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REVIEW

SPECIAL ISSUE

INTEGRATING BIOMECHANICS, ENERGETICS AND ECOLOGY IN LOCOMOTION

Towards the yin and yang of fish locomotion: linking energetics, ecology and mechanics through field and lab approaches

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ABSTRACT

Most of our understanding of fish locomotion has focused on elementary behaviors such as steady swimming and escape responses in simple environments. As the field matures, increasing attention is being paid to transient and unsteady behaviors that characterize more complex interactions with the environment. This Commentary advocates for an ecologically relevant approach to lab studies. Specific examples have brought new understanding to the energetic consequences of fish swimming, such as (1) station holding around bluff bodies, which departs drastically from steady swimming in almost all aspects of kinematics, muscle activity and energetics, and (2) transient behaviors such as acceleration and feeding, which are critical to survival but often neglected because of challenges in measuring costs. Beyond the lab, a far richer diversity of behaviors is available when fish are given enough space and time to move. Mesocosm studies are poised to reveal new insights into fish swimming that are inaccessible in laboratory settings. Next-generation biologgers that incorporate neural recordings will usher in a new era for understanding biomechanics in the wild and open the door for a more mechanistic understanding of how changing environments affect animal movement. These advances promise to allow insights into animal locomotion in ways that will mutually complement and accelerate laboratory and field studies in the years to come.

KEY WORDS: Biologging, Biomechanics, Ecology, Energetics, Fish, Locomotion

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 (Irschick, 2003).

The Taoist principle of yin and yang may help to 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 fishes that we bring into the lab for experimentation (Fig. 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 white yang swirl disappears in the larger context of nature, which extends beyond the lab in time, space and complexity. Indeed, all our labs are embedded in nature and our experiments exist because our animals do, reminding us of the important ramifications of conservation in this day and age.

This Commentary will cover three promising approaches for the future of fish biomechanics research: (1) comparing unsteady movements across diversity; (2) bringing hydrodynamic complexity into the lab; and (3) studying animals in larger spaces with new technologies to expand insight into natural behaviors. Written from the perspective of a lab-based biomechanist with field aspirations, these directions will be critical to advance our understanding of the energetics and ecology of fish locomotion in the years to come.

Momentary movements: diversity, hydrodynamics and energetics

Accelerating fish

We know remarkably little about how swimming fish change their swimming velocity in the laboratory, and even less about how often they accelerate and decelerate in nature. Ecologically, it is important to understand how fish change speed, because this fundamental ability is tied to their survival, such as maneuvering, intercepting prey, escaping from predators and switching to more energetically favorable gaits (Domenici and Blake, 1997; Puy et al., 2024; Webb, 1983; Wu et al., 2007). Often, speed changes are initiated ‘on the fin’ while fish are already swimming (Drucker and Lauder, 1999; Hale et al., 2006; Peake and Farrell, 2004), as opposed to a C-start escape or ambush attack from a standstill.

What ecological insights can we glean from lab experiments on acceleration? First, note that when fishes swim steadily, they keep

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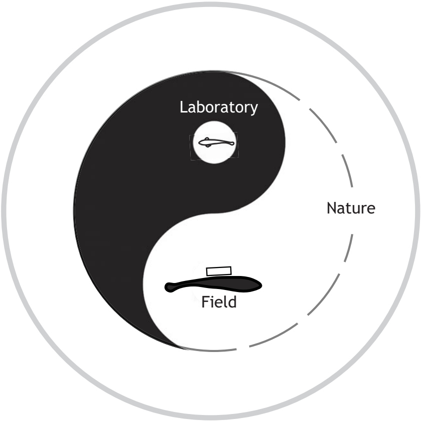

Fig. 1. A yin and yang perspective of laboratory and field studies. The Taoist symbol represents two complementary approaches to understanding the ecology and energetics of fish biomechanics. By bringing fish and salient aspects of their natural environment (white dot) into the lab (black swirl), an experimental understanding of the mechanisms of behavior can be achieved. By bringing technology (white tag on black fish) into the field (white swirl) in the form of biologgers, new insights into the ecology and energetics of fish physiology and behavior can be revealed. Because all labs are embedded in nature, an awareness of the mechanisms of behavior can contribute to conservation issues.

their tailbeat amplitude and frequency low and constant, a strategy that maximizes efficiency while minimizing energetic investment. A survey of over 40 species shows that when they accelerate, fish increase both tailbeat amplitude and frequency, using a different movement strategy that increases propulsion despite incurring higher drag costs (Akanyeti et al., 2017). Does acceleratory propulsion affect the distribution of fishes in their native habitats, or partition their food resources depending on their performance? We are still not able to directly make these connections, but some fundamental observations, currently only possible with flow visualization techniques in the lab, bring us closer to these and other ecological insights.

