Towards the Yin and Yang of fish locomotion: linking energetics, ecology, and mechanics through biomechanics and biologging

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Abstract

Fish locomotion has been studied since the time of Aristotle, drawing interest from across disciplines, from mathematics to physiology, fluid dynamics and evolution. The topic is complex, involving fluid-structure interactions of flexible bodies as well as sensory feedback and active control. As such, most of our understanding has been focused on elementary behaviors like steady swimming and escape responses in simple environments. As the field matures, increasing attention is being paid to transient, unsteady behaviors that are involved in more complex interactions with the surrounding environment. This commentary will argue in favor of studying ecologically relevant behaviors, which can bring new understandings of the energetic consequences of fish swimming. Specific examples will be discussed, such as station-holding around bluff bodies, which departs drastically from steady swimming in almost all aspects of kinematics, muscle activity, and energetics. The energetics of transient behaviors such as acceleration and feeding will also be discussed, highlighting two ways of directing measuring locomotory costs. Beyond the lab, a far richer diversity of behaviors is available when fish are given enough space and time to move. To this end, mesocosm studies are poised to reveal new insights into fish swimming that are out of reach for laboratory situations. Ultimately, biologgers provide a way to study the complete diversity of behavior in wild fishes, with improvements to technology allowing insights into ecology, energetics, physiology and neuroscience in ways that will strongly complement and accelerate lab studies in the years to come.

Introduction:

Comparative biomechanists are interested in understanding the grand diversity of organisms and how they work. Inspired by the natural world, biomechanists have a rich history of looking at anatomy and behavior through the lens of engineering and physics. Burgeoning advances in technology have given us new eyes to look at how animals move, from the moving image (Batty, 1984; McHenry and Hedrick, 2023) to measuring forces (Drucker and Lauder, 1999; Heglund, 1981; Stamhuis and Videler, 1995; Warfvinge et al., 2021) and muscle physiology ((Altringham et al., 1993; Gibbs et al., 2024; Hughes and Ballintijn, 1968). These approaches have been cultivated in the laboratory, where aspects of animal locomotion are interrogated in controlled environments. Importantly, many of the breakthroughs in our field would be impossible without such a reductionist approach. And yet natural behavior is the language of biomechanics. Animals evolved to move in the wild, in lockstep with often complex environments. Animals carry that response in their bodies and nervous systems, even as they are brought inside. For only natural behavior can reveal the breadth of mechanisms and ranges of performance that animals have evolved to execute over millions of years.

The Taoist principle of Yin and Yang may help visualize a new era for comparative biomechanics, one in which we strive to integrate field and laboratory perspectives. The black swirl of Yin represents the laboratory and its powerful technologies, which encloses a white dot that represents the fish that we bring into the lab for experimentation (Figure 1). The white swirl of Yang represents Nature, enclosing a black dot which can be a "lab on a chip" such as a biologger, which is mounted on the fish to reveal its behavior in the wild. Much of our progress lies historically in the Yin approach, where fish are interrogated in the lab. At times, this includes a salient aspect of the environment, such as naturalistic visual stimuli or physical terrain. Advances in biologging (Wilmers et al., 2015), natural neuroscience (Cisek and Green, 2024) and movement ecology (Nathan et al., 2008) are poised to pull traditional biomechanics towards a Yang approach. Fittingly, the border of the Yang swirl disappears when pasted onto a white background, reminding us that Nature extends beyond the lab both in time, space and complexity. Indeed, all our labs are embedded in Nature.

This commentary will cover three promising approaches for the future of fish biomechanics research. 1) Bringing Nature's complexity into the lab 2) understanding unsteady behaviors across a greater range of diversity and 3) studying animals in larger spaces to reveal a greater range of natural behaviors. Written from the perspective of a largely lab-based biomechanist, these directions will be critical to advance our understanding of the energetics and ecology of fish locomotion in the years to come.

