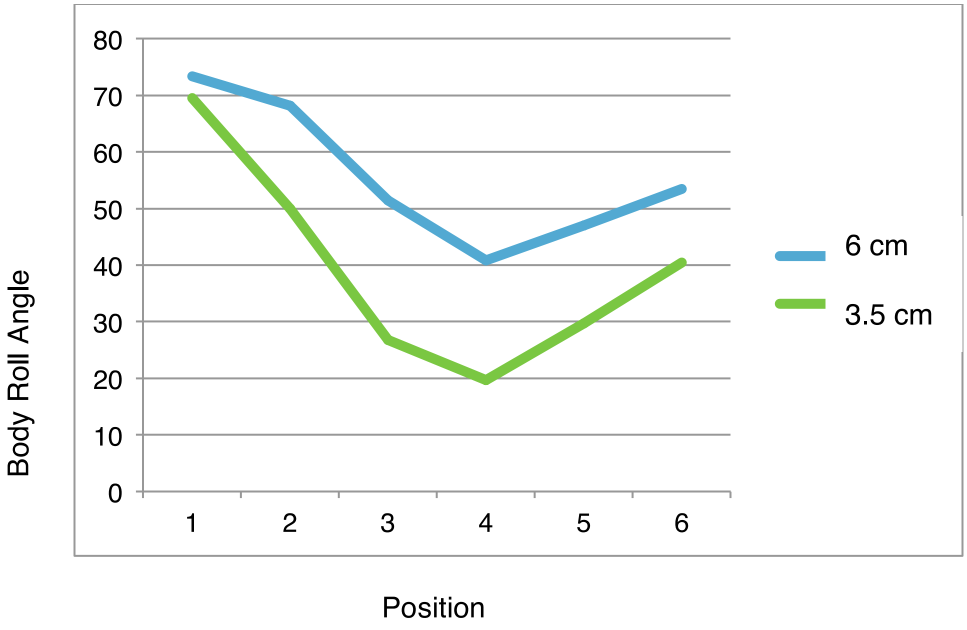

Figure 10. Changes in the fish body roll angle over time. These numbers represent an average of all trials conducted with bluegill A. See text corresponding to table 1 for an explanation of Positions 1-6 (T1-T6).

The angles depicted in Table 2 represent the average angles of roll, pitch, and yaw at each point in time as the fish passes under the obstacle. The roll of the fish follows a consistent trend during swimming past the horizontal obstacle. The fish begins its swim with a 73 degree angle and rotates its body away from vertical until the point at which its nose begins to exit the obstacle. This is its maximum roll and on average is 24.9 degrees. The fish then regains its upright position as it unrolls past the horizontal obstacle.

Table 2. Average rotational angles for roll, pitch, and yaw.

	T1	T2	T3	T4	T5	T6
Roll	73.0	62.5	31.0	24.9	35.1	47.5
Pitch	35.1	47.5	64.88	78.01	-36.60	35.1
Yaw	10.89	12.13	12.28	10.48	6.76	9.96

Note. This represents an average of all BG-A trials combining both full-body and half-body heights. Numbers are in degrees with respect to the floor of the tank.

The pitch of the fish swimming under the obstacle demonstrated a gradual increase as the nose of the fish descended to the bottom of the tank in order to swim under the tank. The fish propelled downwards and the nose of the fish consistently made contact with the floor of the tank

Table 3 represents the change in angle in three dimensions as the fish passes under the obstacle. Of most significance, the rate of rolling changes significantly as the fish moves under the obstacle. The rate of rolling increases from T1-T2 (64.88 deg/s) to T2-T4 (78.01 deg/s), demonstrating that the fish rolls more rapidly as it approaches the obstacle. The unrolling rate is depicted as a negative rate (T4-T6) and is significantly slower (-36.6 deg/sec) than the rolling rates. See the text corresponding to table 1 for an explanation of the Positions T1-T6.

Table 3. Average change in angle for roll, pitch, and yaw.

	RollRateT1-T3 (deg/sec)	RollRateT2-T4	RollRateT4-T6
Roll	64.88	78.01	-36.60
Pitch	6.35	1.51	-18.94
Yaw	-3.62	9.37	2.64

The pitch changes to a small degree initially until the nose or mouth of the fish has made contact with the floor, after which the pitch does not change as the fish moves past the obstacle. Once the body of the fish has past the obstacle, the fish readjusts its pitch in the upward direction, depicted as a negative value (-18.99 deg/sec).

Changes in yaw are generally minimal throughout the swimming process. These changes are most significant from the time between the nose of the fish entering the obstacle and exiting the obstacle during the fish employs an undulating pattern of locomotion known as body and caudal fin swimming.

Bluegill sunfish demonstrated different maneuvering patterns in comparing their movements between the full-height and half-height horizontal obstacle (Figures 11 and 12, respectively). The posterior view displayed in Figure 11 demonstrates the change in upright position as the fish moves through the full body height horizontal obstacle. The positions correspond to the following: (A) Fish right before it enters the horizontal obstacle (movie frame time (t)=291). (B) Fish nose lines up with the obstacle just before it enters the horizontal obstacle post (t=371). (C) Fish is under the horizontal obstacle and base of dorsal fin lines up with the edge of horizontal obstacle at its entrance (t=474). (D)

Fish is under the vertical obstacle and nose lines up with the obstacle as it exits the horizontal obstacle post (t=561). (E) Fish leaving the obstacle and base of dorsal fin lines up with horizontal obstacle post (t=681). This represents the minimum angle required for the fish to pass through the obstacle. (F) Fish has crossed horizontal obstacle and base of anal fin lines up with horizontal obstacle as it leaves it (t=771).

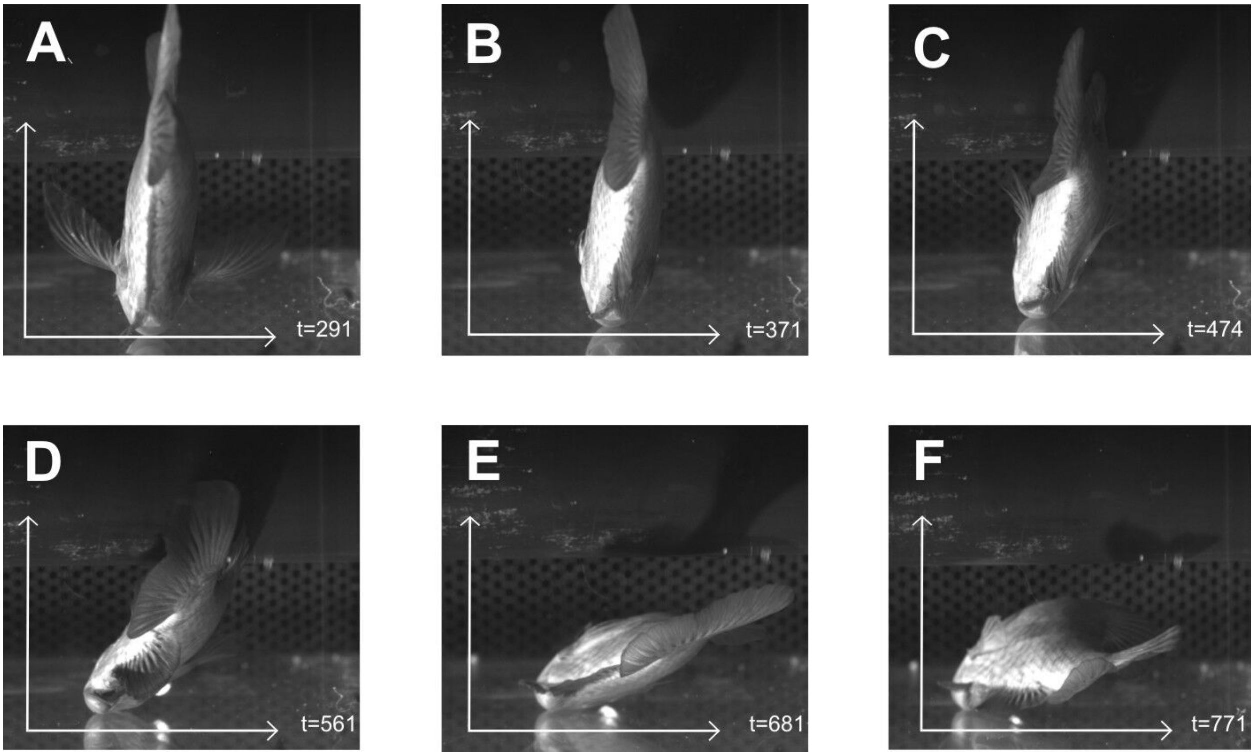

Figure 11**.** Posterior view of bluegill sunfish swimming under a horizontal obstacle.