When species with different body shapes, swimming styles and ecological niches accelerate, they reveal a convergence of hydrodynamics in their wake by leaving similar footprints (Akanyeti et al., 2017). This holds true for elongate fishes such as moray eels (*Gymnothorax vicinus*), laterally compressed fishes such as spadefish (*Chaetodipterus faber*) and fusiform fishes such as red drum (*Sciaenops ocellatus*). Evolution in different habitats does not seem to make a difference either, as surface fishes such as needlefish (*Strongylura marina*), demersal fishes such as oyster toadfish (*Opsanus tau*) and riverine fishes such as rainbow trout (*Oncorhynchus mykiss*) all revert to the same fluid principle when accelerating. When these fishes transition from steady swimming to acceleration, they do so by generating different vortex rings (momentary, doughnut-shaped structures in the flow behind the tail), as revealed by flow visualization techniques such as digital particle image velocimetry (DPIV). When fish diversity is married to flow visualization in the lab, we gain insight into how different fishes influence the water as they swim in real time (Drucker and Lauder, 1999; Nauen and Lauder, 2002; Wilga and Lauder, 2002). A comparative, experimental approach has revealed a unifying hydrodynamic principle for accelerating animals in fluids. Specifically, the diversity of fish swimming wakes collapses during acceleration, made possible by the production of more forceful, symmetrical vortex rings (Fig. 2A–D). For example, in rainbow trout, the ratio of ring height to width (d/D) approaches 1.0 (e.g. the value shifts from 0.66 to 0.88) when transitioning from steady swimming to acceleration (Akanyeti et al., 2017). The force imbued by a vortex ring also depends on the 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 to 0.37 when transitioning from steady swimming to acceleration. Other species across different phylogenetic memberships, body shapes, swimming modes and ecological niches (e.g. clown knifefish, crevalle jack, Florida gar and Indo-Pacific tarpon) demonstrate a similar trend. This unifying principle implies that the fluid medium can reveal strong constraints on behavioral performance that act broadly across phylogenetic membership. These quantitative comparisons are currently only possible in the lab. Field applications of flow visualization are growing in capacity and ease, promising to provide a much-needed addition of hydrodynamic field studies in the future (Creutin et al., 2003; Katija and Dabiri, 2008).

Using robots to reveal energetics

The energetic consequences of swimming behaviors such as chasing prey or fleeing danger are important to understand, as predator–prey processes are thought to drive ecological dynamics (Harper and Blake, 1988; Townsend and Winfield, 1985). Yet, the cost of swimming acceleration is difficult to directly measure given its transient and unpredictable nature. One alternative is to use soft robots (Fig. 2E) to link swimming kinematics with performance and costs. By independently controlling heave and head yaw, one can replicate similar motions to those observed in live fish (Fig. 2F). The parameter space can be explored to discover which swimming movements cause the model, equipped with a force transducer, to hold station ('self-propelled speed' where thrust equals drag; Fig. 2F–I), accelerate ('thrust') or drift downstream ('drag'). At self-propelled speeds, certain heave and yaw combinations result in the highest power efficiency and therefore lowest cost of transport (Fig. 2F,G). During acceleration, different heave and yaw combinations generate high propulsive efficiency (i.e. net force multiplied by speed divided by power). For the remaining motion combinations, the drag incurred by swimming is greater than the thrust produced (Fig. 2F). Mapping propulsive efficiency onto head yaw values in live fish reveals that increased head yaw can increase efficiency by 100% (Fig. 2J), though this comes at a 50% increase in mechanical power investment (Akanyeti et al., 2017) (Fig. 2K). Controlling fish-like motions and evaluating energetic investment with robotic platforms remains a viable approach to understanding the costs of momentary behaviors until measurements on live fish are made.

The cost of foraging: swimming and feeding

One such measurement has been made: for foraging trout accelerating to attack drifting prey. Measuring the physiological cost of attacking prey is challenging, but laboratory respirometry can be applied to directly measure the cost of feeding behaviors. Small trout holding station behind a cylinder in a large flow tank respirometer will repeatedly feed on artificial prey, actively swimming out from the cylinder wake before opening their mouths to intercept a particle, and then returning to the cylinder (Fig. 2L). While swimming behind a cylinder is less costly than swimming in uniform flow, during feeding the opposite is the case (Fig. 2M,N; Johansen et al., 2020). 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, prey