Bringing unsteady flows into the lab.
When fish are exposed to unsteady flow in the wake of a stationary cylinder, they adopt a novel gait called the Kármán gait, During this behavior, fish slalom around and exploit the energy of vortices in a von Kármán vortex street (Figure 2A) (Liao et al., 2003a; Liao et al., 2003b). This ability to surf is possible when the ratio of body length is about twice that of the cylinder diameter. Compared to swimming in uniform (freestream or FS) flow, Kármán gaiting fish can hold station (e.g. not drift downstream in the Earth frame of reference) by shutting down red axial muscle activity along most of the body (Liao, 2004)(Figure 2B). Specifically, the classic pattern of sequential red muscle activity disappears when the same fish Kármán gaits in the vortex street behind a cylinder, where the posterior half of the body undulates with no muscle activity. Indeed, only the anterior-most electrode site exhibits activity despite the body undulating with a larger amplitude than seen during freestream swimming. In this case, the fish is swimming through the largely passive interaction of the vortices bending the body, and not by active muscle contractions. During times when the pectoral fins of Kármán gaiting fish are active, no axial muscle activity is observed. Tellingly, a dead fish towed behind a cylinder displays similar kinematics to a live fish (Liao, 2004). The intrinsic musculoskeletal compliance of the body, devoid of actuation from the nervous system, is sufficient to drive Kármán gaiting -like behavior and even upstream swimming (Beal et al., 2006).

This simple abstraction resulted in profound implications for the ecology and energetics of fish swimming, even though single cylinders are rarely found in nature. These laboratory results can then be used to generate ecological hypotheses and tested in the field: fish sort themselves behind appropriately sized rocks in a river. This size-related rule of habitat-selection may be suggestive of a broader principle affecting how species and life-history stages are distributed across current-swept environments.

Behavior wants to emerge when given enough space. When given free range in a large flow tank, fish will choose where they want to swim. Relating to a single cylinder, fish show at least 4 behaviors (Taguchi and Liao, 2011)(Figure 2C). They can choose to swim away from the cylinder in a region of uniform flow (FS). Around the cylinder, they can swim in the vortex street (KG), entrain just downstream from the cylinder (EN), or in the high-pressure bow wake region in front of the cylinder (BW).

Many flows, many costs

Electromyography recordings indicate which muscles are active and when, but cannot be relied on to measure intensity of activation or the physiological cost of activity. For this, oxygen consumption measurements are the most direct, and least invasive, way to measure behavioral costs in aquatic animals. Respirometry studies have revealed that trout can lower energetic costs by 50% when Kármán gaiting as compared to FS swimming. At moderate swimming speeds (3.5 L s^{-1}), this savings can also be achieved by entraining (Taguchi and Liao, 2011)(Figure 2C). At lower and higher flows, Kármán gaiting is not sustainable: either the vortex street is not sufficiently developed in strength, or it becomes too turbulent for a fish to maintain stability, respectively. Thus, at low flow speeds (1.8 L s^{-1}) , swimming in the FS is the least energetically costly. At higher speeds (5.0 L s^{-1}), swimming in the bow wake is the least costly. In this way, the most favorable regions around a cylinder to hold station change dynamically with flow speed. When applied to the field, this suggests that when current velocity changes during different times of the tidal cycle on a reef or during spring runoff in a river, station-holding fish benefit energetically by shifting positions around the physical habitats with which they associate. This ecological hypothesis remains to be tested and could reveal the mechanisms for spatial distribution of fishes.

Are there more ideal wakes for a fish than that shed from a single cylinder? When fish are exposed to 2 cylinders arranged in tandem in the flow, they prefer cylinder spacings (in the streamwise direction) that are closest together (Stewart et al., 2016). Computational fluid dynamics modeling reveals that the strongest vortex street signature occurs when 2 cylinders are closest together, as if they were a single cylinder, creating extended body and reattachment regimes that are more conducive to Kármán Gaiting (Figure 2D-E). Larger cylinder spacings cause the vortex street from the upstream cylinder to interact destructively with the vortex street from the downstream cylinder. This creates a co-shedding regime in which the vortex wake that a fish experiences behind the downstream cylinder is too weak to harness (Figure 2E). It turns out that 2 cylinders are not better than 1.

Single or even and double cylinders are not common in nature. Rather, aggregations of bluff bodies, like branches from a tree limb or an array of staghorn corals, more commonly present themselves to flow refuging fishes. Using computational fluid dynamics, the wake behind different cylinder arrays can be systematically explored (Figure 2F). For example, the vorticity contours for a 5x3 cylinder array configuration (Re# = 10,000) with spacing in the x and y direction of 1.9D and 3.1D, respectively, where D represents the diameter of the cylinder. In this configuration, complete vortices form between each cylinder before impingement on the downstream cylinder. Additionally, vortices from the top and bottom cylinder rows feed into vortices of the central row, creating a vortex street in the wake of the array. Next, specific cylinder spacing configurations can be fabricated and then tested in a flow tank with live fish to investigate the effect of different wakes on swimming kinematics (Sparks et al., 2024). More naturalistic structures like arrays of bluff bodies, with an understanding of the mechanistic basis for choosing them, promise to advance our knowledge of fish swimming in an ecological context.