In Figure 12, both lateral (A) and posterior (B) views depict the rotation of the fish about the x-axis in the rolling motion. The differences between fish swimming in the full-body height and half-body height obstacles can be seen when comparing the degree of maximum rotation (Figure 11E vs. Figure 12 A3, B3),

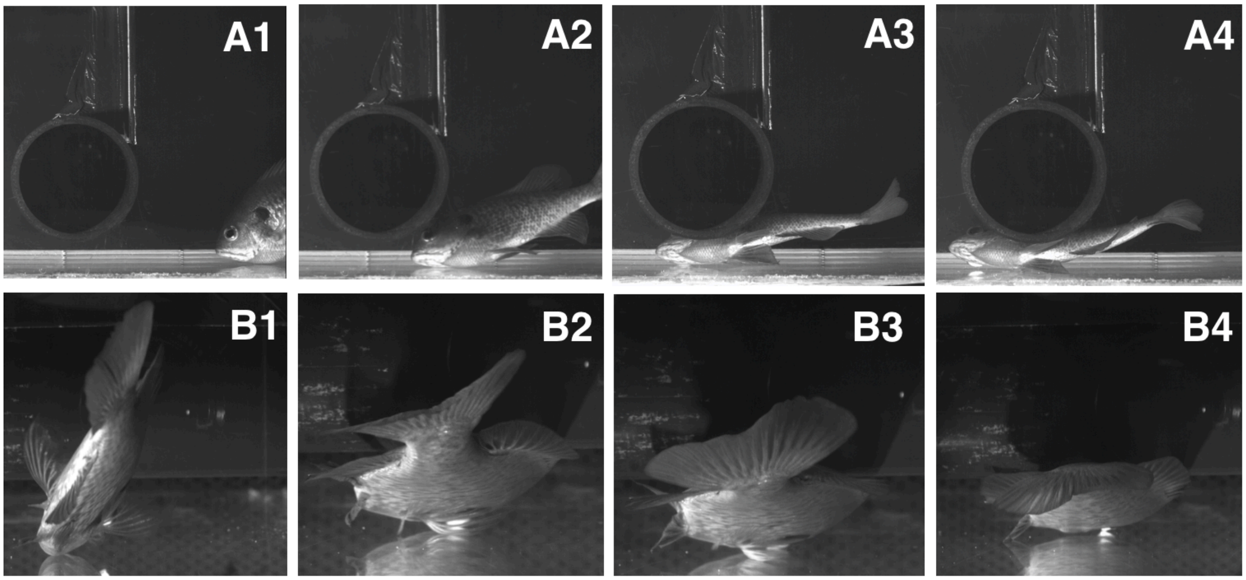

Figure 12. Lateral and posterior views of bluegill sunfish swimming under a horizontal obstacle at half-body height. from the bottom seen in both the lateral (A1-A4) and posterior (B1-B4) views. A3 and B3 depict the rotation of the fish required in order to pass through the obstacle sideways.

As the fish moved under the horizontal obstacle, its velocity changed over time. Using the nose of the fish as a reference point along the x-axis, displacement is graphed over time in Figure 13. Slope of the displacement curve represents the relative velocity. There was an observed increase in velocity as the fish traversed the obstacle. The initial velocity of ~75 mm/sec (blue line) was more than doubled to ~175 mm/sec as the fish approached and passed the obstacle (red line).

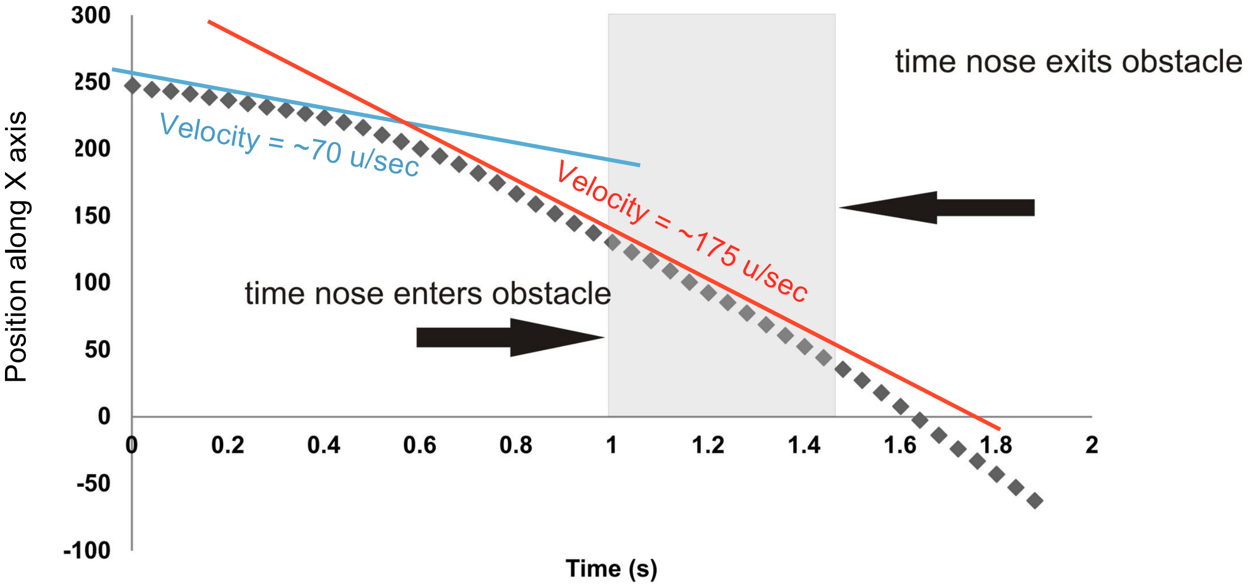

Figure 13**.** Velocity of the bluegill sunfish swimming under the horizontal obstacle. The position of the bluegill sunfish nose tip is noted as it moves through space along the x axis over time. The blue and red lines on the graph depict estimations of the change in position over time, which are approximations of relative velocity.

Fin Kinematics

This section will highlight my analysis of fin kinematics. First, I will characterize the nature and regulation of multifin control. I will then analyze the role of pectoral fin cupping during swimming under a horizontal obstacle.

Multifin control

Bluegill sunfish utilized all fins in a coordinated series of movements to navigate under the horizontal obstacle. The gait diagram for a fish swimming under a horizontal obstacle is depicted in Figure 14. Each panel represents one sequence of bluegill sunfish and each colored bar represents the duration of the fin beat cycle away from the body.

