Ecology and biomechanics of locomotion and feeding in fishes

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Chapter outline

Fishes evolved in nature, but are most conveniently studied in a laboratory. In nature, fishes perform biomechanically-based behaviors in the face of harsh and extreme environmental conditions, many of which relate to locomotion or feeding. Despite the rich body of literature examining the mechanisms underlying these behaviors in a laboratory setting, we know much less about how these behaviors occur in nature. Now, emerging technological advancements are allowing researchers to quantify function in naturalistic conditions, and even the wild. Our chapter will focus on how ecology has shaped the biomechanics and morphology of swimming and feeding in fishes. Specifically, we will focus on extremes, including high pressure (deep sea), high flow (intertidal, rivers, etc.), high/low temperatures (tropics to polar), and low density and viscosity (aerial feeding). These habitats provide valuable case studies in which to understand how environmental factors influence function in driving evolution.

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1 Introduction

Fishes make up more than half of all living vertebrates, with approximately 36,000 extant species alive today (Facey et al. 2023). Most of these species live in water which can vary widely in temperature, density, pressure, turbidity, flow speed and direction, pH, salinity, viscosity, light transmission, and oxygen content (Fig. 1). Impressively, fishes often live at the extremes of many of these variables, such as from very cold (e.g., Eastman, 1991) to hot environments (e.g., Blanchard et al., 2024). Some fishes live under high pressure (e.g., the deep sea Günther, 1887; Priede, 2017) or low pressure (e.g., at high altitudes Kang et al., 2017), while others experience extreme water motion daily in environments such as rocky intertidal zones (Webb et al., 2010). Although these habitats seem extreme from a human perspective, adaptations across biological scales have evolved to meet these physiologically challenging conditions. To fishes, these environments are simply home. Not only can fishes thrive at extremes, but some are capable of dealing with extreme environmental fluctuations, requiring adaptations to meet broad ranges of conditions that impact their physiology on short temporal scales (Brown and Feldmeth, 1971). Understanding the biomechanical responses of fishes to these extremes will allow us to better predict the future of fish diversity and provide a window into rapid evolution, informing conservation efforts by building our understanding of how and which species will survive in a rapidly changing world. Indeed, much of fish diversification stems from adapting to positions on environmental gradients.

Extreme habitats arouse both public curiosity and scientific interests. These habitats not only provide interesting studies of adaptation themselves but also as natural systems in which to test hypotheses of evolution. All animals are subject to physical laws, resulting in 'hard' constraints on their adaptability and plasticity (Alexander, 1985, Taylor and Thomas, 2014, Higham et al., 2021). These constraints are thought to prevent certain phenotypes from emerging. However, evolution is also influenced by 'soft' constraints that arise from ecological, developmental, and evolutionary processes that determine which phenotypes are adaptive under certain conditions. Therefore, the realized phenotype of a fish will result not only from what is biologically possible, but from the context in which the fish performs tasks related to growth, survival, and reproduction. This context is often characterized by multiple ecological variables simultaneously (e.g., temperature, flow, pressure, etc.). Disentangling the responsible variable(s) is a challenge of evolutionary biologists, physiologists, and biomechanists.

Ecomechanics (or mechanical ecology) is the study of how organisms interact with their biotic and abiotic environment (Wainwright, 1976, Bauer et al., 2020, Higham et al., 2021, Ferry and Higham, 2022). Fishes have evolved a vast range of morphologies and mechanics across environmental conditions, making this group a valuable study system to increase our

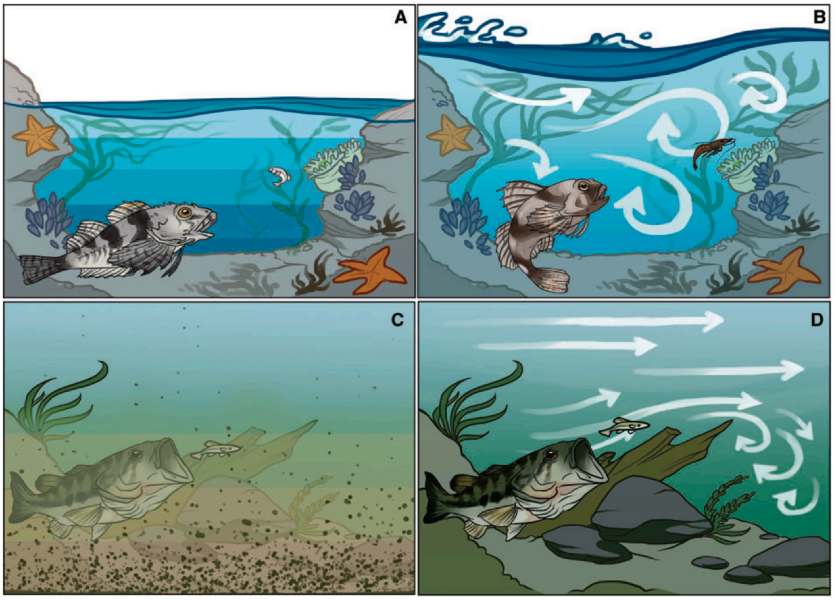

FIG. 1 Illustrations of ecological variables of interest to fish biomechanists, including temperature changes (A) and flow (B) in tidepools, turbidity in a river (C), and flow in a river (D). These environmental conditions each impact fish biomechanics, as shown here with the example of prey capture. *From Higham et al. (2015) (with permission from Oxford University Press).*

understanding of how form and function are influenced by the environment. To understand these relationships, researchers can use ecomechanical models, biophysical models that incorporate both organismal traits and environmental variables (Higham et al., 2021). These models are key tools in understanding the relative contributions of environmental and ecological conditions to the evolution of form and function in fishes. To fully implement such models, fishes should be measured in ecologically-relevant conditions or directly in their natural habitats. However, experimental biomechanics is extremely challenging to accomplish in the field. First, effective experimental design requires reproducibility and the ability to understand trends through repeated observations. In nature, the repeatability of both animal movements and environmental variables poses great challenges (Venerus et al., 2024). These challenges can be overcome in laboratory studies (Oufiero Garland, 2009). Second, physically following fishes in their large-volume habitats requires advanced technology. Acoustic telemetry is traditionally used to quantify movements of fishes in nature and—with the appropriate design—can be used to quantify swimming speed in fishes (Hanson et al., 2010). However, tagging technologies can limit broad application due to their high expense, and sensor sizes can be bulky and invasive to attach. Recent technological advances have led to the development of smaller and more powerful portable devices to measure fish movements in the field, facilitating studies of ecomechanics under fully natural conditions (Bauer et al., 2020). These new technologies include calibrated wireless accelerometry that can recover data on fish swimming kinematics and performance with great resolution (Brownscombe et al., 2018; Gleiss et al., 2019; Venerus et al., 2024). Given these advancements, our understanding of the ecomechanics of fishes is likely to increase substantially in coming years.