Beyond steady swimming: when fish change speeds

Watch a fish in nature, and it's apparent that they do not swim steadily for long. Instead, they turn, pause and accelerate as they go about the important business of surviving. Fishes have been chasing each other since before the Devonian period, using their ability to accelerate to ensure successful catching of prey as well as successful evading of predators. Often fishes do not have the luxury of sitting around before bursting towards or away from another fish: they must give chase and be chased while already on the move. And yet our understanding of how swimming fishes change speed and surge forward towards survival is relatively unknown.

When fish swim steadily, they keep their tailbeat amplitude and frequency low and constant, a

strategy that maximizes efficiency while minimizing energetic investment (Akanyeti et al., 2017). Acceleration represents a different movement strategy that increases propulsion (by increasing tailbeat amplitude 34% *L*) despite incurring higher drag costs. When tail beat amplitude is plotted as a histogram, these two behavioral strategies form distinct, overlapping clusters that have significantly different mean values.

Steadily swimming fishes produce wake structures that resemble vortex rings. Using time-resolved, planar Particle Image Velocimetry, a fish wake reveals itself as a backwards jet surrounded by 2 counter-rotating vortices: in three-dimensions this takes the shape of a toroid, or vortex ring (Drucker and Lauder, 1999). How does the wake of an accelerating fish compare? When vortex rings behind accelerating fishes from widely different body shapes, swimming styles and ecological niches were examined, a common shape was revealed (Akanyeti et al., 2017). When a steadily swimming fish transitions to acceleration, they do not generate larger vortex rings, as might be assumed based on the larger tailbeat amplitudes and greater impulses. Instead, accelerating fishes generate more radially symmetrical rings that are directed more downstream with larger diameter vortex cores (Figure 3A-B). Average force, or impulse, can be calculated from the geometry and strength of vortex rings (Drucker and Lauder, 1999). Specifically, the average force applied to the fluid during each tail beat can be retrieved by measuring the circulation, jet angle (θ), core diameter (D_o), and the spacing between the two vortex cores (D) (Figure 3C-D). The impulse calculated during acceleration is about four times higher than during steady swimming. This is due to the generation of stronger vortices (a 172% increase), the direction of the ring (and thus jet) is oriented ~30% more downstream, and the diameter of the ring is reduced by ~25%, from an oval to a circle shape) (Akanyeti et al., 2017).

When the relationship between tail beat kinematics (amplitude and frequency) and ring geometry are modeled, and then compared to live fish and literature values of nozzle-generated rings, we find the following: accelerating fishes reshape their shed vortex rings to approach radial symmetry (Figure 3C-D). Radial symmetry occurs when the ratio between ring height (dictated by tail height) to width (d/D) approaches 1.0. In rainbow trout this value shifts from 0.66 to 0.88 (Akanyeti et al., 2017). Radially symmetric rings possess the maximum amount of energy relative to other ring shapes that maintain the same impulse. The impulse of a ring also depends on ratio of core diameter to ring diameter, D_o/D. When it approaches 0.42, it reaches maximum efficiency based on nozzle-generated ring experiments (Gharib et al., 1998; Weigand and Gharib, 1997). Rainbow trout shift their D_o/D from 0.25 when swimming steadily to 0.37 when accelerating, bringing their wake closer to the optimum value of 0.42. This is not only the case in trout but for 4 other species with very different phylogenetic memberships, body shapes, swimming modes, and ecological niches (e.g. Clown knifefish, Crevalle jack, Florida gar and Indo-Pacific tarpon), suggesting that this is a unifying hydrodynamic principle for accelerating animals in fluids. Still, an unresolved question is how D_o/D scales with body size, since D_o/D is significantly higher for smaller fish, like a zebrafish. One important caveat to keep in mind is that fish wakes are inevitably more complex than single rings, and may not have the same properties of momentum, energy and stability as nozzle-generated rings.