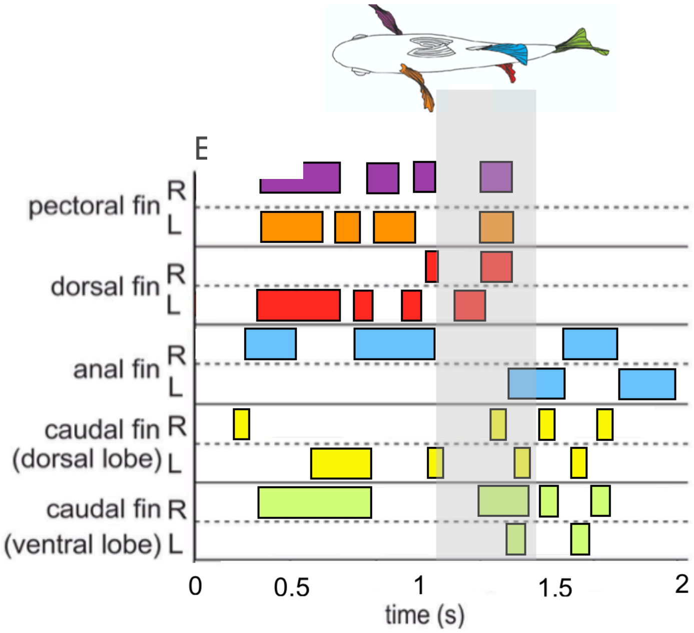

Figure 14. Gait diagram of forward swimming under a horizontal obstacle. The gray bar line represents the horizontal obstacle. Each color of the bar represents each different fin. Purple represents the right pectoral fin, orange represents the left pectoral fin, red represent the dorsal fin, blue represents the anal fin, yellow represents the dorsal lobe of the caudal fin and green represents the ventral lobe of caudal fin. BG-D trial 13 is depicted here as an example.

The rolling motion is achieved with multifin control to create a combination of thrust and drag forces. The left pectoral fin strokes precede the right fin strokes as the fish rolls toward the right. There is an increased frequency of pectoral fin movements as the fish enters and completes the roll, as well as enters and passes through the obstacle. The pectoral fin movement is known as “cupping” and is described below.

The dorsal fin makes predominantly leftward motions to create thrust that leads to rightward rotational motion. The anal fin has a long rightward stroke just prior to entering the horizontal obstacle. The fin is extended outward to create drag as the fish rolls, functioning as a rudder. To propel under the obstacle, the fish utilizes low-amplitude strokes of all fins.

The caudal fin motion is best understood by dividing it along the y-axis between its dorsal and ventral lobes. Initially these lobes work independently to create thrust and drag that achieve the rolling position. The dorsal lobe has a predominantly leftward thrust to create sufficient force to roll the fish in a rightward direction. Meanwhile the ventral lobe functions as a rudder with a long rightward stroke around 0.5 seconds to contribute to this rightward torque. Once the fish has completed the roll, the dorsal and ventral lobes of the caudal fins work in unison in a low-amplitude undulating pattern to propel the fish past the obstacle. At roughly 1 second, the fish has completed the roll and the caudal fin adopts a fast rhythmic pattern (~4-6 beats/sec) to propel the fish under the horizontal obstacle.

Pectoral Fin Cupping

Fish consistently used pectoral fins to rotate their bodies from the upright to lateral position, or roll along the x-axis. The pectoral fin strokes were the primary locomotive forces in moving the position of the fish in order to roll and pass through the horizontal obstacle. The pectoral fin motion observed in maneuvering past the horizontal obstacle was a complex, coordinated pattern described as “cupping” in Figure 15. The yellow lines represent the contortions of the pectoral fin to create leading edge vortices in both the upper and lower fin edges, which characterize the pectoral fin cupping motion. This motion involves large bending deformations throughout the fin beat cycle, which are highlighted by the yellow lines in Figure 14. Arrows represent the directions in which the pectoral fins are moving. Pectoral fin outlines (in yellow) correspond to the position of pectoral fins at a specific time. Abduction of the pectoral fin involves a cupped sweeping motion best seen in Frames B, C, and F while adduction involves a paddling motion during adduction seen in Frames D and G. The time it took this individual bluegill sunfish to go under the obstacle (A) to (L) was 0.670 seconds. This is consistent with previously described pectoral fin cupping motions described in blue gill sunfish (Tangorra et al., 2009).

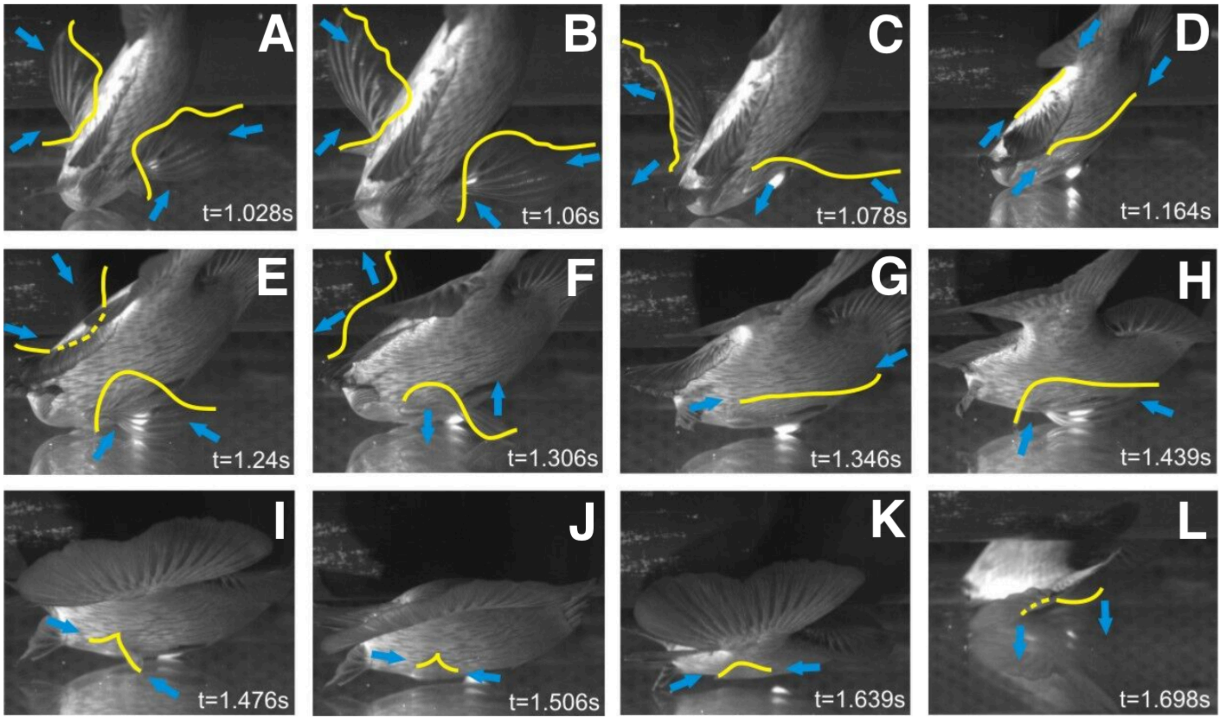

Figure 15. Pectoral fin cupping to maneuver through a horizontal obstacle. From time (t=1.028s), the bluegill sunfish approaches the horizontal obstacle and then passes under the obstacle and out the other side (t=1.698s).

Figure 16 demonstrates the change in position of the left pectoral tip along the z-axis as the bluegill sunfish passed under the obstacle. In the shaded gray area of Figure 15, each rapid upward feature on the graph represents a single pectoral fin beat as the sunfish achieves a rolling motion and passes through the horizontal obstacle. At the beginning of the obstacle, the pectoral fin had the largest stroke, followed by 1-2 additional strokes observed consistently across all trials. Figures 15 and 16 depict the movements of bluegill D under the horizontal obstacle in trials 2 and 12, respectively.