Here, we use examples from a broad variety of habitats, ranging from inshore rivers to the deepest oceans, to explore how extreme conditions in temperature, pressure, fluid density, viscosity, and flow characteristics have influenced the evolution and biomechanics of fishes (Fig. 1). Specifically, we will investigate how fishes deal with the challenges of extreme and fluctuating environmental conditions at both proximate (i.e., immediate impact) and ultimate (i.e., on an evolutionary scale) levels. Significant research has explored fishes' physiological ability to tolerate conditions such as hypoxia and extreme temperatures (e.g., Mandic et al., 2009). Some fishes can tolerate a wide range of conditions over short time periods, whereas others are limited to a narrow range. The variation in thermal tolerance can be linked to a wide variety of traits, including body size, life stage, genetics, and phenotypic plasticity (McKenzie et al., 2021). Other fluctuating environmental variables may also drive variations in biomechanics, although this is much less understood.

Swimming and feeding are especially important aspects of fish behavior and have accordingly received considerable attention for decades (Shadwick and Lauder, 2006; Wainwright et al., 2007; Day et al., 2015; Lauder, 2015). Much of the focus of these biomechanical studies has been on laboratory measurements, including swimming in a flume (Jayne and Lauder, 1995; Drucker and Lauder, 2000) or capturing prey in still water (Wainwright et al.; 2001; Higham et al., 2006a). These studies powerfully advanced our initial understanding of aquatic swimming and feeding. However, key gaps in knowledge remain, specifically in two areas. First, these two behaviors of swimming and feeding are rarely performed in isolation. Capturing prey almost always incorporates locomotion (Higham 2007a, 2007b), which then relies on sensory feedback, motor control, and integration among higher-level complex systems involved, for example, in vision and locomotion (Higham et al., 2015; Martin et al., 2024). Second, both water and fish are rarely moving in steady states, which means more realistic measurements involving acceleration and maneuvering are needed to understand the evolution of morphology and biomechanics among fishes.

It is ultimately the interaction between biomechanics, physiology, and ecology that will determine an organism's survival and success. For almost all fishes, swimming is fundamental for capturing prey, fleeing from predators, mating, migrating, and finding optimal habitats to maintain homeostasis. Here, we aim to review the role of ecology, both biotic and abiotic, in the biomechanics of fish locomotion and feeding. However, we focus largely on the interactions between individuals and their physical environment. We acknowledge that the ecology of a fish also involves interactions with other individuals of the same species as well as individuals of other species. We first focus on the impacts of temperature, a key environmental variable that is the most comprehensively studied. We then focus on the role of water density and viscosity. Finally, we examine the role of environmental flow. Our chapter concludes with an outline of where the field is heading in the coming decades, including some key areas that should be prioritized.

2 Temperature

2.1 Role of temperature on fish performance

Water temperature varies considerably across space, latitude, depth, day, season, and over long timescales. Most fishes conform to environmental temperatures—a strategy known as ectothermic poikilothermy—and will experience changes in body temperature as the ambient temperature changes. Only a few exceptions, such as tunas and lamnid sharks, are regionally homeothermic, regulating internal body temperatures to support exceptionally high swimming performance (e.g., Bernal et al., 2001). Even these exceptions illustrate the importance of temperature on fish physiology and biomechanics. Indeed, temperature has been labeled the "master factor" controlling fish performance and behavior (Brett, 1971). The exponential increase in the rates of reactions, described using Arrhenius kinetics, has been used in many models for rates of metabolism, growth, development, performance, and fitness (Knies and Kingsolver, 2010). Once the optimal temperature is exceeded for a given process, proteins become overly flexible, reducing substrate affinity by disrupting the active site and ultimately causing critical proteins to denature (Hochachka and Somero, 2002). Although temperature changes can influence many physiological processes, the direct impacts of temperature on muscle performance and function likely have the largest biomechanical consequences. In general, increases in temperature are associated with an increase in muscle contraction frequencies across a range of species (Rome, 1990, Rome and Swank, 1992, Altringham and Block, 1997, Syme, 2006, Donley et al.. 2007). Specifically, temperature will impact the ability of a muscle to generate power (muscle force x muscle shortening velocity) by altering the rate of cross-bridge cycling. Temperature's effect on the speed of cross-bridge cycling is likely due, in part, to colder temperatures slowing the release of Ca^{2+}, the diffusion of Ca^{2+} to the actin and myosin, and the reuptake of Ca^{2+} by the sarcoplasmic reticulum (Brill and Dizon, 1979). Therefore, higher temperatures result in higher power until temperatures exceed an optimal value, after which a sharp decrease in power is expected (Donley et al.. 2007). This will ultimately play a critical role in how fishes respond to warming temperatures across the globe (Fig. 2).

Numerous studies have examined the role of temperature on the swimming performance of fishes, which is more completely reviewed elsewhere (Syme, 2006). In general, maximum swimming speed is significantly reduced in cold water due to the negative impacts on muscle contraction frequency (Wardle, 1980, Claireaux et al.. 2006). The effects of temperature are often represented by Q_{10} values, which represent the rate at which a biological process increases when temperature is raised by 10 °C. The following equation is used:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{10^{\circ}\mathrm{C}/(T_2-T_1)}$$

where R is the rate and T is the temperature in Celsius. In a study of maximum tail beat frequency of cod (*Gadus morhua*) in relation to

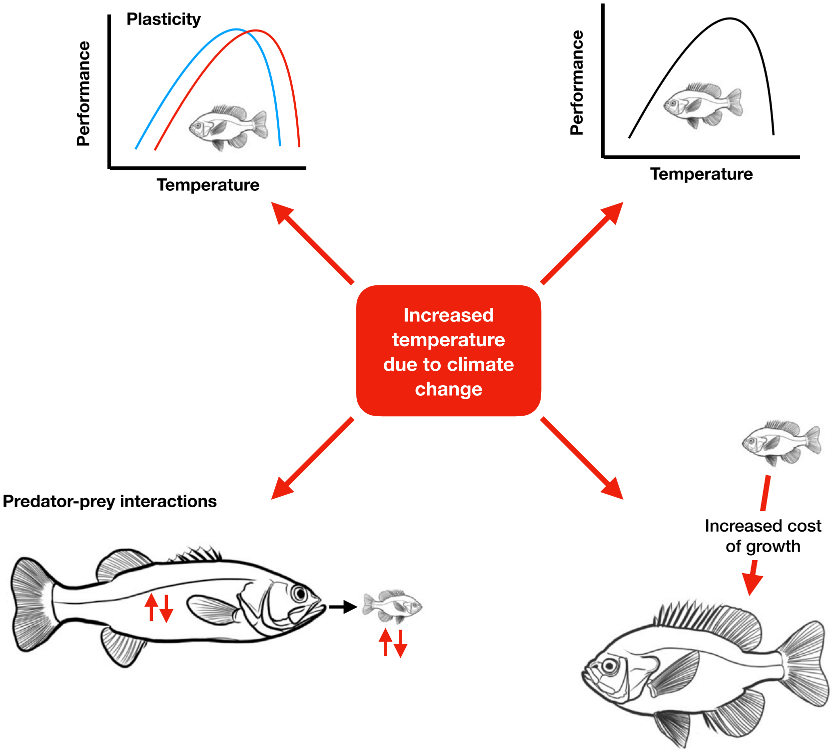

FIG. 2 The role of increased temperature due to climate change on fish physiology and biomechanics. Temperature will impact performance (e.g., suction feeding, maximum locomotor speed), such that performance increases with temperature up to a point, after which there is a sharp decline. Fishes often exhibit plasticity in their thermal response curve, acclimating to new environments within short periods of time. Based on previous work, changing temperatures can both increase and decrease predator and prey success, depending on the study. Finally, increases in temperature will likely make growth more costly in fishes.