Optimal ring geometry does not reveal the overall swimming efficiency of an accelerating fish because the motions that produce them may be costly. Additionally, the cost of performing these transient movements are difficult to capture using traditional intermittent respirometry. One alternative is to hijack the shape and motions of the fish by molding and then actuating soft physical robots (Figure 3E). A single actuation point connected to a 6-axis force transducer allows the control of heave and head yaw independently. By driving yaw amplitudes at similar values to that observed in live fish during steady swimming and acceleration (10° and 20° Figure 3F), it is possible to link swimming kinematics with performance and costs. For example, by plotting propulsive thrust as a function of phase difference (between heave and yaw) and heave oscillation frequency, a relatively small horseshoe-shaped region of the parameter space

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emerges in which swimming movements generate thrust that matches drag ("self-propelled speed" Figure 3F-G). Certain motion combinations result in the highest power efficiency and therefore lowest cost of transport (dot in blue region where dashed circle equals 90% similarity, Figure 3F-G). During acceleration, swimming motions generate thrust that is sufficient to overcome drag ("thrust" Figure 3F&H). Certain heave and yaw combinations generate high propulsive efficiency (e.g. net force multiplied by speed divided by power), identified as the dot in red region where the dashed circle equals 90% similarity (Figure 3H). For the rest of the parameter space, the drag incurred by swimming is greater than the thrust produced (dark blue "drag" Figure 3F). Soft robotic models can be used to explore the effects of swimming kinematics on acceleration in ways that would be challenging in live fishes due to the transient and unpredictable nature of the behavior.

The cost of transient behaviors:
What is the cost of a fleeting behavior such as acceleration? When propulsive efficiency is measured for head yaw values of the physical model and then mapped onto head yaw values in live fish, we see that increased head yaw can increase efficiency by 100% (Figure 3J), though this comes at a 50% increase in mechanical power investment (Akanyeti et al., 2017)(Figure 3K). How different this mechanical cost is as compared to the biological cost in a real fish awaits respirometry studies.

Some progress has been made in understanding the energetics of transient behaviors. Feeding is often a fast, temporary behavior, and yet food is a vital resource that must be continuously acquired throughout the lifetime of motile animals. Small trout holding station behind a cylinder in a large flow tank respirometer will repeatedly feed on artificial prey (Figure 3L). Swimming behind a cylinder is less costly than swimming in uniform flow (Figure 3M, Johansen et al., 2020). However, during feeding, the cost of being behind a cylinder is greater than not (Figure 3N). This is likely due to the stability and control costs of transitioning into and out of the vortex street to intercept the unpredictable trajectory of food. In addition, the capture success is lower when attacking from behind the cylinder, especially at higher speeds (Figure 3O). Here, behavior changes the energetic landscape, making it more favorable to feed in uniform flows despite the higher costs associated with it when only locomotion is considered.

In rivers trout routinely hold station in the riffles created behind rocks and large woody debris throughout the day (Gibson, 1978; Keenleyside, 1962). In the mornings and evenings, they move to pool regions marked by more uniform flows where they feed on insect hatches(Regal, 1992). Whether they are driven to partition behavior and make habitat decisions based on energetics measured in the lab could now be tested in the field. For example, do wild trout in pools feed more than when they are station-holding behind rocks, and would the latter decline experimentally introduced food relative to when swimming in pools? In this way, data generated in the lab can be used to refine data-driven models to generate testable hypotheses of favorable strategies in nature.

A mini-ocean:
There are only so many behaviors a fish will exhibit in an aquarium or flow tank. Fish reveal new behaviors when given time and space. The distinction between *any* behavior and behavior when fish are *comfortable* is often invisible to those who do not have the opportunity to observe the natural behavior of wild fish. As such, the majority of fish locomotion research has centered on basic behaviors that fish can perform soon after placing them in an experimental tank, such as steady swimming or C-start escapes. But by simply giving fish more space and time, one can access more diverse behaviors, such as schooling or predator-prey interactions. When wild bluefish and their prey were allowed to recreate attack and evasion strategies in a 22' diameter, 27,000 gallon flow-through outdoor seawater mesocosm (Figure 4A), new insights into the

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pursuit algorithm of how fish chase down their prey were revealed ((McHenry et al., 2019)).

Video is traditionally the currency that biomechanists use to measure behavior. The challenge is that recordings are constrained to ample light availability, and many behaviors occur at night, in the deep ocean, or in murky water and lie beyond what we can observe visually. One promising approach is to attach accelerometers onto fish placed in larger spaces to better understand their locomotor repertoire in ways that would be impossible in the lab. Behaviors such as steady swimming at different flow velocities can be calibrated with video first in the laboratory (e.g. flow tank) before release into a mesocosm (Figure 4B), as well as other variables of interest such as heart rate or oxygen consumption (Doherty et al., 2022). Additional kinematic behaviors observed and annotated in the mesocosm such as maneuvering, resting, and feeding, can establish a better understanding of behaviors.