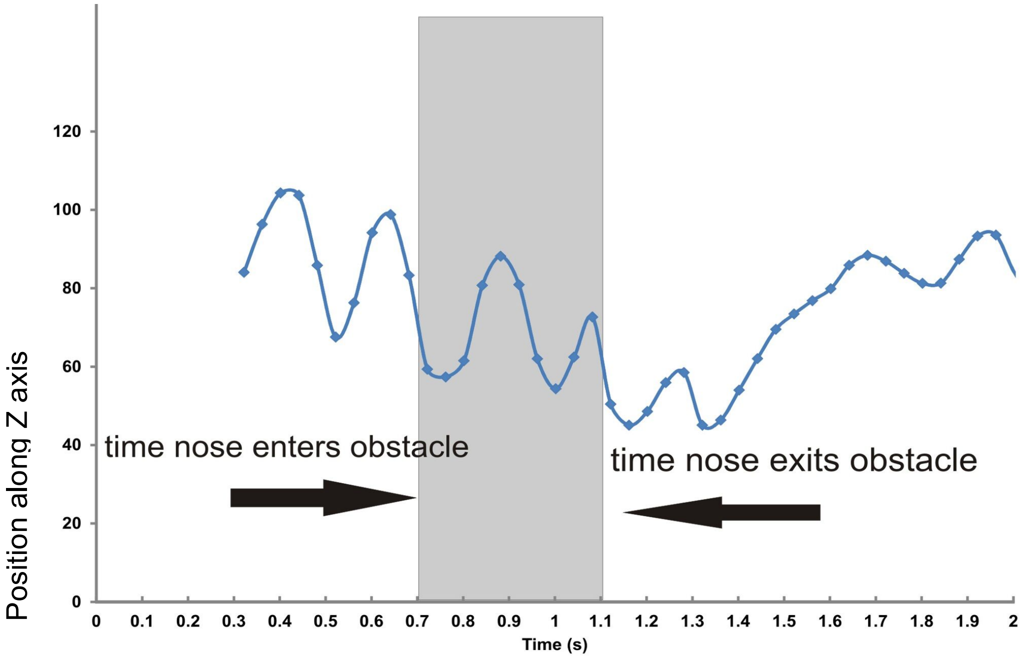

Figure 16. Pectoral fin movements while swimming under the horizontal obstacle (BG-D, trial 2). The graph represents the position of the left pectoral tip along the Z axis as the blue gill sunfish swims through the horizontal obstacle over time. This graph depicts the movements of fish BG-D during the second trial as an example.

Each figure demonstrates the low-amplitude, high frequency flapping of pectoral fins that rotates this fish from upright swimming to sideways swimming. On average, 2-3 pectoral fin movements were observed while the fish passed under the obstacle, during which the fish was primarily utilizing body and caudal fin swimming. The graph in Figure 17 represents the movements of Fish D during trial 12 as an example compared to the movements of the same fish during trial 2 in Figure 16.

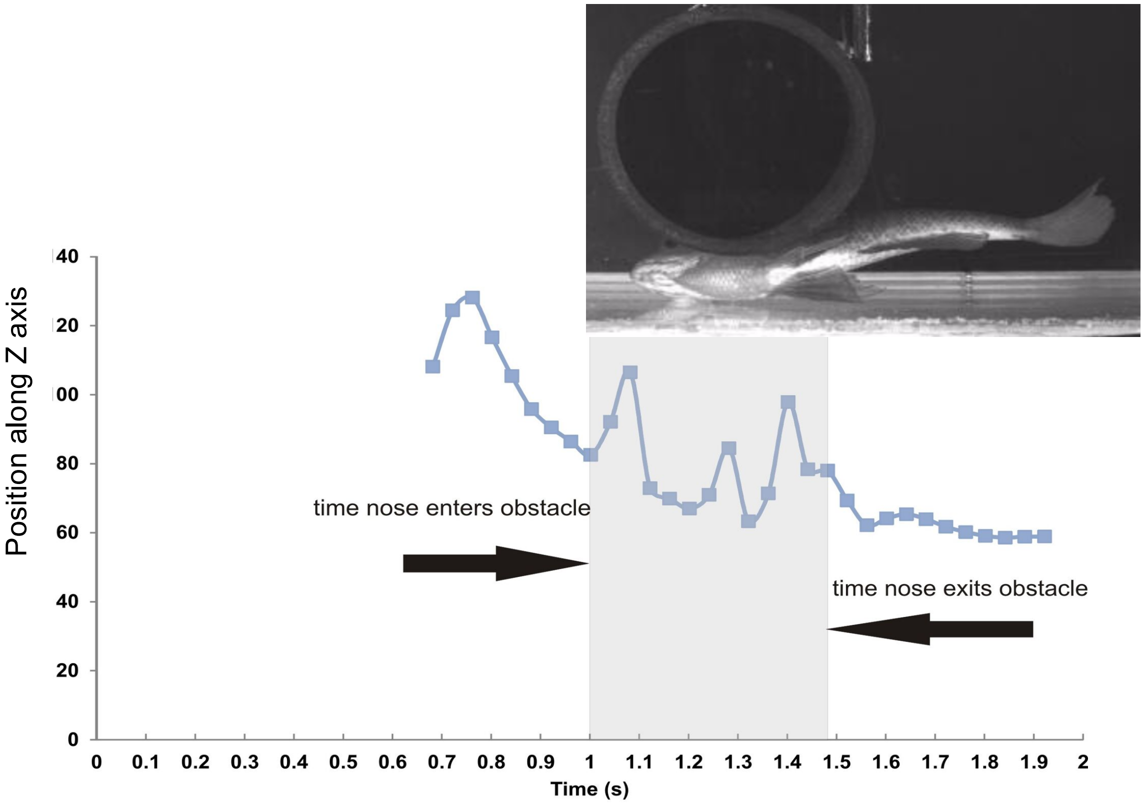

Figure 17. Pectoral fin movements while swimming under the horizontal obstacle (BG-D, trial 12). This represents fish BG-D swimming under the obstacle during trial 12. The image depicts one video frame at the point in time when the nose of the bluegill sunfish has exited the obstacle.

Results Summary

The focus of this study was to understand body kinematics and multifin control of bluegill sunfish swimming under a horizontal obstacle. Analysis of high-speed videography revealed a series of coordinated movements of all fins to achieve rolling, propulsion under the horizontal obstacle, and unrolling. While all fins were utilized to adjust pitch, roll, and yaw, pectoral fins were the primary locomotive fins in creating rolling and unrolling via a complex fin motion described as cupping. Body and caudal fin swimming drove propulsion under the horizontal obstacle during sideways swimming. During the rolling and propelling process, the blue gill sunfish increased its velocity in transitioning from slow-speed median and paired fin swimming driven by pectoral fins to propulsion under the obstacle using body and caudal fin swimming.

Chapter IV

Discussion

This study examined the kinematics of forward swimming of bluegill sunfish through a horizontal obstacle. I will first discuss the findings of my current investigation in the context of prior studies on blue gill sunfish locomotion. Next, I will highlight some of the key findings from this investigation with regard to complex fin movements and maneuverability. I go on to demonstrate how this knowledge may form the basis for new biorobotic design. Finally, I will consider some of the limitations of this study and areas for future investigation.