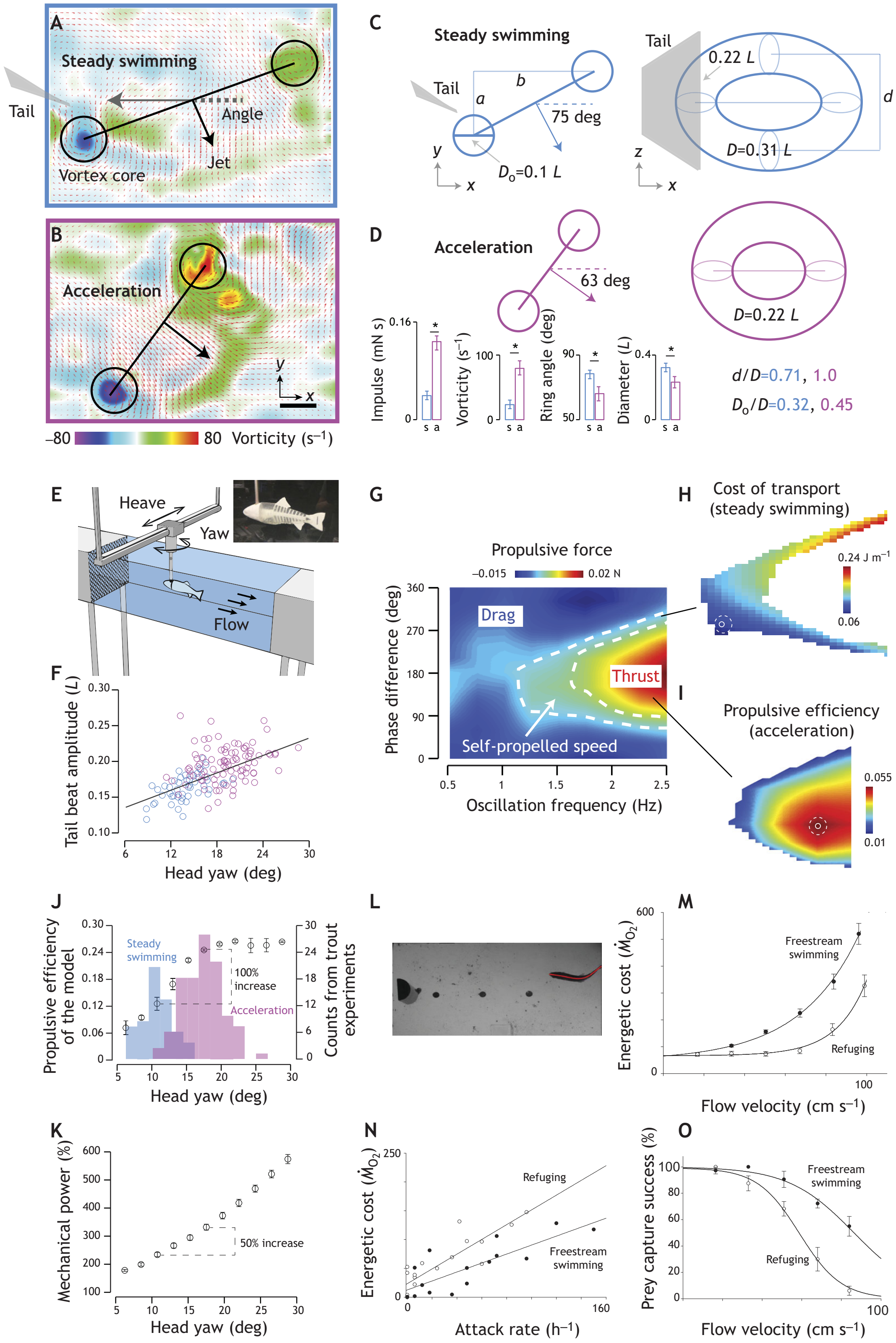

Fig. 2. See next page for legend.

capture success is lower for Kármán gaiting trout; thus, it is also more energetically favorable to feed in uniform flows (Fig. 2O). In rivers, trout hold station behind rocks and large woody debris (Gibson, 1978; Keenleyside, 1962), and feed on insect hatches in pools (Regal, 1992). Results from the lab can be used to generate ecological hypotheses that can be tested in the field, another promising way that can begin to bridge the inside and outside worlds of research.

Fig. 2. Different laboratory approaches to understanding ecologically relevant behaviors such as acceleration and feeding. To eat or avoid being eaten, to keep up with the school or to maneuver through complex habitats, fish need to modulate their swimming speed. Digital particle image velocimetry across a diversity of species shows that the vortex ring shed behind steadily swimming fishes (A) differs from that shed by accelerating fishes (B) (Akanyeti et al., 2017). Steady swimming rings (C) are more elliptical and directed more laterally than rings generated by acceleration (D), which have higher vorticity, lower ring angle and smaller diameter. Acceleration rings contain an average force that is 4 times greater than steady swimming, with thicker vortex cores that approach maximum efficiency values of 0.42. d/D, ratio of ring height to width; D_o/D, ratio of core diameter to ring diameter; s, swimming; a, acceleration. (E) A robotic model approach to energetics can proceed by first understanding the correlation between the degree of head yaw and tailbeat amplitude in live fish (F) swimming steadily (blue) and accelerating (pink). (G) Driven at these head yaw values, a performance space can be rendered by a soft robot molded from a 3D scan of a real trout. When the phase difference between heave and yaw is plotted against the oscillation frequency, steady swimming ('self-propelled speed', where thrust=drag) is revealed as a light blue C-shaped region delineated by dashed lines. (H) Within this region, the cost of transport is minimal at certain combinations of heave–yaw phase differences (~90 deg) and oscillation frequency (~1.5 Hz), 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 region in G). Within this region, propulsive efficiency (net force multiplied by speed divided by power) is maximal at certain combinations of phase differences (~180 deg) and oscillation frequency (~2.5 Hz). This is seen in the red region in I, where the white dot represents the maximum efficiency and the dashed circle encloses a region of 90% similarity. Leveraging robotics allows us to understand swimming movements in terms of mechanical performance. (J) Next, linking back to live fish kinematics, plotting robot head yaw against yaw values from real fish shows that a yaw increase from 10 to 20 deg provides a 100% increase in propulsive efficiency. However, this increase in propulsive efficiency comes with a 50% increase in mechanical power input (K). (L) Fish must accelerate to feed, but the energetic costs of feeding are challenging to measure. One approach involves presenting artificial prey to trout holding station in a flow tank respirometer. (M) These types of predator–prey experiments are possible in the laboratory, and reveal that while swimming behind structures is more energetically favorable than swimming in uniform flow (Johansen et al., 2020), feeding is both less energetically favorable (N) and less successful (O). Panels A–K are from Akanyeti et al. (2017) and panels M–O are from Johansen et al. (2020).