Mesocosms could be populated with native forage and habitat to look at preferred swimming speeds and daily time budgets of behaviors across longer timescales, from multiple days to months. This could reveal the effect of physiological states on locomotion during ecologically-important seasons (spawning, migration,etc.), as has been demonstrated for the upregulation of hormones on communication in midshipman fish (Forlano et al., 2015; Sisneros et al., 2004). With accelerometers synchronized to video recordings, behaviors in a mesocosm can be annotated and quantified. Computational advances in automated recognition make it possible to uniquely identify and track individuals in three-dimensions and reveal body kinematics in response to varying biotic and abiotic parameters (Congdon et al., 2022; Mathis et al., 2018; Pérez-Escudero et al., 2014). Integrating existing technologies can open the door to understanding how the presence of prey, light and flow can impact or predict behavior. Mesocosms need not be a controlled pool in a lab, they could be part of a natural field site. The utility of a mesocosm is primarily to establish an arena to outfit with sensors (e.g. video, sound) or potentially have control over environmental variables (e.g. light, temperature), as well as ensure the ability to retrieve accelerometry tags.

Strategic placement of accelerometers reveals a more nuanced understanding of behavior (Broell et al., 2012; Kawabata et al., 2014). By placing multiple accelerometers onto both the tail and the operculum of a fish, swimming and respiratory activity can be monitored independently (Gibbs, Strother and Liao in prep). This enables the differentiation of swimming (e.g. higher tail beat and opercular pumping acceleration) from resting (e.g. lower tail beat and opercular pumping acceleration). Unique behaviors are revealed based on *a priori* calibrations in the flow tank based on a probability density function plot of the tail and opercular acceleration (Figure 4C).

The Ocean:

And still, no mesocosm is big enough. Fish have an uncanny ability to quickly know the bounds of any experimental enclosure. There is no substitute for studying animals in the wild, where their bodies and brains have evolved. In lab experiments, we try our best to ensure that the animal is comfortable and behaving normally and that we choose an appropriate stimulus. This is not required in nature, where the validity of behavior is never in question.

The advent of biologgers, which can record temperature, depth, acceleration, heart rate, and light levels among other parameters for extended periods, has provided a secret window into how aquatic animals move in the wild (Block, 2005; Campbell et al., 2008; Hvas et al., 2020; Whitford and Klimley, 2019; Williams and Ponganis, 2021; Williams et al., 2020). For example, tuna tagged off the coast of Novia Scotia were observed to swim with intermittent rather than continuous locomotion, using their negative buoyancy to glide passively while diving (Gleiss et al., 2019), where dives were likely in response to foraging and thermoregulation. Advancing technologies promise to expand the types and quality of data collected in the field (Brodie et al., 2018; Hussey et al., 2015; Whitford and Klimley, 2019). However, biologging data

have traditionally lacked the spatial and temporal resolution that is sought by biomechanists to understand the proximate mechanisms of behavior.

Devoid of the luxuries of satellite GPS tracking systems enjoyed by terrestrial animal research, acoustic telemetry has emerged as the primary technique to follow the movements of individual fish for up to several years. Briefly, acoustic telemetry involves collecting a wild fish, inserting or attaching a small coded tag to the body, and releasing it back into their habitat where receivers are placed to listen to their presence (Figure 4D). Each tag is programmed with a unique acoustic ID and can also record temperature and pressure. Tags reveal the location and time of arrival of specific fish near receivers, with a transmission range of several hundred meters depending on water depth, turbidity and current. Analogous to an electronic highway toll system, fish "check in" as they pass receivers, often for several years. The spatial resolution of tracks depends largely on the density of the receiver array and how well each fish is detected based on ping rate and movement behavior. To this end, a global partnership that shares networks of receivers (e.g. Ocean Tracking Network) have revolutionized the ability to track individual aquatic animals across long distances at an economical price point (Iverson et al., 2019). Similarly, a satellite-based animal surveillance systems (e.g. ARGOS) has allowed windows into aquatic animal movement (Benson, 2012; Watanabe and Papastamatiou, 2023).