temperature, an average Q_{10} of 2.06 was found, indicating that tail beat frequency approximately doubled with an increase of 10 °C (Videler and Wardle, 1991). Similarly, temperature was found to be a significant predictor of critical swimming speed, the speed at which a fish can no longer hold position against a laminar flow current or U_{crit}, from 204 studies of freshwater fishes from the Iberian Peninsula (Cano-Barbacil et al., 2020). Another study showed that chub mackerel (*Scomber japonicus*) swim slower at 18 °C (52.5–97.5 cm s^{-1}) than at 24 °C (70–120 cm s^{-1}) (Dickson et al., 2002). Using high-speed videography, Dickson et al. (2002) also examined the swimming kinematics in relation to temperature. Interestingly, temperature did not impact tail-beat frequency or stride length, but warmer temperatures were associated with an increase in the propulsive wavelength (Dickson et al., 2002). Thus, both maximum speed and maximum sustainable speed are commonly dependent on ambient water temperature. Although power output of muscle decreases at lower temperatures, some fishes can compensate for decreased power output by compressing their recruitment order into a narrow range of locomotor speeds (Rome, 1990). In other words, they can recruit more muscle fibers and faster fiber types at a given speed. For example, a fish at 10 °C must recruit 1.53-fold greater fiber cross section of muscle than at 20 °C (Rome, 1990).

Temperature not only has short-term impacts on animal performance, but can potentially lead to habitat expansion over evolutionary time scales. Modern sharks became pelagic in the early Cretaceous (122.6 mya, Barremian; Sternes et al., 2024), a time when the sea surface temperature was a maximum (28.2 °C, Cretaceous thermal maximum; Scotese et al. 2021). When swimming speed was modeled as a function of temperature based on previous studies of shark muscle (Donley et al., 2007), the authors found that pelagic species swam fastest during this warm period. Therefore, the increased water temperature may have permitted the niche expansion via increased swimming performance and improved predatory capabilities (Sternes et al., 2024).

Despite the significant impacts of temperature on performance, many temperate-zone fishes can acclimate to short-term cold conditions to enhance locomotor activity (Johnston, 1993, Domenici and Blake, 1997; Fig. 2). For example, cold acclimation (at 5 °C compared to 15 °C) enhanced maximal oxidative capacity of red muscle from short-horned sculpin (*Myoxocephalus scorpius*; Guderley and Johnston, 1996). At colder temperatures, the oxidation rates of mitochondria from cold-acclimated sculpin muscle were comparable to rates at warm temperatures (approximately 5 °C warmer) for mitochondria from warm-acclimated sculpin muscle (Guderley and Johnston, 1996). These compensatory changes in mitochondrial capacity may be linked to an increase in mitochondrial volume density. These findings are one of several that illustrate the thermal robustness of some fish muscle to changes in temperature (concept reviewed in Olberding and Deban (2021)). At the organismal level, some fishes can adjust to colder temperatures to maintain their locomotor performance. For example, goldfish acclimated to 35 °C can swim 0.2 ms^{-1} at

10 °C (Johnson and Bennett, 1995). However, when acclimated to 10 °C, these fish could swim at speeds up to 0.9 ms^{-1}. These experiments demonstrate extreme temperature compensation and suggest that thermal responses in fishes are complex, varying by species and season.

Yet another way for fishes to adapt to cooler temperatures is to exhibit regional or whole-body endothermy, as exhibited by some sharks, billfishes, tuna, and other species such as the louvar (*Ouvarus imperialis*) and opah (*Lampris guttatus*) (Donley et al., 2004, Graham and Dickson, 2004, Wegner et al., 2015, Stoehr et al., 2020, Arostegui et al., 2023). Typically, fish red muscle lies close to the lateral edges of the body. In these endothermic species, however, large bundles of red muscle are arranged deep in the body, internally along the spine, allowing the fish to conserve heat generated by these active tissues. Additionally, these fishes maintain elevated internal tissue temperatures by conserving metabolically derived heat through vascular countercurrent heat exchange (Dickson and Graham, 2004, Harding et al., 2021). While regionally endothermic fishes tend to swim faster (about 1.6 times) than ectothermic fishes in nature (Harding et al., 2021; Fig. 3), endothermic fishes have not expanded their thermal niche, occupying similar environmental temperature regimes to poikilothermic taxa.

Another way in which fish can cope with extremely cold water is with antifreeze proteins, which bind to ice crystals in the body fluids and inhibit their growth, thereby preventing organismal freezing (DeVries and Cheng, 2005). Notothenioid fishes of the Southern Ocean surrounding Antarctica are one of the most famous examples of how fish can adapt to extreme cold. In fact, this marine environment is the coldest and harshest in the world, with perennial freezing seawater temperatures of −1.91 °C. They do this, in part, with novel ice-binding proteins (antifreeze glycoprotein) (Cheng and Detrich, 2007; DeVries, 1971). The blood serum of notothenioid fishes freezes at −2 °C, a point at which most fish would die (DeVries, 1971). Instead, antifreeze proteins allow these fish to occupy a region inhospitable to other fishes.

Predator-prey interactions, although not studied as frequently as swimming, can also change in response to changes in temperature (Domenici et al., 2019; Figs. 2 and 4). Grigaltchik et al. (2012) examined both swimming performance and predator-prey interactions under different temperature acclimation conditions. Australian bass (*Percalates novemaculatus*) was the predator and eastern mosquitofish (*Gambusia holbrooki*) was the prey. They acclimated prey and predators separately (to either 25 °C or 15 °C) and then exposed each to acute test temperatures of 10 °C, 15 °C, 20 °C, 25 °C, and 30 °C. They found that warm-acclimated fish swam faster at warmer acute temperatures, whereas cold-acclimated fish swam faster at colder acute temperatures (Grigaltchik et al., 2012). Maximum escape speeds of mosquitofish during predation trials exceeded burst swimming speeds in swimming trials. However, the maximum attack speeds of bass were lower than the burst swimming speeds from the swimming trials. Consequently, the maximum absolute attack speeds of bass

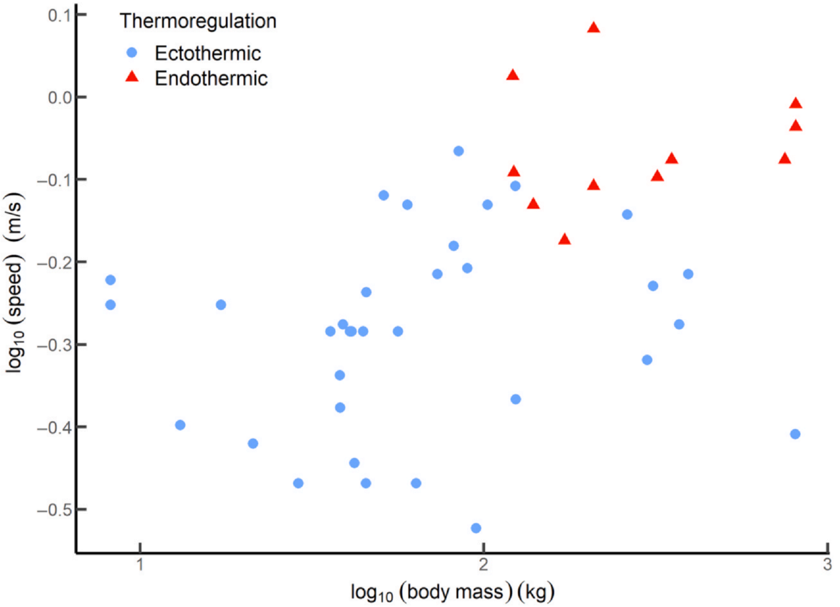

FIG. 3 Cruising speed of fishes with regional endothermy and those without it. *From Harding et al. (2021) (reproduced with creative commons license CC BY 4.0).*

were lower than the escape speeds of mosquitofish. This likely leads to decreased predation pressure with increased temperatures.