Bringing flow complexity into the lab

Using a cylinder to create unsteady flows

Fish vary their swimming velocity, but water also moves. Flows in nature are often unsteady, where fluid velocity varies in space and time. Wild fish are often attracted to these flows in rivers, lakes and oceans (Jowett and Richardson, 1995; Marchetti and Moyle, 2001). This is evident when fishes in rivers refuge behind rocks, boulders and large woody debris, and when marine fishes hold station behind coral branches and vegetation during tidal flows. Because freely behaving fishes congregate where flow and bluff bodies intersect (Pavlov et al., 2008), it is tempting to assume that they derive a benefit, perhaps energetically for locomotion, ecologically with increased feeding opportunities or both. Critical in understanding the link between biomechanics, ecology and energetics is our ability to re-construct unsteady flows in the lab to elucidate the mechanisms that attract or repel fish to flow.

When fishes as diverse as rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*), alewives (*Alosa pseudoharengus*), bluegill sunfish (*Lepomis macrochirus*) and yellow perch (*Perca flavescens*) are exposed to unsteady flows behind a stationary bluff body such as a cylinder, they can exploit the energy of vortices in its wake (Fig. 3A) (Liao et al., 2003a,b). Cylinders represent a good experimental approach to approximating natural habitat such as submerged vegetation (branches, roots, etc.), rocks and corals, in that discrete, predictable vortices are shed. Experiments with cylinders reveal that rainbow trout can surf when their body length is about twice that of the diameter of the vortex-shedding structure. By doing so, they can hold station (e.g. Kármán gaiting trout can resist drifting downstream in the Earth frame of reference by exploiting vortices in a von Kármán street) by shutting down red axial muscle activity along the entire posterior half of the body (Liao, 2004) (Fig. 3B). When this occurs, only the anterior-most red muscles are active, despite the body undulating with a larger amplitude than seen during swimming against uniform flow (e.g. freestream swimming). When exposed to certain vortical flows, trout can swim by relying on passive interactions of vortices bending the body instead of active muscle contractions. Unsteady flows in the lab reveal a need to understand both passive and active components of very complex, and often unintuitive, fin and body movements. For example, the intrinsic musculoskeletal compliance of a dead trout, devoid of actuation from the nervous system, is sufficient to create upstream swimming (Beal et al., 2006; Liao, 2004). Moreover, fishes swimming in unsteady flows that use swimming modes other than body undulation (e.g. gymnotiform locomotion) may face unique challenges and costs that are only starting to be understood (Ortega-Jiménez and Sanford, 2021). These laboratory results have important implications for the energetics and ecology of fish swimming, such as suggesting that fish save energy and relate to habitat structures according to their body size and swimming mode. Future experiments that (1) look at simultaneous, real-time muscle activity, kinematics and flow field around the body, (2) expand the diversity of experimental species, and (3) look at fluid structure interactions beyond cylinders such as substrate roughness and compliant vegetation (Cameron et al., 2013; Carlson and Lauder, 2011) promise to shed deeper insight into the ecology and energetics of fish locomotion. In the field, these principles of fish and unsteady flow interactions could be applied to enhance the ecological context of stream restoration or augment fish passageway designs to decrease the energetic costs of fish migration.

Many flows, many costs

Behavioral diversity emerges when given enough space. When given free rein in large tanks, rainbow trout show new ways of relating to habitat and flow that can have important energetic implications. For example, trout display at least four behaviors around a single cylinder in flow (Taguchi and Liao, 2011) (Fig. 3C). They can Kármán gait behind, entrain to the side, swim in the front bow wake region or swim away in a region of uniform flow (freestream swimming). Kármán gaiting and entraining trout consume 50% less oxygen as compared with freestream swimming. Flow velocity shifts the energetic consequences of these behaviors profoundly. At lower flow speeds, swimming in uniform flows is the least costly, while at higher speeds, swimming in the bow wake is the least costly. In this way, the energetics of swimming change with flow speed in ways that cannot be predicted by simply studying fish swimming in uniform flows. This gives us insight into habitats in nature, where tides and river runoff create flows that are either not strong enough or too turbulent, which can drive fish populations to alter their daily spatial distributions to save energy.