Comparing Gaits of Upright, Sideways, and Reverse, Non-linear Swimming

The data from our previous work on the kinematics of normal forward and backward swimming with and without an obstacle demonstrates very different patterns of swimming in each of the five conditions (Figure 17). This highlights the importance of fin regulation in order to maintain fish dynamic stability in all conditions. There are a variety of ways to maintain stability of the center of mass by various alterations in fin surface, beat frequency, and coordination with other fins. Figure 18 summarizes the work of the Lauder laboratory over several different experiments in comparison to the current investigation.

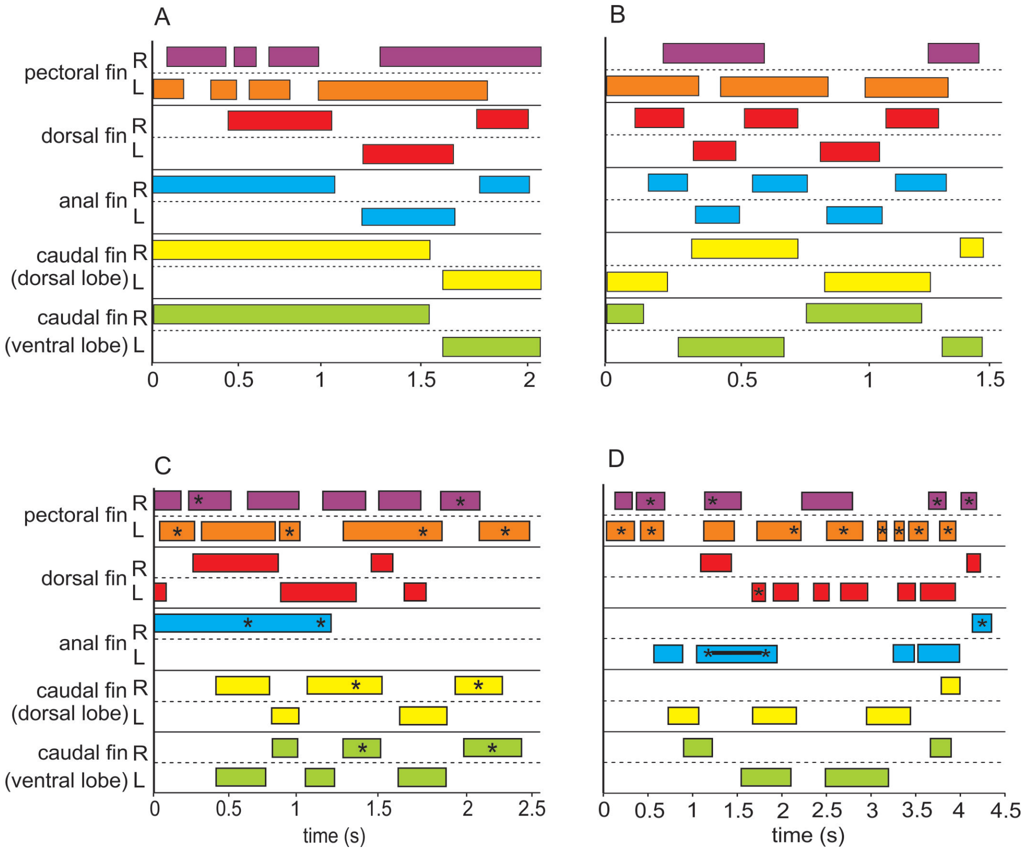

Figure 18. Gait diagram: comparison of kinematic patterns of bluegill sunfish swimming. A represents forward normal swimming, B represents backwards normal swimming, C represents forward swimming through a, D represents backward swimming through an obstacle course. See Figure 13 for details on colors corresponding to fins.

Forward swimming in the upright position appears to be the most efficient and physiologic form of movement. Panel A represents forward swimming of bluegill sunfish normally without an obstacle. The y-axis represents pectoral, dorsal, anal and caudal fins and the x-axis represents time in seconds. Each bar represents a full fin beat from the start to the end of the sequence. The total time it took the fish to swim through the flow tank was about 2 seconds. In forward swimming, the dorsal, caudal, and anal fins were all working in phase with each other with respect to right and left strokes aligning in time. Note that the dorsal and ventral aspects of the caudal fin utilize long strokes in phase with each other. Pectoral fins beat with the most frequency alternating in time throughout the sequence.

Backward swimming involved asynchronous pectoral fin movements with left and right fins abducted and adducted, respectively, in an alternating pattern, along with synchronized median fin activity of dorsal, anal and, caudal fins. Panel B represents bluegill swimming backwards without obstacles. Each bar as in A represents the full duration of a fin beat from the beginning of the sequence till the end. It took 1.5 seconds to swim the entire sequence. The dorsal and anal fins continue to beat in phase with shorter strokes, averaging 4 Hz, compared to 1-1.5 Hz in forward swimming. In comparison to forward swimming, the caudal fin's ventral and dorsal components alternate in sequence between right and left strokes. Unlike forward swimming, which utilizes primarily in phase motions of multifin control and is mostly propelled by pectoral fins, backwards swimming in blue gill sunfish uses alternating motions of pectoral, dorsal, anal, and caudal fins (Flammang and Lauder, 2016).

A combination of forward and backward swimming maneuvers was utilized to navigate through an obstacle course. Panel C represents bluegill sunfish forward swimming through an obstacle course. Y-axes as in A and B represent all fins involved in maneuverability and the x-axis represents the time it took to swim backwards through the entire flowtank. The stars represent when the fins touch an obstacle. The gait diagram in Panel C demonstrates numerous short, high frequency strokes across all fins to navigate through the obstacle course. Pectoral, anal, and caudal fins made contact with the obstacle as a means of navigating and maneuvering through the obstacle course. Pectoral fins, which primarily utilized quick, alternating strokes, made most frequent contact with the obstacles. This is consistent with previous studies demonstrating that pectoral fins are dominant locomotor forces at slow speeds in blue gill sunfish (Flammang and Lauder, 2016). The lobes of the caudal fin demonstrated both in phase and out of phase motion as the fish maneuvered through the obstacle.

Panel D demonstrates the gait diagram of blue gill sunfish swimming backward through an obstacle course. The gait diagram is in many ways similar to forward swimming through an obstacle course given the pectoral fins utilize rapid strokes with frequent touches of obstacles to navigate the obstacle. The time to cross the obstacles was longer than in forward swimming through the obstacle course. Pectoral fins were used more predominantly and in open areas between the obstacles. The caudal fin lobes also demonstrate a combination of in phase and out of phase movements through the obstacle array. Tapping of fins was observed in pectoral, anal, and dorsal fins. Fish used pectoral fins more often than median fins to tap objects. The number of pectoral fin taps in backwards swimming was significantly different from the number of taps in forward swimming (Kalionzes et al., in preparation).

The results of the current study of blue gill sunfish swimming under a horizontal obstacle are previously noted in Figure 14. Bluegill sunfish utilized a combination of synchronous and asynchronous fin activity to pass under the horizontal obstacle. Rolling motion required asynchronous fin activity, such as opposing dorsal and anal fin movements, to achieve non-zero rotational torque along the x-axis. Once the rolling motion was complete, the bluegill sunfish used synchronous activity of all fins in sideways body and caudal fin swimming.

Bluegill sunfish are designed for efficient maneuverability by minimizing angular momentum by utilizing all of their fins and their deep-bodied shape. In open spaces, they use median and paired fins swimming in a synchronous pattern driven by its pectoral fins at slow speeds. Blue gill sunfish revert to body and caudal fin swimming in narrow spaces such as the horizontal obstacle in this study, a phenomenon that has been previously observed in various fish species (Schrank et al., 1999).