In a more recent study, Allan et al. (2017) investigated the effects of temperature and elevated CO_2 on the predator-prey interactions between a coral reef predator (*Pseudochromis fuscus*) and prey (*Pomacentrus wardi*). They measured capture success, predator attack distance, and predator attack speed. For the prey, they measured reaction distance, escape distance, and escape speed. Capture success and predation rate increased with both temperature and CO_2 levels (Allan et al., 2017), which may have stemmed from decreased prey escape speed and prey responsiveness, but could also be due to increased motivation from the predator given that higher temperatures cause an increase in metabolic rate. These complex interactions between predators and prey are an important area for future research aiming to understand the mechanisms by which global warming will impact ecosystems, conservation, and management.

Temperature also has a strong influence on suction feeding in fishes. Several kinematic variables of bluegill sunfish all increase with decreasing temperature, including time to peak gape, time to maximum lower jaw depression, and time to mouth closing (Wintzer and Motta, 2004). Similarly, largemouth bass experience a decrease in mouth opening performance with acute deviations (higher or lower from 25 °C; DeVries and Wainwright, 2006).

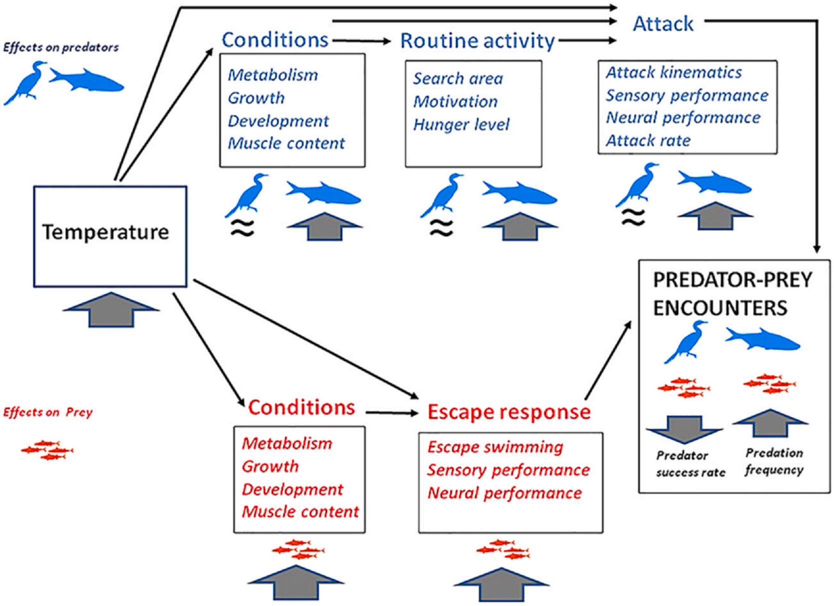

FIG. 4 How predator–prey interactions might respond to changes in temperature, based on fish as prey, and fish or an endotherm (e.g., a bird) as predators. This is based on the prediction that the climate is warming. Downwards and upwards arrows indicate a decrease and an increase, respectively. A ≈ sign indicates no significant change. At high temperatures, prey conditions (growth and metabolism) increase and so does escape performance, also because of the direct effect of temperature. Temperature has similar positive effects on fish predator attacks (via direct effects and because of decreased body conditions). In addition, because of their higher routine activity and higher hunger level (due to higher metabolism), the frequency of predator–prey interactions increase (though they may decline at high temperatures that exceed acclimation temperatures; see main text). Temperature has little effect on performance and hunger level on endotherms (compared to the effect on ectotherms), and therefore predator success rate is expected to decrease at high temperature because of the positive effects of temperature on prey escape performance. *From Domenici et al. (2019) (reproduced with creative commons license CC BY).*

However, the value of Q_{10} was lower than expected (1.28 for values between 15 °C and 25 °C), suggesting some type of physiological adaptation to a predatory lifestyle in a thermally variable environment. Regardless, the reduced suction feeding performance suggests that extreme water temperatures could reduce capture success, or alternatively, shift prey selection. Future investigations in this area would inform our understanding of temperature effects on feeding, providing important insights into aquatic food webs.

Finally, in addition to influencing the contraction of swimming and feeding muscles directly, temperature can impact locomotor and feeding performance by altering the function of other complementary systems, such as the visual system. For example, swordfish (*Xiphias gladius*) exhibit a specialized heating system in an extraocular muscle that warms the eyes and brain up to

10 °C–15 °C above the ambient water temperature (Fritsches et al. 2005). Using electroretinograms, the authors examined the temporal resolution of the visual system via the flicker fusion frequency, the stimulus frequency at which the retina can no longer resolve a sinusoidally modulated light stimulus. They found that flicker fusion frequency was 5 Hz or less at 10 °C and over 40 Hz at 20 °C, suggesting substantial improvement in visual function under warmer conditions (Fritsches et al., 2005). By keeping their eyes at temperatures between 19 °C and 28 °C, swordfishes can maintain their visual abilities in colder water, which likely conveys an advantage for detecting prey.

2.2 The roles of hydrostatic pressure

Like temperature, hydrostatic pressure influences biological processes by affecting the volume in which chemical reactions occur (e.g., Macdonald, 2021; Somero, 1992; Yancey, 2020). These effects translate across biological scales, from DNA to ecosystem properties, and impact the locomotion of fishes and other deep-sea organisms. Water is nearly incompressible throughout the habitat range of bony fishes, making it unlikely that pressure physically constrains a fish's ability to move through water. However, the physical properties of cells and proteins that underlie the ability of fishes to swim and feed *are* greatly influenced by hydrostatic pressure. The most well studied of these proteins is actin, which binds with myosin in the cross-bridge cycling process that allows muscles to contract (e.g., Somero, 1992; Macdonald, 2021). Fish actins are known to be sensitive to changes in hydrostatic pressure, with deep-sea fishes displaying adaptations to maintain actin stability under high pressures and cold temperatures (Bourns et al., 1988; Gao and Winter, 2015; Morita, 2003; Swezey and Somero, 1982). Additional molecular adaptations to high pressure, including the accumulation of stabilizing solutes such as the osmolyte trimethyl-amine-N-oxide (Kelly and Yancey, 1999; Yancey, 2001, 2005; Yancey et al., 2014; Yancey and Siebenaller, 2015), pressure-adapted forms of enzymes involved in energy metabolism such as lactate dehydrogenase (Brindley et al., 2008; Gerringer et al., 2020; Siebenaller, 1984; Siebenaller and Somero, 1978; Somero and Siebenaller, 1979), and other protein and cellular-level changes that have yet to be studied likely combine to support full swimming and feeding function for fishes living under high pressures.