When trout are exposed to more complex physical structures in flow, they choose configurations that generate the strongest, most predictable vortices (Stewart et al., 2016) (Fig. 3D,E) and avoid structures that create vortices that are too weak to harness (Fig. 3E). Opportunities exist to efficiently investigate the hydrodynamics around more intricate habitats, approximating multiplexed structures such as vegetation or corals, using computation methods (Fig. 3F). These structures can be fabricated and then tested on live fish to investigate the effect of more

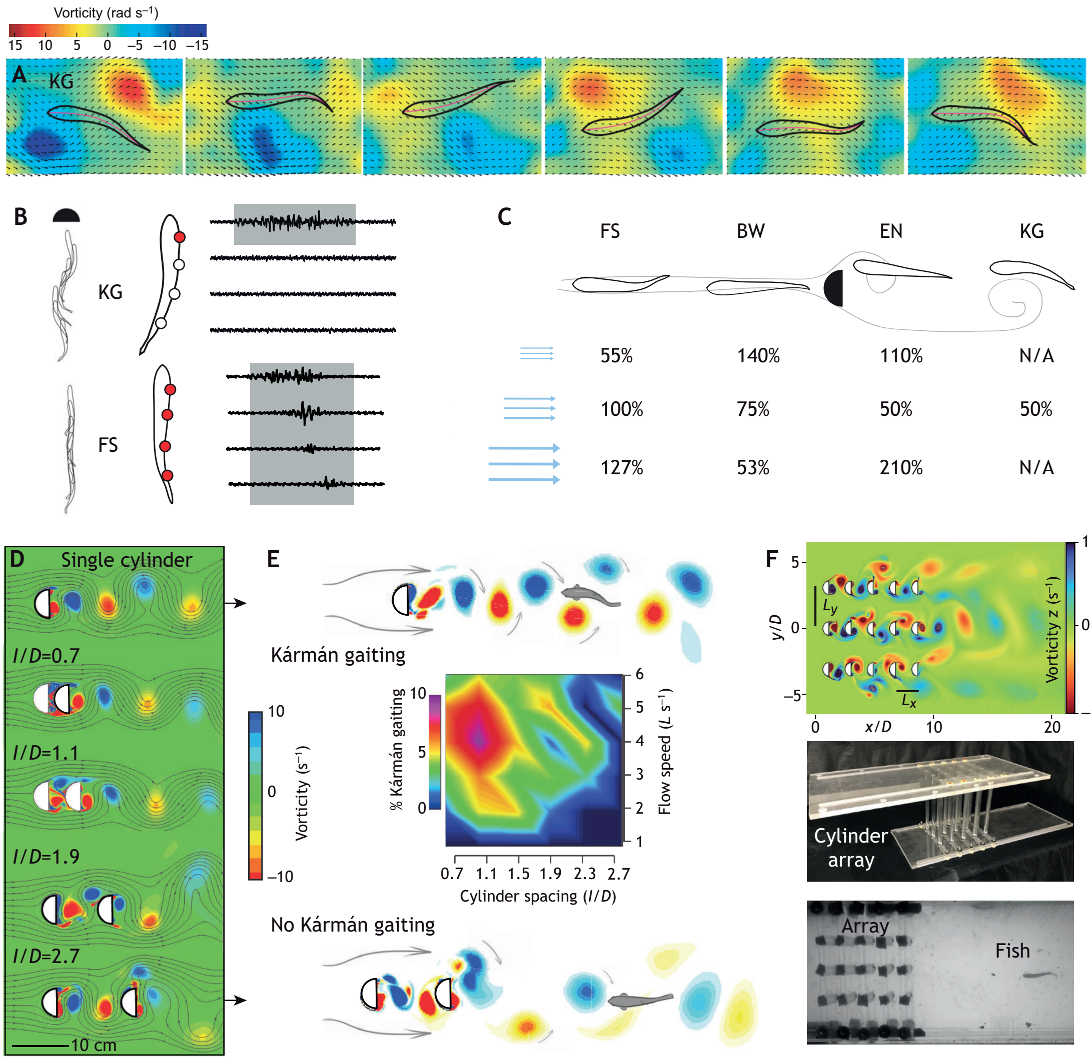

Fig. 3. Fish swimming in the lab under ecologically relevant, unsteady flows reveal unique body kinematics, muscle activity, energetics and behaviors. (A) Flow visualization of a trout slaloming around vortices shed behind a cylinder (e.g. Kármán gaiting, KG). From Liao et al. (2003b). Reprinted with permission from AAAS. (B) KG fish alter both their kinematics and axial red muscle activity patterns as compared with swimming in freestream flow (FS) conditions (modified from Liao, 2004). (C) Even with a single cylinder, fish adopt several positions around the structure, saving energy to different degrees depending on the flow velocity (modified from Taguchi and Liao, 2011). When the energetics of FS swimming is set at 100%, the relative costs of different behaviors can be seen (BW, bow wake; EN, entrain), illustrating the complex relationship between how fish relate to structure and the flow velocity. This observation provides a foothold to begin to understand more intricate fluid–structure–energetics interactions in nature, where similar behaviors likely shape ecological relationships at the population level. (D) Computational fluid dynamics (CFD) model of more elaborate structures in flow. Tandem cylinders placed close together generate a strong vortex street that trout prefer to KG behind (Stewart et al., 2016). *l* is the length between two cylinders in the downstream–upstream direction (cylinder spacing). This is normalized/divided by the cylinder diameter *D* to give the final number. (E) Trout do not KG behind widely spaced cylinders at any flow velocity tested. Modified from Stewart et al. (2016). (F) The wake behind multiplexed structures approaching coral branches or submerged tree branches can be efficiently explored with CFD simulations, where L_x is the downstream spacing and L_y is the cross-stream spacing. Cylinder arrays can then be fabricated and used in live fish experiments to improve our understanding of how fish relate to intricate structures in nature (Sparks et al., 2024).

intricate wakes on swimming kinematics (Sparks et al., 2024). Future work adopting a comparative framework, in addition to investigating how fish relate to natural structures that vary in composition or compliance, will undoubtedly reveal new mechanisms of energy savings.

Studying animals in bigger spaces

Mesocosm as mini-ocean

Much of our understanding of fish locomotion is based on steady swimming or C-start escapes: behaviors that fish can perform soon after placing them in an experimental tank. But by simply giving fish more space and time, more diverse behaviors are revealed. For example, when wild bluefish (*Pomatomus saltatrix*) were left to interact with native killifish (*Fundulus heteroclitus*) in a large outdoor mesocosm (Fig. 4A), new insights were gained into the pursuit algorithm of how fish attack their prey (McHenry et al., 2019).

With accelerometers synchronized to video recordings, locomotory 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