When receivers are placed in confined bodies of water such as a river system instead of the open ocean, it becomes possible to generate new understanding of fish movements (Figure 4E). For example, by placing receivers along a 40-mile stretch of the Intracoastal Waterway, a marine river system with inlets connecting it to the Atlantic Ocean, the movements of individual fish relative to tidal flow cycle and particular habitats (e.g. oyster reef, or mud flat) can be recorded (Goturk, Clark and Liao in prep). Tidal transport has been shown to save energy for migrating fishes (Gibson, 1992; Weihs, 1978). Receivers can be coordinated with water monitoring stations from government agencies (e.g. NOAA) or local conservation groups to gain a better understanding of the environmental conditions that influence fish movement.

Sydney Brenner, the American scientist and entrepreneur, famously said: "Progress in science depends on new techniques, new discoveries and new ideas, probably in that order." New technologies have ushered more interest in understanding how fish move in the wild, as evidenced by the over 6-fold increase in aquatic telemetry from 2005-2015 (Hussey et al., 2015). Building on a rich history of tagging fish (Thorstad et al., 2014), there is now an increase in experimental versus observational studies, where comparisons can be made between treatment groups (Cooke et al., 2008). Importantly, telemetry can open the door for a more mechanistic versus correlational understanding of how changing environments affect animal movement (Block et al., 2019; Brodie et al., 2018; Lowerre-Barbieri et al., 2021). A biomechanist asking "How do animals move?" in the field may develop interests and recognize applications in conservation and ecology. This shift in perspective is not trivial: an ecological perspective sees habitat as drivers of locomotion, behavior and migration strategy, not just variables that affect movement mechanics (Brownscombe et al., 2022; Huey, 1991). A mechanistic approach to conservation becomes more likely if we drive our perspective back and forth between the lab and the field, as well as between disciplines. In the example of marine fish conservation, a deeper understanding of how swimming energetics is connected to migration and survival could generate population models that better predict future numbers in the ocean at a time of climate change.

It is hard to gain a comprehensive understanding of the ecology and energetics of locomotion without considering the brain. Animals take in sensory input and make movement decisions based on this information. From moment to moment, animals must make correct choices to ensure their survival, and this continues over the course of their lifespan. With this perspective, biologgers with eventual capabilities to record sensory inputs and physiological states, from spikes to neurotransmitter levels that drive arousal or fear, will usher in a new era

for understanding biomechanics and behavior in the wild. In this regard, biomechanists would do well to link arms with neuroscientists who ask questions in natural environments (Berman et al., 2019; Cisek and Green, 2024; Dennis et al., 2021). By recording from the brain in freely moving animals in natural habitats, spike activity from individual and populations of neurons in the brain have revealed processes about animal navigation that are beyond the reach of traditional indoor laboratory studies that rely on model organisms. For example, by making recordings in a freely flying bat in a naturalistic mesocosm, a new population of neurons in the hippocampus was discovered that helps to explain goal-directed navigation and provided evidence for a cognitive map on the scale of hundreds of kilometers (Geva-Sagiv et al., 2015; Tsoar et al., 2011). Underwater, advances have also been made, with wireless recordings revealing the activity of place cells and sensory cells for navigation and feeding in fishes (Takahashi et al., 2021; Vinepinsky et al., 2017). A recent advance in the fabrication of a slim, low-cost head-stage amplifier has enabled brain activity recording in swift-swimming fishes (Figure 4F-H) (Gibbs 2024). With modification, the head stage can be converted to a wireless, data logging device that can be incorporated into a biologger to record the neural activity of wild fish. In concert with long-term mesocosm observations, next-generation biologgers can be used to reveal patterns of behavior that are inaccessible in walled laboratory settings. Beyond biomechanics, how do sensory inputs and physiological states affect locomotion in ways that influence habitat choice or the seasonal pursuit of prey? Instead of recording the electrical outputs of firing neurons in the tradition of electrophysiology, an electrochemical technique called fast-scan cyclic voltammetry can be employed to identify neurotransmitters such as dopamine or serotonin (Rodeberg et al., 2017). Parameters such as light levels, threat of predators and temperature fluctuate both daily and seasonally and play deciding roles in locomotion and behavior through the alteration of physiological states, which are sculpted by neurotransmitter levels (Brown and Bolivar, 2018; Guh et al., 2021; Reid et al., 1998). Examining these relationships in greater detail in freely swimming fishes capable of making real-time movement decisions with give us greater insight into the descending control and modulation of locomotion. This knowledge will play an important role in contextualizing and better understanding the ecology and energetics of fish locomotion in years to come.