In the deep ocean, a collection of habitats loosely classified as depths greater than 200 m, the interacting effects of cold temperatures and high hydrostatic pressures can be challenging to disentangle, and these factors combine to influence fish activity, physiology, and biomechanics. Cold temperatures and high pressures can slow biological processes through these volume changes and through the reduction of particle kinetic motion (e.g., Macdonald, 2021). However, the extent to which hydrostatic pressure and temperature can be considered comparable as evolutionary drivers remains unknown. For example, both high pressures and cold temperatures impact membrane fluidity, an essential parameter for cellular function (e.g., Cossins and Macdonald, 1989; Sinensky, 1974). The effects of high pressure on lipid structural properties have been hypothesized to relate directly to temperature, with a 100 MPa increase in hydrostatic pressure—the equivalent of 10,000 m water depth—corresponding to a ~13–21 °C decrease in temperature (Somero, 1992). By this correlation, a membrane at 2 °C in the deep waters of Challenger Deep at 11,000 m would be under an effective temperature between about −11 and −19 °C due to the habitat pressure (Macdonald and Cossins, 1985; Somero, 1992). Yet, the ability of a membrane to maintain the correct fluidity under high pressure is not achieved with the same structural changes as those required by a membrane under cold temperatures (Winnikoff et al., 2021). Development of a model or equation that accurately predicts the combined effects of pressure and temperature on biological reaction rates will require considerably more data (Gerringer et al., 2017). Future research should carefully consider the influence of both habitat temperature and habitat pressure on fish biology to unravel the effects of these similar variables.

Deep-sea fishes are incredibly diverse, with many captivating morphologies and behaviors (e.g., Priede, 2017; Fig. 5). The deep sea is made up of multiple diverse habitats, each with their own suite of evolutionary drivers, from hydrothermal vents to deep-sea trenches, topographically complex seamounts, submarine canyons, mesopelagic habitats, the deep bathypelagic, and the abyssal plains. This broad range of ecological niches that make up the deep sea have led to high biological diversity. In fishes, high rates of body shape evolution have been shown across deep-sea taxa in comparison to shallow-living species (Martinez et al., 2021), further demonstrating the diversity of form and function across deep-sea habitats. The swimming and feeding ecology of deep-sea fishes remains understudied, but a few important investigations have begun to reveal how deep-sea conditions influence fish biomechanics. Observations of fishes by remotely operated vehicles (ROVs), submersibles, and free-vehicle landers each provide opportunities to study fish biomechanics in the wild. A few studies have documented swimming kinematic parameters of single deep-sea fish taxa that live near the seafloor, such as the abyssal rattail *Coryphaenoides armatus* at 4800 m (Gadiformes, Macrouridae), the blue hake *Antimora rostrata* (Gadiformes, Moridae) at 2500 m (Collins et al., 1999), and an aphyonid cusk eel (Ophidiiformes, Bythitidae) (Mundy et al., 2018). The deeper-living *C. yaquinae* swam at a speed of 0.17 body lengths per second, while the bathyal *A. rostrata* swam at 0.39 body lengths per second (Collins et al., 1999). For the cutthroat eel *Synaphobranchus kaupii* (Anguilliformes, Synaphobranchidae) at depths 775–2467 m, average swimming speed was 0.55 ± 0.03 body lengths per second (Bailey et al., 2005). At a similar depth of 2504 m, the aphyonid species (*Barathronus* sp. or *Nybelinella* sp.) swam at speeds of 0.33 ± 0.15 body lengths per second (Mundy et al., 2018), demonstrating that phylogeny and morphology also influence swimming

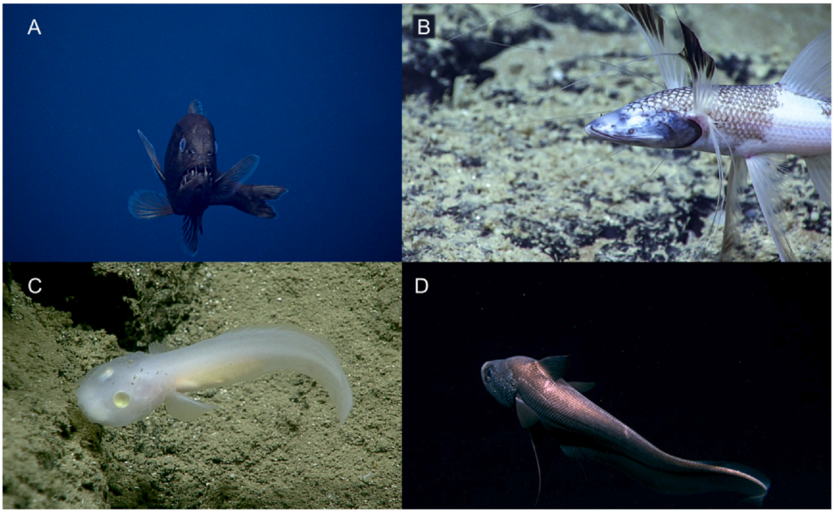

FIG. 5 (A) A pelagic fangtooth, *Anoplogaster* sp. (Anoplogasteridae) seen at 800 m during a midwater transect. Image courtesy of the NOAA Office of Ocean Exploration and Research, Deep-Sea Symphony: Exploring the Musicians Seamounts. (B) A tripodfish, *Bathypterois viridensis* (Ipnopidae) is a deep-sea ambush predator, adopting this posture to sense potential prey. Image courtesy of the NOAA Ocean Exploration, Windows to the Deep 2019. (C) Aphyonid fish observed at 2500 m in the Mariana Archipelago (*Barathronus* sp. or *Nybelinella* sp., Bythitidae, Ophidiiformes). In the only observation of this fish alive, the animal swam slowly, ~0.33 body lengths per second (Mundy et al., 2018). Image courtesy of the NOAA Office of Ocean Exploration and Research. (D) Rattails like this fish, *Coryphaenoides lateralis* (Macrouridae) are important members of the deep-sea fish community (e.g., Priede, 2018). Many deep-sea fishes, like these rattails, have elongate bodies, believed to be an adaptation for swimming efficiency. Image courtesy of NOAA Ocean Exploration/Global Explorer.

speed, in addition to habitat depth. Additionally, deep-sea fishes have been shown to be adept at backward swimming, an important adaptation for escape and maneuverability (Priede and Jamieson, 2025). Backward swimming by reverse undulation occurs in multiple deep-sea taxa across orders, including the rattail *Coryphaenoides yaquinae* (Macrouridae, Gadiformes), the cutthroat eel *Ilyophis robinsae* (Synaphobranchidae, Anguilliformes), and the cusk eels *Barathrites iris* and *Bassozetus* sp. (Ophidiidae, Ophidiiformes). Backward swimming appears to be aided by axial elongation in these deep-living taxa, with contributions from the pectoral fins in the rattails (Family Macrouridae) and cusk eels (Family Ophidiidae). These findings highlight that maneuverability, in addition to efficiency, is likely an important driver of the evolution of deep-sea fish swimming (Priede and Jamieson, 2025). In a recent study, to assess the influence of habitat depth on swimming speeds within constrained phylogenies, swimming kinematics of fishes were recorded from opportunistic observations of four major orders of deep-sea fishes across a broad depth range, from the intertidal to depths almost 6000 m. This analysis revealed that deep-living fishes tend to swim more slowly than their shallow-living relatives (Woodworth et al., 2024). This decline in swimming speed seen across the seafloor-associated Gadiformes and Perciformes corresponds closely to habitat temperature, showing a dramatic decrease at shallow depths, followed by stable, slow swimming speeds at depths >1000 m. If hydrostatic pressure were directly impacting swimming performance in deep-sea fishes, swimming speed would decrease linearly with increasing habitat depth. Instead, the declines in swimming speed across observed taxa appear more similar to a temperature-depth profile, variable in surface waters and stably low at great depths. These results suggest that pressure effects on swimming speed in the deep ocean are likely either insignificant or are much lower than the effects of temperature (Woodworth et al., 2024). This study illustrates the importance of considering how environmental variables interact to influence fish activity and behavior, as factors such as temperature, light and nutrient availability, oxygen concentration, and hydrostatic pressure all influence organismal biology in the deep ocean.