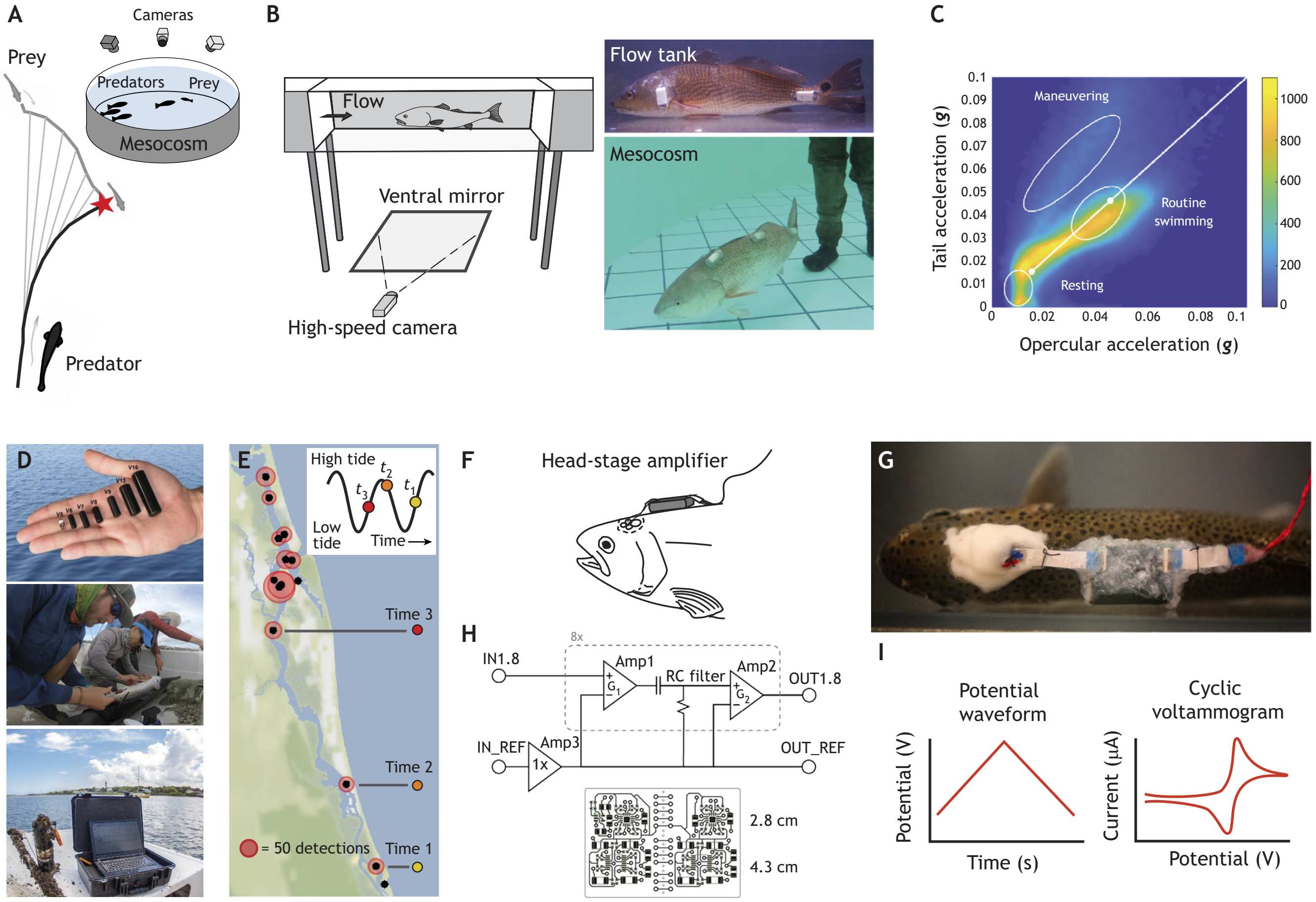

Fig. 4. Observing natural behaviors is facilitated in large spaces where animals have more space and time. (A) Video observation of wild bluefish attack strategies on natural prey requires enough space to allow for behavior decisions, which can be done in large outdoor mesocosm pools (McHenry et al., 2019). (B) To extend our observation of fishes where enough time, space and visibility pose challenges (i.e. small lab tanks, field behaviors in low water clarity, deep water or at night), multiple accelerometers can be placed on fish. Then, velocity-specific swimming movements can be calibrated in a flow tank before release of the fish into a mesocosm. Modified from Stewart et al. (2016). (C) Accelerometers from two positions, the operculum and tail, are used to generate a probability density function plot. By doing so, persistent surveillance of wild fishes can be accomplished for weeks, months or years. (D) Acoustic telemetry uses receivers to track unique ID tags inserted into 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, USA (E. Goturk, C. Morgan and J.C.L., unpublished). The timing (t_1–t_3) 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 fish (modified from Gibbs et al., 2023). (G) The streamlined amplifier can be attached to fast-swimming fishes such as rainbow trout and allows them to swim against different velocities, perform C-starts, or feed on drifting prey (modified from Gibbs et al., 2023). (H) Chip design allows for wireless data logging capabilities (modified from Gibbs et al., 2023). (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 fish.

reveal body kinematics in response to varying biotic and abiotic parameters (Congdon et al., 2022; Mathis et al., 2018; Pérez-Escudero et al., 2014). Many behaviors, however, occur at night, in the deep ocean or murky water, and lie beyond what we can observe visually. One promising approach to realize more behaviors is to attach accelerometers onto fish placed in larger spaces. Behaviors can be first calibrated with video in the laboratory before fish are released into a mesocosm or the wild (Fig. 4B). Examples include steady swimming at different flow velocities in a flow tank, as well as other variables such as heart rate or oxygen consumption (Doherty et al., 2022). Strategic placement of accelerometers can reveal 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 (B. J. Gibbs, J. Strother and J.C.L., unpublished). 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 using *a priori* calibrations in the flow tank based on a probability density function plot of the tail and opercular acceleration (Fig. 4C).

Mesocosms could be populated with native forage and habitat to look at preferred swimming speeds and daily time budgets of behaviors across longer time scales, from weeks to months. This could reveal the effect of physiological states on locomotion during across 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). Looking forward, more studies of tagged, lab-calibrated fish released into mesocosms or the wild promise to reveal new insights into locomotion.