Concluding thoughts

Locomotion is a fundamental aspect of life, crucial to almost every aspect of an animal's ecology and evolution. It is important to realize that by bringing animals into the lab, we also bring their natural environment with them, in so much that their bodies and nervous systems have been sculpted by their habitat over evolutionary time. Their bodies must navigate not only through complex physical habitats that interest biomechanists, but also move through space during sophisticated predator-prey interactions and social interactions. As we continue experiments indoors, we must also learn to recognize when our animals are "out of tune". A guitar that is out-of-tune will still make a sound if strummed. Similarly, an animal will respond to any stimulus in a testing room, artificial or otherwise. In an era where the environment itself threatens to be out of tune, we must be stewards of natural movement and behavior, always mindful that our experimental reductionism occurs within a larger ecological perspective. While walled experiments remain essential, we would do well to adopt a more holistic perspective of fish biomechanics. Asking lab questions in a field context ensures we add complexity to experiments that generate hypotheses with direct ecological relevance.

Understanding the energetic and ecological consequences of animal biomechanics also requires expanding from an engineering perspective to incorporate an understanding of physiology and neuroscience. In the parable of three blind men, each man imagines what an elephant is by running his hands over different parts of the body. Each proceeds to describe a different beast based on limited experience. Along with field and lab perspectives, we can look

to advance the field of comparative biomechanics by always trying to move our hands to another part of the elephant. The field needs the lab as much as the lab needs the field, with technologies once reserved for the lab now fast approaching field readiness. Rather than eliciting performance in the small confines of laboratory tanks, studying fishes in larger spaces allows them the opportunity to reveal their behavioral preferences. Looking forward, advances in telemetry technology promise next-generation "lab-on-a-fish" capabilities that will enhance collaborations between neuroscientists, biomechanists and movement ecologists. The effect will be to usher in a new, more nuanced and accurate understanding of how and why animals are designed and move.

   The experiments we choose shape our individual careers. But the questions we ask and the perspectives we have while asking them, drive and define the direction of our field. We stand to enrich our understanding of animals when we open our doors and eyes to what is happening in the wild.

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Acknowledgments

Figure 1: A Yin and Yang perspective of fish biomechanics research in the laboratory and in the field. The Taoist symbol of dualism represents two approaches to understanding the ecology and energetics of locomotion. By bringing fish and salient aspects of its natural environment (white dot) into the lab (black swirl), an experimental and mechanistic understanding can be gained. By bringing technology (black) into nature (white swirl) in the form of biologgers on wild fish, new insights into the ecology, energetics and evolution of fish physiology and behavior can be revealed. Because all labs are embedded in nature, ecologically-relevant findings have the opportunity to address applied issues in conservation.

Figure 2: Fish swimming around cylinders alter their body kinematics, muscle activity, energetics and behavior. A. Particle Image Velocimetry shows how Kármán gaiting (KG) fish slalom around vortices shed behind a single cylinder (Liao et al., 2003b). B. KG fish altering their kinematics significantly compared to when they swim in the freestream flow (FS) and shut down most of their axial red muscle activity (Liao, 2004). C. Fish adopt four positions around a cylinder at three different flow velocities, revealing the relative energetic costs of station-holding (Taguchi and Liao, 2011). At an intermediate flow speed (3.5 L s^{-1}) where the energetics of FS swimming is set at 100%, KG and entraining (EN) require half (50%) the energetic investment, and bow waking (BW) requires 75% of the energy of FS swimming. This relationship changes with flow speed. At a lower flow (1.35 L s^{-1}), fish do not KG because the vortex street behind the cylinder is not developed. Here, FS swimming saves the most energy, where BW and EN is more costly. At a higher flow (5.0 L s^{-1}), fish do not KG because they become unstable in a turbulent vortex street. Instead, BW is the most energetically favorable behavior, followed by FS and then EN.D. Computational fluid dynamics model of tandem cylinders with variable spacing at Reynolds # 42,000, revealing that closer spacings preserve a strong vortex street signature similar to single cylinders (Stewart et al., 2016). E. Fish prefer to KG behind closely spaced cylinders at intermediate flow velocities (*slightly higher than for single cylinders), and do not KG behind widely spaced cylinders at any flow velocity tested. F. Computer simulations of 5x3 cylinder arrays with variable downstream and cross-stream spacings to allow for efficient exploration of wakes (Re = 10,000). A vortex street is generated for a configuration with a downstream cylinder spacing (Lx) of 1.9 D and a cross-stream spacing (Ly) of 3.1, where D is the cylinder diameter. Select array configurations are then fabricated and used in live fish experiments in a flow tank (Sparks et al., 2024).