In addition to *in situ* observations of fishes swimming in the deep ocean, trends in fish morphology with increasing habitat depth also provide clues as to how deep-sea conditions have driven animal evolution. In the deep ocean, many fishes have elongated bodies, either eel-like or elongated with tapering tails. This strong trend toward axial elongation at great depths occurs in both the true eels (Anguilliformes) and other unrelated taxa such as the Gadiformes, Ophidiiformes, and Osmeriformes, suggesting evolutionary pressures toward elongate forms in the deep ocean (Neat and Campbell, 2013). The prevalence of elongated fishes at great depths is not fully understood and could include phylogenetic considerations. It is hypothesized to relate to swimming efficiency, with elongated fishes being capable of swimming long distances at slow, sustained swimming speeds (Neat and Campbell, 2013). The need for swimming efficiency, rather than fast speeds, could reflect the physically closer interaction distances between predator and prey in the dark deep ocean when compared to shallow-living depths. In the well-lit environment of the surface oceans, organisms often sense one another through visual cues, leading to long chases. In the deep oceans, mechanosensation and chemosensation dominate organism's sensory landscapes, which is hypothesized to reduce evolutionary pressure for fast swimming speeds, known as the visual interactions hypothesis (Childress, 1995; Drazen and Seibel, 2007; Seibel and Drazen, 2007). Additionally, elongated body forms and their corresponding high swimming efficiency (Vorus and Taravella, 2011) may be valuable in the deep ocean due to the slight increase in water viscosity at high pressure, which may favor anguilliform swimming (Borazjani and Sotiropoulos, 2009; Neat and Campbell, 2013). Morphological analyses have shown that deep-sea fishes do tend to have longer body forms, lending potential support to this efficiency hypothesis (Friedman et al., 2020; Martinez et al., 2021). Future work should directly measure oxygen consumption under high pressure to test these energetic hypotheses, particularly as one study has shown that the European eel, *Anguilla anguilla*, was able to maintain the same swimming speed with reduced oxygen consumption under high pressure (Sébert et al., 2009). Experiments that measure the energetics of fish swimming and feeding behaviors should apply deep-sea conditions of cold temperatures and high pressures to understand the evolutionary influence of these factors and to inform understanding of energy flow through the deep ocean, Earth's largest habitat.

Pressure impacts fish biology directly by influencing molecular and cellular processes. Additionally, high pressures in the deep ocean can also indirectly influence evolutionary processes, with the potential to affect fish ecomechanics. For example, although pressure itself does not seem to directly change fish swimming speeds (Woodworth et al., 2024), pressure does influence buoyancy in fishes, which has implications for locomotion and energetics. Most fishes are neutrally or slightly negatively buoyant, which helps them to avoid excess energy expenditure maintaining their vertical position. This neutral or near-neutral buoyancy often relies on the fish's ability to inflate a gas-filled swim bladder. However, these swim bladders become increasingly difficult to inflate under the high pressures of the deep sea (Scholander, 1954). Interestingly, some deep-sea fishes can use gas-filled swim bladders in the deep sea, even at great depths (Priede, 2018), while many others rely on watery, gelatinous tissues (Gerringer et al., 2017), high lipid stores and muscle water content (Drazen, 2007), and low-density bones (Denton and Marshall, 1958; Gerringer et al., 2021; Martin et al., 2022) to maintain buoyancy. Many of these adaptations are thought to be accompanied by reduced muscle strength and lower activity rates (Drazen et al., 2015; Drazen et al., 2013; Gerringer et al., 2017). This potential evolutionary trade-off between reducing buoyancy and swimming capacity remains an important line of investigation for future studies. Importantly, many deep-sea fishes may not need to be fast swimmers, in large part due to a shift in feeding ecology, with multiple deep-sea fishes being sit-and-wait ambush predators that interact with prey across short spatial scales (e.g., Childress, 1995; Drazen and Sutton, 2017).

Fishes in the deep sea feed via diverse methods (Drazen and Sutton, 2017; Gartner et al., 1997). These deep-sea fishes often have dramatic feeding morphologies. For example, the loosejaw dragonfish (Stomiidae) of the mesopelagic have large, fanged jaws and lack skin between the mandibular rami, leading to a completely open oral floor. This extreme adaptation allows the fish to close this large mouth by reducing drag, lowering the surface area of the closing jaw (Kenaley, 2012). Many deep-sea fishes are sit-and-wait predators with upturned mouths (e.g., the attenuated spider fish, *Bathypterois atricolor* and the pelagic humpback anglerfish, *Melanocetus johnsonii*, Fig. 6). Even within one clade, deep-sea fishes can have vastly different feeding morphologies, as seen for example in the Lophiiformes (e.g., Miller et al., 2025). In demersal fishes that live in association with, but often do not rest on,

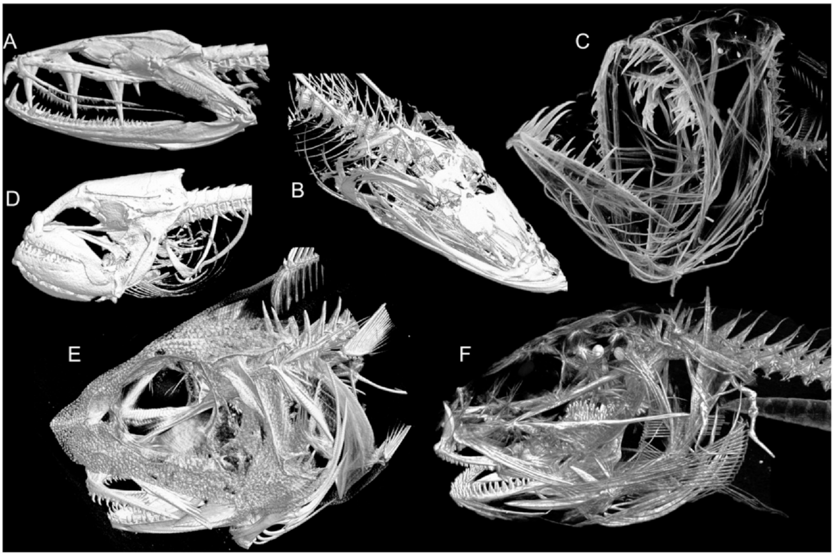

FIG. 6 Example morphology of deep-sea fishes shown in micro-computed tomography (micro-CT) scans. (A) *Dysomma polycatodon*, Synaphobranchidae, SIO 00-35, 100–200 m, Taiwanese fish market, South Pacific Ocean, up to 29.4 cm SL. (B) *Bathypterois atricolor*, Ipnopidae, SIO 68-537, 5486 m, Central Pacific Ocean, 14.5 cm SL. (C) *Melanocetus johnsonii*, Melanocetidae, UW156286, Eastern North Pacific, 9.5 cm SL. (D) *Simenchelys parasiticus*, Synaphobranchidae, SIO 05-133, collection depth to 1000 m, Tasmania, South Pacific Ocean, 11.6–14 cm standard length (SL). (E) *Malacocephalus laevis*, Macrouridae, SIO 00-200, 500 m, Fieberling Guyot, North Pacific Ocean, 35.6 cm SL. Scans by Mackenzie Gerringer, SUNY Geneseo. (F) *Pseudoliparis swirei*, Liparidae, USNM 438975, 7949 m, Mariana Trench, Pacific Ocean, 11.2 cm SL. Scan by Adam Summers, Friday Harbor Labs, University of Washington.