Comparing the durations noted in the gait diagrams across various scenarios in Figure 18, some general trends were observed. Backward swimming is less efficient than both forward upright swimming and sideways swimming. Swimming backward is different from swimming forward because there were shorter durations of strokes and more fin cycles over time. Notable differences existed in upright and sideways swimming. Upright swimming was primarily driven by pectoral fin propulsion using median and paired fin swimming, while sideways swimming utilized body and caudal fin swimming. Despite these differences, there was comparable efficiency between these forms of swimming at the slow speeds observed in this study. Future studies must observe blue gill sunfish at faster speeds and over longer durations to capture differences in speed between upright and sideways swimming.

As the complexity of the obstacle array increased, from forward swimming to backward swimming through an obstacle course, the duration of time to complete the obstacle array also increased. This is consistent with the notion that atypical swimming patterns, such as swimming backwards or in a non-linear direction, would be less efficient. The most complex task, backwards swimming through an obstacle, had the shortest and fastest fin beats per excursion. These quick movements may enable the fish to make small corrections in order to maintain its stability and center of mass in complex movements such as moving in reverse and navigating around obstacles in a non-linear path.

Pectoral Fin Movements and Cupping

Rolling, or rotating about the x-axis, was the primary maneuver utilized to navigate under the horizontal obstacle in this study. Rolling of bluegill sunfish involved coordinated multifin control driven primarily by pectoral fin locomotion. In my observations, I noted complex changes in pectoral fin modulations to swim under the obstacle. The fish at times utilized up to 4 cupping motions to be able to make the necessary motion changes to maneuver under the obstacle. While this study focused on rolling maneuvers, previous studies on yawing maneuvers in various fish demonstrate that effective median and paired fin swimming depends on the integrated contribution of multiple propulsors (Schrank et al., 1999).

The pectoral fins of bluegill sunfish have multiple uses and can undergo complex conformational changes depending on the context. Pectoral fins are used as primary propulsors in slow-speed swimming, while also functioning as rudders used by fish to create drag or slow down the swimming speed, as evidenced by my experiment. They appear to be used for tactile sensation, perhaps via mechanoreceptors, as seen in the tapping of obstacles in previous experiments. Pectoral fins are known to be jointed and can reduce their surface area up to 30%. This investigation demonstrated how pectoral fins operate in the context of complex multifin control to navigate under the horizontal obstacle. This coordination is highly adaptive and offers significant insight into the hydrodynamics of fish locomotion.

Cupping of fish fins has been previously described in the literature and been found to be a highly effective means of generating force. The cupping motion of pectoral fins has been demonstrated to minimize lift forces generated by asymmetrical fin motions and increase thrust of the outstroke. Lauder and Madden suggest that cupping and bending motions of pectoral fins may help modulate both positive and negative lift forces during both outstroke and instroke, as the simultaneous up and down forces may minimize oscillations in center of mass (Lauder and Madden, 2007). Biorobotic models created by Tangorra and Lauder have demonstrated roughly 26% superior thrust created by the cupping motion compared to other fin movements, including flat, undulating, and rolling movements (Tangorra et al., 2009). A recent study using a biorobotic model comparing cupping fin motion to flat fin motion found a 78% increase in thrust force and 16% increase in thrust efficiency (Hu et al., 2016). These dramatic differences account for the primary role that pectoral fins play in rolling past the horizontal obstacle.

The kinematics of pectoral fin cupping has been well-described previously. Experimental fluid dynamic analysis of sunfish pectoral fin locomotion have shown that these fins generate thrust throughout the fin beat cycle, and that the upper and lower edges each produce distinct simultaneous leading edge vortices (Lauder, 2006). It has been proposed that the funneling motion of the vortices produced by the cupping motion caused an increase in fluidic velocity between the dorsal and ventral fin margins (Esposito et al., 2012). Pectoral fin thrust is produced throughout the fin beat cycle. This unique vortex structure may explain why cupping is able to produce higher thrust forces than other fin movements. The results of the current study further reinforce the prominent role of pectoral fin locomotion and cupping in complex maneuvering for bluegill sunfish.

This study demonstrated that fish roll only as much as they need to in order to pass under an obstacle. This was evidenced by the differences in rolling angles utilized by fish depending on whether they were passing under a full body height or half body height horizontal obstacle. This is consistent with the idea that rolling involves a deviation from the fish's typical body mechanics, altering its center of mass and the interaction with the multifin propulsion system. It suggests that sideways swimming is not preferable to normal forward swimming. Although there were no significant differences in the duration of time required to cross the obstacle.

Understanding Fin and Body Contact

The transition from slow-speed upright swimming driven by pectoral fins to sideways swimming via body and caudal fin movements involved complex, simultaneous alterations in the fish's pitch and roll that consistently involved the fish making contact with the glass tank floor and the horizontal obstacle. As the nose of the fish touched the bottom of the tank, it began to correct its pitch, initiate its roll, and transition to body and caudal fin swimming.

This was a consistently observed phenomenon in all fish in the current study and is consistent with our previous investigations on fin tapping. Our previous studies have observed tapping in all fins, including pectoral, anal, caudal, and dorsal fins. As the complexity of the array increased, the number of times that fins made contact with the obstacle also increased (see Figure 17). The frequency and duration of pectoral fin tapping was greatest amongst all fins which suggests the primacy of these fins in navigating complex environments. From our previous work on blue gill sunfish swimming backwards through obstacles, we speculated that fins may be used as mechanoreceptors that offer feedback to the fish about the surrounding environment (Kalionzes et al., in preparation). This study also may suggest that fin and body tapping may offer stability, maneuverability, and navigability to move through complex environments. Further investigation using biophysical tools such as electromyography and nerve conduction studies are necessary to understand the biofeedback achieved by tapping at the neuronal level.

Speed and Maneuverability Under a Horizontal Obstacle

The velocity of the fish swimming through the tank changed as fish navigated under the obstacle. One of the unexpected results of my experiment was the change in velocity that was observed as the fish swam under the horizontal obstacle. I hypothesized that the fish would slow down or remain at the same speed while passing through the obstacle. However, as noted in Figure 12, swimming velocity increased prior to entering the obstacle. This increased speed was sustained through the entire course of the obstacle until the nose of the fish reached the other side.

Shrank and Webb previously studied fish moving through both vertical and horizontal tubes, and my results are consistent with their findings. In their experiment, fish had to swim on their sides in a stable position in order to swim through horizontal tubes up to 20 cm in length. Goldfish were able to navigate the narrowest tubes when swimming horizontally. Goldfish are fusiform fish known to use primarily body and caudal fin swimming as compared to angelfish and silver dollars who utilize paired fin swimming (Webb and Shrank, 1998). When faced with confined spaces, all fish relied more heavily on body and caudal fin swimming. I observed the same phenomenon in my experiment as the fish turned on their sides and utilized body and caudal fin swimming to surpass the horizontal obstacle.

My study examined the nature of body mechanics and fin control with horizontal slit widths. Previous studies on teleostean fish have analyzed fish with various body and fin forms to determine the maneuverability of fish through vertical and horizontal slits (Webb et al., 1996). Webb et al. found that there was no difference between maneuverability through vertical and horizontal slits widths, suggesting that fish were equally adept at swimming on their sides. My study results are consistent with these findings. Blue gill sunfish, as deep body fish, did not lose speed while traversing the horizontal obstacle in this study. The horizontal obstacle creates a tight space that requires the fish to roll on its side and alter its biomechanics to maintain its center of mass and velocity. My results demonstrate that fish are able to optimize this angle of roll based on the size of the horizontal slit, while maximizing efficiency by maintaining and even increasing velocity. The fish were able to transition from slow-speed swimming driven primarily by pectoral fins to body and caudal fin swimming in order to pass under the narrow slit underneath the horizontal obstacle.