Figure 3: Energetics of acceleration and feeding. Digital particle image velocimetry reveals 2 counter-rotating vortices representing a vortex ring generated behind the tail of a steady swimming (A) and accelerating (B) fish (Akanyeti et al., 2017). Models of ring geometry illustrate that vortex rings from steady swimming (C) are more elliptical and directed more laterally than rings generated by acceleration (D), which have higher vorticity, lower ring angle and smaller diameter. These create an impulse (average force) that is 4 times greater during acceleration. Accelerating rings also possess thicker vortex cores, which approach efficiency values of 0.42 found in nozzle-generated rings. E. An actuated, soft robotic model molded from a 3-D scan of a real trout was used to reveal the performance and costs associated with steady swimming and acceleration. In rainbow trout as well as across a diversity of species, head yaw is correlated to tailbeat amplitude during acceleration (F). G. A plot of the phase difference between heave and yaw against the heave frequency. Steady swimming occurs at self-propelled speeds (light blue "horseshoe" shaped region, thrust = drag). H. Within this space, the cost of transport is minimal at certain combinations of heave-yaw phase differences (~90°) and oscillation frequency

(~1.5Hz), where the white dot represents the minimum cost of transport and the dashed circle encloses a region of 90% similarity. The model accelerates (thrust > drag) when propulsive force is highest (red, G.). I. Within this acceleration space, propulsive efficiency (net force multiplied by speed divided by power) is maximal at certain combinations of heave-yaw phase differences (~180°) and oscillation frequency (~2.5Hz). This is seen in the red region, where the white dot represents the maximum efficiency and the dashed circle encloses a region of 90% similarity. J. Propulsive efficiency increases with head yaw up to 20°. An increase of 10° to 20° in head yaw represents a 100% increase in propulsive efficiency when plotted against yaw values from real fish. K. This increase in propulsive efficiency comes at a 50% increase in mechanical power input. L. Trout holding station behind a cylinder in a flow tank respirometer will feed on artificial prey. M. Swimming behind a cylinder is less costly than swimming in uniform flow (Johansen et al., 2020), but is more costly during feeding (N). Capture success is lower when swimming behind a cylinder (O).

Figure 4: Observing natural behaviors is facilitated in large spaces where animals have more space and time. A. Video observation of predator attack strategies on prey requires appropriate space to allow for behavior decisions, as evidenced in an outdoor mesocosm where wild bluefish chase natural prey (McHenry et al., 2019). B. Multiple accelerometers can be placed on fish and their velocity-specific swimming movements calibrated in a flow tank before their release into a mesocosm. C. A probability density function plot of accelerometry data from the operculum and tail. Behaviors can be recovered under circumstances that are unfavorable for video recording (nighttime, low water clarity, great depths), allowing persistent surveillance of wild fishes over days or weeks. D. Acoustic telemetry uses receivers to track unique ID tags inserted wild red drum and tracked with receivers (tag image credit: Innovasea). E. Time, date, location and number of detections of an individual red drum as it moved across a receiver array in St. Augustine FL. The timing (t1-t3) and location of detection can be cross-referenced with tide cycle on a given day (inset) to gain a better understanding of fish movements relative to tidal flow cycles. F. A customized, waterproof, streamlined head stage amplifier can record neural activity in the brain for freely swimming fishes (Gibbs et al., 2024). G. The streamlined amplifier can be attached to fast swimming fishes such as rainbow trout and allows it to swim against different velocities, perform C-starts, or feed on drifting prey. H. Chip design allows for wireless datalogging capabilities. I. By applying voltage sweeps instead of recording neural spike activity, the head stage can act as a neurologger to identify neurotransmitters such as dopamine or serotonin in the brain of freely moving fishes.

Figure 5: Bringing fishes into the controlled environment of the laboratory yields powerful insights into behavior, but often at the cost of reducing ecological perspective. Bringing technology into the wild opens up a rich and relevant suite of natural behaviors, but often results in data with low spatial or temporal resolution. Between the lab and the ocean lies a "zone of difficulty." Mesocosms, large experimental spaces that approach natural habitat complexity, have proven to be a productive middle ground for experiments. Future research progress will depend on leveraging the strengths of both perspectives, where we can bring experimental approaches into the field as well as mine the cornucopia of natural behaviors of the field in a laboratory context.