Spying on wild fish with telemetry

There is no substitute for studying animals in the wild, where their bodies and brains have evolved. The advent of biologgers, which can record temperature, depth, acceleration, heart rate and light levels among other parameters for extended periods, has provided a rare 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). In addition, 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).

Acoustic telemetry is a popular approach to understanding underwater animal movement, as satellite technology used in terrestrial tracking is ineffective. Briefly, acoustic telemetry involves attaching a uniquely coded tag to the fish and releasing it back into its habitat, where receivers are placed to listen to its presence (Fig. 4D). 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. The advent of a global partnership that shares networks of receivers (e.g. Ocean Tracking Network) has revolutionized the ability to track individual aquatic animals across long distances at an economical price point (Iverson et al., 2019). This infrastructure has provided new insights into the migration patterns of fishes and thus serves as a powerful conservation tool, separating stocks for better management and revealing important spawning grounds that can be protected (Gunn and Block, 2001; Matley et al., 2022).

What can telemetry tell a biomechanist? Acoustic tags equipped with temperature and pressure sensors can reveal where and when fish move across oceans, but lack the spatial and temporal resolution sought by biomechanists to understand the proximate mechanisms of behavior. One work-around is to place receivers that have detection spans that cover confined bodies of water such as a river. For example, by placing receivers in the Intracoastal Waterway, a narrow marine river along the Atlantic Ocean, the movements of individual fish can be tracked with high fidelity, enabling average ground speeds to be calculated (Fig. 4E). In addition, fish swimming speeds relative to tidal flow cycle and specific habitats (i.e. oyster reef) can be identified (E. Goturk, C. Morgan and J.C.L., unpublished). Given that tidal transport has been shown to save energy for migrating fishes (Gibson, 1992; Weihs, 1978), receivers can be coordinated with flow velocity monitoring stations to gain a better understanding of what flow conditions fish must contend with in nature. By doing so, we begin to establish a species-specific context for the prevalence of certain swimming speeds. How fast do fish choose to swim when left to their own devices? By studying volitional behaviors in wild places, we meet the fish where it is, rather than design laboratory experiments *a priori*. Understanding the prevalence and importance of swimming speed may help us better interpret the role that specific anatomical or physiological attributes, such as fin shape or red muscle distribution, play in enhancing or constraining locomotion.