the seafloor, feeding morphology is also highly variable. For example, the pugnose eel, *Simenchelys parasitica* (family Synaphobranchidae) has a robust, blunt cranial morphology (Fig. 6) and is believed to feed by biting off sections of its prey's flesh via rotational feeding (Eagderi et al., 2016). There is significant room for advancement in research to understand how deep-sea conditions have influenced the evolution of feeding biomechanics. Although very little research has been conducted on the biomechanics of feeding in deep-sea fishes, some studies have used functional morphology to explore deep-sea fish feeding ecology, complementing other methods including stomach contents analyses, direct observation, and stable isotope analyses (reviewed by Drazen and Sutton, 2017). For example, in the hadal zone, depths greater than 6000 m, snailfishes in the family Liparidae have been found to have strong, well-ossified pharyngeal jaws, hypothesized to be a key factor in the group's evolution into these deep-sea trenches because these jaws allow snailfishes to effectively feed on amphipod crustaceans that are abundant in hadal habitats (Gerringer, 2019; Gerringer et al., 2017). Future work should combine these morphological analyses with computational fluid dynamic modeling and *in situ* studies of fish feeding to understand how hydrostatic pressure influences processes like suction feeding and the evolution of feeding ecology at depth.

3 Viscosity and density

3.1 Viscosity

Aside from its physiological effects, temperature also influences fish performance and kinematics by changing water viscosity (Fuiman and Batty, 1997; Johnson et al., 1998). A conservative estimate might suggest that most teleosts reside in environments where sustained temperatures range from between 0 °C and 30 °C (Hunt von Herbing, 2002). As temperature decreases through this range, the viscosity of seawater approximately doubles (Dorsey, 1968; Hunt von Herbing, 2002; Podolsky, 1994). Several fishes, however, inhabit more extreme habitats and experience temperatures that fall outside this range or fluctuate widely. For example, some of the coldest aquatic environments on earth are occupied by species of the family Nototheniidae, which live in temperatures as low as −1.9 °C (DeVries and Wohlschlag, 1969), while desert pupfish (*Cyprinodon macularius*) occupy bodies of water that can reach 44 °C (Schoenherr, 1988). The habitats of *C. macularius* also fluctuate seasonally in temperature, exposing the species to variations of nearly 40 °C (Schoenherr, 1988). Although the range of fluctuations in their habitats is slightly smaller, swordfish (*Xiphias gladius*) can experience changes of nearly 20 °C over just a few hours during their vertical migrations from surface waters to depths of over 400 m (Carey and Robinson, 1981), and tidepool fishes are exposed to heating and cooling of 10–15 °C daily (Arakaki and Tokeshi, 2006; Sidell et al., 1983). Based on the physical properties of water, viscosity should vary by a factor of three across these extreme environments, impacting the flow regimes under which fishes are swimming and feeding. Further, due to seasonal and diel fluctuations as well as changes in the fluid environment organisms experience at different body sizes, individual fish may experience substantial variations in viscosity throughout their lifetimes (Johnson et al., 1998).

Understanding the influence of viscosity on fish swimming and feeding requires disentangling the interacting effects of temperature. Methyl cellulose solutions often exhibit shear-thinning or viscoelastic properties, which deviate from the Newtonian behavior of water. This means that the viscosity of methyl cellulose solutions can vary with the flow rate, potentially altering the hydrodynamic conditions experienced by swimming fish in ways that are not directly comparable to natural aquatic environments. Keeping this potential limitation in mind, it is possible to isolate the physiological and hydrodynamic it is possible to isolate the physiological and hydrodynamic effects of temperature from those of viscosity by adding thickening substances such as dextran or methyl cellulose to the water to manipulate both viscosity and temperature independently (Fuiman and Batty, 1997; Johnson et al., 1998). Johnson et al. (1998) tested the escape performance of goldfish at 5 °C, 20 °C, and at 20 °C with dextran added to mimic the viscosity at 5 °C and found no effect of viscosity on any measured parameters. The same study, however, then examined the escape response of smaller guppies (*Poecilia reticulata*), which had a mean length of 2.0 cm compared to 7.7 cm for the goldfish, and found that viscosity negatively affected burst swimming speeds. Similarly, investigations of Atlantic herring (*Clupea harengus*) and Atlantic haddock (*Melanogrammus aeglefinus*) larvae of different sizes found that viscosity caused greater reductions to voluntary swimming speeds in smaller larvae, while temperature had minimal effects on these size groups (Fuiman and Batty, 1997; Hunt von Herbing and Keating, 2003). Swimming kinematics follow similar trends, with stride length and tail beat frequency decreasing more strongly with increasing viscosity in smaller larvae (Fuiman and Batty, 1997; Osse and van den Boogaart, 1999).

The consistent findings that smaller fish are more strongly affected by viscosity are likely due to their comparatively low Reynolds number (Re) (Fuiman and Batty, 1997; Higham et al., 2015; Johnson et al., 1998). The dimensionless Reynolds number describes the fluid environment a body in water experiences by representing the ratio of inertial forces to viscous forces, and is calculated as $Re = \rho UL/\mu$ where ρ is the fluid density, U is the swimming speed, L is the characteristic length (total length of the fish or square root of its frontal area) and μ is the dynamic viscosity (Fuiman and Batty, 1997; Hunt von Herbing, 2002; Yavno and Holzman, 2018). At low Re, viscous forces dominate, such that small, slow-moving fishes can be imagined as moving through honey compared to at high Re, where inertial forces dominate and large, fast-moving fishes can glide through water on the merits of their momentum. Thus, the small size and low speeds of fish larvae cause them to experience water as a relatively viscous medium (Müller and Videler, 1996), which appears to be detrimental to their swimming performance, including their voluntary swimming speed (Fuiman and Batty, 1997) and maximal escape speed (Johnson et al., 1998). Along with the negative effects of low Re on prey capture (reviewed in Holzman et al., 2025), this loss of performance may also act as a selection pressure on growth rate, where marine fish larvae that grow quickly improve their fitness by escaping the viscous regime (Müller and Videler, 1996; Yavno and Holzman, 2018). These examples illustrate the importance of considering not only the multi-faceted drivers of evolution across fish habitats, but the importance of size both to our own conceptual understanding of fish biomechanics and to the evolution of fish form and function.