Biorobotic Applications

My research has implications for biorobotic models that attempt to efficiently navigate past obstacles, while optimally modulating their speeds to maximize efficiency. Based on the findings of this study, further investigations in blue gill sunfish and robotic models could determine points in time and space when a swimming object would need to alter its speed in tandem with the rolling, propelling, and unrolling phases of navigating past horizontal obstacles in order to maximize speed and efficiency.

AUVs are one area of biotechnology in which the application of knowledge on aquatic locomotion may yield significant rewards for mankind. AUVs are of special interest to the military that employs these devices to achieve tasks like sweeping for mines or patrolling harbors. These devices have been crucial to mapping the ocean floor and surveying shipwrecks, amongst many other tasks. While tethered AUVs are limited in dexterity because they are attached to the surface, remote-controlled URV's have a limited energy supply so energy efficiency is a key limitation. A bio-inspired underwater vehicle developed at the Indian Institute of Technology Madras, India, has already demonstrated a 1.5 times increase in energy efficiency compared to equivalent conventional underwater vehicles (Deccan Chronicle, July 13, 2016). The goal for these devices is to allow them to hover, turn swiftly, and conserve energy in movement.

Conventional underwater vehicles have difficulty operating effectively in complex environments. They often require a large radius of curvature to make sharp turns and rely on multiple propellers to increase speed and mobility. Underwater vehicles need the ability to rotate ninety degrees and move without compromising speed and balance in order to fit through crevices in caves, shipwrecks, and for other deep-sea missions. On the other hand, fish can actively control characteristics of their propulsive surfaces such as fin surface area (Lauder and Madden, 2006), which takes advantage of drag principles to maneuver through complex environments and dramatically improve hydrodynamic efficiency. An AUV prototype that incorporates this innovation is currently in development (Lauder Laboratory, 2016).

In a review article by Lauder and Madden in 2006, a series of key findings from the past two decades of fish biomechanics studies are highlighted as insights to inform robomimetic fish design. Amongst these important findings include the knowledge that fish actively control the curvature of their fins, making them distinct from insect wings or bird feathers, in order to alter propulsion based on hydrodynamic flow and movement. Fish fins are flexible and move in three-dimensional space. Finally, multifin control is extremely complex and interdependent: for example, dorsal and anal fins alter the flow past these structures to potentially increase thrust at the tail fin. These insights and numerous others that can come from our current investigation on multifin control in yaw, pitch, and roll can provide the engineers with essential principles to develop more efficient and effective underwater machines that incorporate multifin function.

The goal of my research in this thesis is to develop an understanding of the orchestration of fin mechanics employed by the bluegill sunfish to change speed and body rotation in order to navigate under a horizontal obstacle. Robotics research does not seek to necessarily copy these biologic models directly, but rather to distill the fundamental principles that govern the function of biological systems, and apply them to robotic design.

Study Limitations

Although a great deal of work has been done on the biomechanics of fishes, the complex motion of fins and fishes bodies is still poorly understood, especially when fish execute complex maneuvers. At the current time, we lack data on the sensory information available to fishes from the surface of fins (Lauder and Madden, 2006). We have little understanding of whether fish are able to sense the position of their pectoral, dorsal, caudal and anal fins during navigation with or without obstacles, but I speculate that fish are aware of such sensations and are able to use them in order to navigate efficiently. From what we know so far, motor output and sensory input are limited to the lateral line, which forms sensors on the surface of fishes and in canals that extend down each side of the body (Lauder and Madden, 2006; Coombs and Van Netten, 2006; Curcic-Blake and Van Netten, 2006). However more extensive work is needed to be able to link the motor output and sensory input of fins through specific biomechanical movements such as swimming under or through obstacles. Additional sensors on or in fish fins would allow them to sense where fins are in space and if contact is made with objects in their immediate environment.

Other experimental methods of analysis could lend further insight into this investigation. For example, electromyograms (EMGs) of individual muscles utilized during complex pectoral fin movements such as cupping behavior may lend greater insight into how these fins produce rolling behavior and how this cupping phenomena differs from other pectoral fin movements utilized by bluegill sunfish.

Another method that would lend further insight in this investigation is the utilization of particle image velocimetry (PIV). This optical method of flow visualization could provide information about specific vectors created by each of the fins during complex fin movements, such as rolling. In this study, the bluegill sunfish appeared to utilize body and caudal fin swimming while sideways, along with minimal pectoral fin movements. PIV would be particularly useful in determining which fins primarily provide thrust vs. drag forces during complex movements like sideways swimming under a horizontal obstacle. PIV could help elucidate whether additional fins like dorsal, anal, and pelvic fins generate locomotor forces. I also observed asymmetric pectoral fin movements during rolling and unrolling. This analysis could also clarify exact angles at which these forces are directed in asymmetric cupping of pectoral fins to achieve rolling and unrolling.

Another limitation of the study is that the real world is far more complex than the laboratory experimental conditions used here. In reality, changes in aquatic environments such as temperature, salinity, and pH of water may alter fish behavior in ways that have not been accounted for in our laboratory experiments. In addition, predation and interactions with fish in the ecosystem further dictate fish behavior and biomechanics. For example, our previous studies and the current one focus on individual fish swimming behavior. However many fish swim in schools, which involve communication and coordination through complex mechanisms that are not well understood. Subsequent investigations may seek to capture these complex phenomena by recreating laboratory environments more analogous to rock or coral reef systems and include multiple fish in the same environment. Analysis of high-speed camera footage may allow us to study how fish move individually or collectively in their natural environments, outmaneuver their prey, and evade predators.

In addition, in natural bodies of water that fish inhabit, such as streams, lakes, and oceans, hydrodynamic forces from water currents are far more complex than what we have created in the laboratory. It is likely that fish account for multiple simultaneous force vectors, along with turbulent flow, in order to utilize multifin control to be able maneuver efficiently. We are only beginning to understand how fish respond to simple obstacles and controlled hydrostatic force vectors in laboratory conditions, and future work extending these studies to more natural environments is likely to yield many new insights into fish swimming behavior.

References

Biewener, A. (2003). Animal Locomotion. Oxford University Press. Great Britain.

Coombs, S. A., and Van Netten, S. M. (2006). The Hydrodynamics and Structural Mechanics of the Lateral Line System, Fish Biomechanics. Fish Physiology, R. E. Shadwick, G. V. Lauder, Eds., *Academic Press*, San Diego. *23*,103−139.

Crowder, L., and Cooper, W. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, *63,*1802-1813. doi: 10.2307/1940122

Curcic-Blake, B., and Van Netten, S. M. (2006). Source Location Encoding in the Fish Lateral Line Canal. *Journal of Experimental Biology*, *209*(8),1548−1559.

Dang, Z., Richmond, M. C., Guensch, G. R., and Muller, R. P. (2004). Study of fish response using particle imaging velocimetry and high-speed, high-resolution imaging. U.S. Department of energy: Energy efficiency and renewable energy. *Wind and Hydropower technologies.* U.S.A.

Drucker, E. G., and Jensen, J. S. (1996). Pectoral fin locomotion in the striped surfperch. *Journal of Experimental Biology, 199*(10), 2235– 2242.

Drucker, E. G., and Lauder, G. V. (2000). A hydrodynamic analysis of fish swimming speed: wake structure and locomotor force in slow and fast labriform swimmers. *Journal of Experimental Biology*, *203*, 2379-2393.