New technologies have increased interest in understanding how fish move in the wild, as evidenced by the over 6-fold increase in aquatic telemetry from 2005 to 2015 (Hussey et al., 2015; Thorstad et al., 2014), and continued advances promise to enable more mechanistic studies in the field. Already this has resulted in an increase in experimental versus observational studies in the wild, where comparisons can be made between treatment groups (Cooke et al., 2008).

Last but not least, a biomechanist dabbling in telemetry may discover new interests in conservation, while an ecologist recording field behaviors may realize an interest in biomechanics. This is a much-needed perspective for both fields. This shift in outlook is not trivial: an ecological perspective sees habitats 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.

Neuroscience meets ecology

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, and neuroscientists are revealing new insights by asking questions in natural environments (Berman et al., 2019; Cisek and Green, 2024; Dennis et al., 2021). For example, freely flying bats in a naturalistic mesocosm were instrumental in discovering a new population of neurons in the hippocampus that is part of a cognitive map that encompasses 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 fast-swimming fishes (Fig. 4F–H) (Gibbs et al., 2024). With modification, the amplifier can be incorporated into a next-generation biologger to record neural activity in wild fishes to reveal how sensory inputs and physiological states influence, for example, habitat choice or the seasonal pursuit of prey patterns of behavior.

Beyond recording the electrical activity of neurons, the head-stage amplifier could additionally be used to perform an electrochemical technique called fast-scan cyclic voltammetry, in which voltage sweeps can be employed to identify neurotransmitters such as dopamine or serotonin in the brain (Rodeberg et al., 2017). Neurotransmitter levels play deciding roles in locomotion and behavior through the alteration of physiological states (Brown and Bolivar, 2018; Guh et al., 2021; Reid et al., 1998). Examining brain states in freely swimming fishes capable of making real-time decisions will give us greater insight into descending control and modulation. This knowledge will play an important role in contextualizing and better understanding the ecology and energetics of fish locomotion in the years to come.

Concluding thoughts

The field of fish biomechanics is spreading its fins. More attention is being paid to understanding the mechanisms and costs of complex and unsteady behaviors that have ecological relevance (Fig. 5). Laboratory experiments using more naturalistic conditions are deepening our knowledge of the energetics of locomotion. Soft robotic models can be used to explore the effects of swimming kinematics on acceleration in ways that would be challenging in live fish because of the transient and unpredictable nature of the behavior. As we continue experiments indoors, we must also learn to recognize when 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 the lab. 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. Asking lab questions in a field context ensures we add complexity to experiments that generate hypotheses with direct ecological relevance.

In addition to laboratory experiments, studying fishes in larger spaces reveals a greater diversity of behaviors and performance. A more holistic understanding of fish locomotion also requires

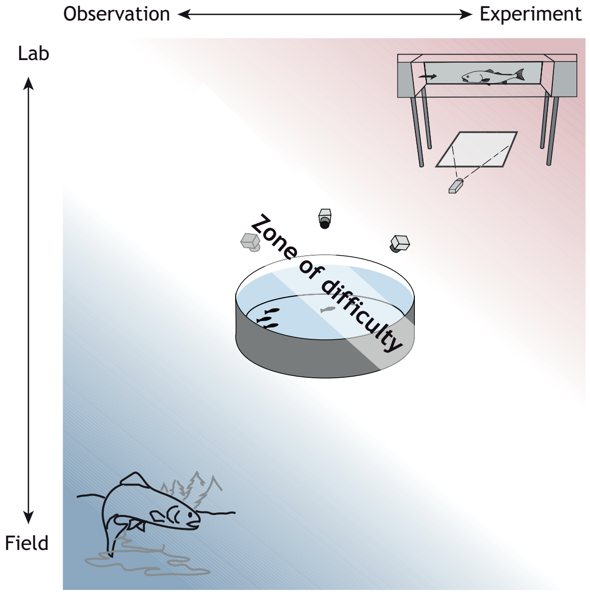

Fig. 5. Bringing fishes into the controlled environment of the laboratory yields powerful insights into behavior, but often at the cost of reducing ecological perspective. Bringing technology into the wild opens up a rich and relevant suite of natural behaviors, but often results in data with low spatial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

incorporating an understanding of neuroscience. 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 animal movement when we integrate technologies and open our doors and eyes to what is happening outside our immediate labs.

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Competing interests

The author declares no competing or financial interests.

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