Ellerby, D. J., and Gerry, S. P. (2011). Sympatric divergence and performance trade-offs of bluegill ecomorphs. *Journal of Evolutionary Biology*, *38*, 422-433. Doi: https://doi.org/10.1007/s11692-011-9130-y

Esposito, C. J., Tangorra, J. L., Flammang, B. E., and Lauder, G. V. (2012). A robotic fish caudal fin: effects of stiffness and motor program on locomotor performance. *Journal of Experimental Biology*, *215*, 56-67. doi:10.1242/jeb.062711

Flammang, B. E., and Lauder, G. V. (2008). Speed-dependent intrinsic caudal fin muscle recruitment during steady swimming in bluegill sunfish, *Lepomis macrochirus*. *Journal of Experimental Biology*, *211*, 587-598. doi: 10.1242/jeb.012096

Flammang, B. E., and Lauder, G. V. (2009). Caudal fin shape modulation and control during acceleration, braking and backing maneuvers in bluegill sunfish, Lepomis macrochirus. *Journal of Experimental Biology*. *212*, 277-286; doi: 10.1242/jeb.021360

Flammang, B. E., and Lauder, G. V. (2013). Pectoral fins aid in navigation of a complex environment by bluegill sunfish under sensory deprivation conditions. *Journal of Experimental Biology*, *216*, 3084-3089. doi: 10.1242/jeb.080077

Flammang, B. E., Lauder, G. V. (2016). Functional morphology and hydrodynamics of backward swimming behavior of bluegill sunfish. *Zoology*, *119*(5), 414-420. doi: 10.1016/j.zool.2016.05.002.

Gottlieb, J. R., Tangorra, J. L., Esposito, C. J., and Lauder, G. V. (2010). A biologically derived pectoral fin for yaw turn manoeuvres. *Applied Bionics and Biomechanics*, *7*(1) 2010, 41–55. doi: 10.1080/11762320903537782

Hatze, H. (1974). "The meaning of the term biomechanics". *Journal of Biomechanics*, *7* (12), 189-190. doi:10.1016/0021-9290(74)90060-8

Hedrick, T. L. (2008). Software techniques for two-and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspiration &. Biomimetics*, *3*(3), 034001. doi: 10.1088/1748-3182/3/3/034001

Houssay, F. (1912). Forme, Puissance et stabilité des Poissons. Paris: Herman.

Hu, K., Ren, Z., Wang, Y. (2016). Quantitative hydrodynamic investigation of fish caudal fin cupping motion using a bio-robotic model, *IEEE International Conference on Robotics and Biomimetics* (ROBIO).

Kalionzes, K. N., Flammang, B. E., and Lauder, G. V. Multifin control of bluegill sunfish during backwards maneuvering through an obstacle course. *Zoology*, In Preparation.

Lauder, G. V., and Madden, P. G. A. (2006). Learning from Fish: Kinematics and Experimental Hydrodynamics for Roboticists. *International Journal of Automation and Computing*. *4*, 325-335.

Lauder, G. V., Madden, P. G. A., Mittal, R., Dong, H., and Bozkurttas, M. (2006). Locomotion with flexible propulsors: I. Experimental analysis of pectoral fin swimming in sunfish. *Bioinspiration &. Biomimetics. 1*, 25–34. doi:10.1088/1748-3182/1/4/S04

Lauder, G. V., Anderson, E. J., Tangorra, J., and Madden, P. G. A. (2007). Fish biorobotics: kinematics and hydrodynamics of self-propulsion. *Journal of Experimental Biology*, *210*, 2767-2780. doi: 10.1242/jeb.000265

Love, M. S., and Yoklavich, M. M. (2006). Deep Rock Habitats. In The Ecology of Marine Fishes: California and Adjacent Waters (ed. L.G. Allen, D.J. Pondella, and M. H. Horn). *University of California Press, Berkeley,* 253-266.

Mittelbach, G. G. (1981). Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology, 62*, 1370-1386. doi: 10.2307/1937300

Moyle, B. P., and Cech Jr , J. J. (2000). Fishes: An introduction to ichthyology, 4th edt. Department of wildlife, fish and conservation biology, *University of California, Davis*, Prentice Hall. Upper Saddle River, NJ.

Neveln, I. D., Bai, Y., Snyder, J. B., Solberg, J. R., Curet, O. M., Lynch, K. M., and MacIver, M. A. (2013). Biomimetic and bio-inspired robotics in electric fish research. *Journal of Experimental Biology*, *216*(13), 2501-2514. doi: 10.1242/jeb.082743

Pope, M. H. (2005). Giovanni Alfonso Borelli, the father of biomechanics. *The Spine Journal*. *30*(20), 2350-5. doi: 10.1227/01.NEU.0000249263.80579.F9

Ragu, R. (2016). Deccan Chronicle. “First Bio-Inspired Robot” Retrieved on November 15, 2016 from: http://www.deccanchronicle.com/technology/in-other-news/130716/first-bio-inspired-underwater-robot.html

Shadwick, R. E., and Lauder, G. V. (2006). Fish biomechanics. *Elsevier Academic Press*, 369-423.

Shrank, A. J., and Webb, W. P. (1998). Do body and fin form affect the abilities of fish to stabilize swimming during maneuvers through vertical and horizontal tubes? *Environmental Biology of Fishes, 53*, 365-371. Netherlands.

Schrank A. J., and Mayberry, S. (1999). How do body and paired-fin position affect the ability of three teleost fishes to maneuver around bends? *Canadian Journal of Zoology*, *77*, 203-210. doi.org/10.1139/z98-209

Tangorra, J. L., Davison, S. N., Hunter, I. W., Madden, P. G. A., Lauder, G. V., Don, H., Bozkurttas, M., and Mittal, R. (2008). The Development of a Biologically Inspired Propulsor for Unmanned Underwater Vehicles. *Journal of Oceanic Engineering, 32*(3), 533-550. doi: 10.1109/JOE.2007.903362

Tangorra, J., Esposito, C. J., and Lauder, G. V. (2009) Biorobotic Fins for Investigations of Fish Locomotion. Manuscript submission. [Online] Available: http://www.people.fas.harvard.edu/~glauder/reprints_unzipped/Tangorra.Esposito.Lauder.IROS2009.pdf

Videler, J. J. (1993). Fish kinematics: history and methods. *Department of Marine Biology, University of Groningen*, The Netherlands. Springer Netherlands. 93-112.doi.10.1007/978-94-011-1580-3_5

Webb, P. W., LaLiberte, G. D., and Schrank, A. J. (1996). Does body and fin for affect the maneuverability of fish traversing vertical and horizontal slits?. *Environmental Biology of Fishes*, *46*, 7-14.

Webb, P. W. (2002). Control of posture, depth, and swimming trajectories of fishes. *Integrative and Comparative Biology, 42*, 94-101.

Westneat, M. W. (1996). Functional Morphology of Aquatic Flight in Fishes: Kinematics, Electromyography, and Mechanical Modeling of Labriform Locomotion. *Journal of American Zoologist, 36* (6), 582–598. doi.org/10.1093/icb/36.6.582

Wilga, C. D., and Lauder, G. V. (1999). Locomotion in Sturgeon: Function of the Pectoral Fins. *Journal of Experimental Biology*, *202*(18), 2413–2432.

Wilga, C. D., and Lauder, G. V. (2000). Three Dimensional Kinematics and Wake Structure of the Pectoral Fins During Locomotion in Leopard Sharks Triakis Semifasciata *Journal of Experimental Biology*, *203*(15), 2261–2278.

Wilga, C. D., and Luader, G. V. (2001). Functional Morphology of the Pectoral Fins in Bamboo Sharks, Chiloscyllium plagiosum: Benthic vs. Pelagic Station-Holding. *Journal of Morphology*, *249*(3), 195– 209. doi.10.1002/jmor.1049