In addition to examining the effects of Reynolds number on swimming performance by comparing fish across sizes, it is possible to mimic the viscous low-Re regime of small fish at low temperatures by subjecting larger fishes to highly viscous fluids. The effects of altering fluid viscosity on performance vary. West African lungfish (*Protopterus annectens*) (Horner and Jayne, 2008) and gray bichirs (*Polypterus senegalus)* (Lutek and Standen, 2021) do not show any changes to their spontaneous swimming speeds in high-viscosity environments, due in part to increased muscle activation. Although zebrafish (*Danio rerio*) (Danos and Lauder, 2012) and sea lampreys (*Petromyzon marinus*) (Tytell et al., 2023) experience impaired C-starts and spontaneous swimming speeds (respectively) in viscous regimes, they also appear to compensate through increased muscle activation to outperform expectations set by simulations.

In addition, several distinct kinematic patterns emerge from these experiments. First, body curvature increased and stride length decreased with viscosity in *P. annectens* (Horner and Jayne, 2008)*, P. senegalus* (Lutek and Standen, 2021)*,* and *P. marinus* (Tytell et al., 2023). In the two species that maintained their swim speeds in high viscosity, *P. annectens and P. senegalus*, tail beat frequency and lateral displacement of the body both increased in more viscous regimes, with the largest change in displacement occurring anteriorly in *P. annectens* (Horner and Jayne, 2008; Lutek and Standen, 2021). Interestingly, these kinematic findings in adult fish swimming at low Re closely mirror the swimming modes of larval fishes (Voesenek et al., 2018). Many small larvae, which exist at low Re, display more anguilliform swimming modes characterized by high-frequency undulations, high body curvatures, large lateral displacements that extend anteriorly, and low stride lengths early in development and transition to subcarangiform or carangiform swimming modes as they grow and enter flow regimes dominated by inertial forces (Osse and van den Boogaart, 1999, 2000). In other words, it appears that elongate adult fish and fish larvae both respond to strong viscous forces by adopting similar swimming kinematics (Voesenek et al., 2018). Future work should continue to investigate the role of viscosity as a selective pressure on morphology, mechanics, and life history, especially in extreme environments and smaller fishes.

3.2 Density

Although the density of water can change marginally due to fluctuations in temperature, salinity, and hydrostatic pressure, the largest and most biomechanically significant difference in density that fishes experience exists for species that move between air and water. A wide range of fish taxa can successfully locomote on land (see Kawano and DiSanto, 2025), but some can also capture prey outside of the aquatic environment. Examples of taxa that can leap out of the water to capture flying or suspended invertebrates (and occasionally birds) include the Archerfish (*Toxotes* spp.) (Bekoff and Dorr, 1976; Schuster, 2018), African tigerfish (*Hydrocynus vittatus*) (O'Brien et al., 2014), giant trevally (*Caranx ignobilis*) (Honeyborne and Brownlow, 2017) silver arowana (*Osteoglossum bicirrhosum*) (Goulding, 1980), freshwater butterflyfish (*Pantodon buchholzi*) (Schwab and Saidel, 2003), brown trout (*Salmo trutta),* Atlantic salmon (*Salmo salar*) (Kalleberg, 1958), Hart's rivulus (*Anablepsoides hartii*) (Seghers, 1978), four-eyed fish (*Anableps anableps*) (Zahl et al., 1977), northern pike (*Esox lucius*) (Glegg, 1945), and black basses (*Micropterus* spp.) (Evermann and Clark, 1920; Harrison, 1951; Marshall, 2011). Several other species can capture terrestrial prey by picking them from the substrate with their jaws, including mudskippers (Gobiidae: Oxudercinae), reedfish (*Erpethoichthys calabaricus*), eel catfish (Siluriformes: Clariidae) (Van Wassenbergh, 2019), and the mangrove rivulus (*Kryptolebias marmoratus*) (Pronko et al., 2013). The ability to operate in both air and water is a potentially significant evolutionary innovation for these and other taxa, and requires overcoming distinct biomechanical challenges.

The drastic difference in density between air and water presents several challenges for terrestrial and aerial prey capture and processing. First, virtually all teleosts, including many of the fishes that feed terrestrially or aerially, utilize suction during feeding (Liem, 1980; Wainwright et al., 2007). Suction is generally achieved when fish expand their buccal and opercular cavities, creating a sudden drop in pressure and unidirectional flow into the mouth aperture (Day et al., 2015; Muller et al., 1982). In water, this flow exerts sufficient force on the prey to draw it into the predator's buccal cavity. Air, however, is roughly 800 times less dense than water (e.g., Van Wassenbergh, 2013, 2019). As the kinetic energy of a volume of fluid can be modeled using the equation,

$$E_{kin} = \frac{\rho V v^2}{2}$$

where ρ is density, V is fluid volume, and v is fluid speed, the fluid speed of air would need to be $\sqrt{800}$ or $\sim$28 times faster than that of water to create a flow with the same kinetic energy (Van Wassenbergh, 2013). The rate of buccal expansion necessary to generate flows of air at these speeds would require the muscles that power suction feeding to contract at velocities above their assumed physiological limits (Hill, 1938; Van Wassenbergh, 2013). Further, even if sufficient kinetic energy was generated, the force exerted by flow passing over a prey item would be weaker in air due to its low viscosity (Van Wassenbergh, 2013). Thus, suction feeding is not possible in terrestrial environments (Herrel and Aerts, 2004) and, in air, fishes must feed by other means.

Fishes that feed in air often overcome this first challenge by shifting away from suction feeding. During terrestrial feeding, fishes grab prey items directly with their jaws (Herrel and Aerts, 2004; Van Wassenbergh, 2019), and in the case of aerial feeding, fishes overtake and engulf prey items in the air (Lowry et al., 2005; Axlid et al., In review; Fig. 7). Studies of *O. bicirrhosum* and *M. salmoides* have demonstrated that aerial feeding involves larger and more rapid movements than aquatic feeding, including a larger gape size (Lowry et al., 2005; Axlid et al., In Review). It is unknown whether these trends occur

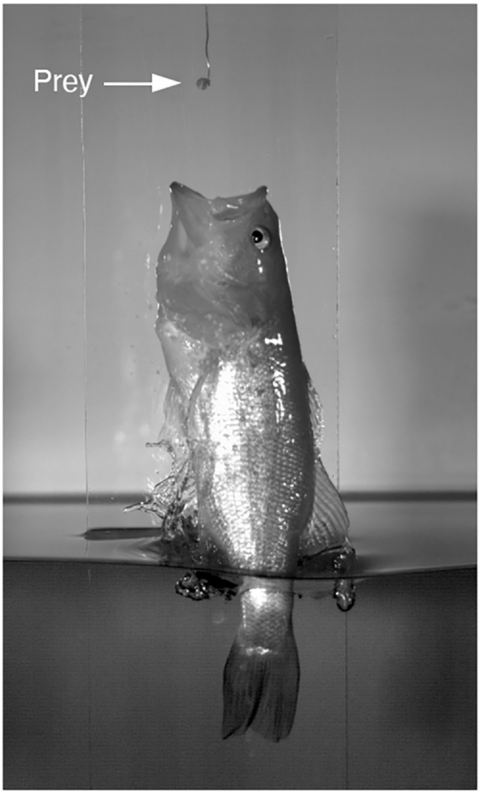

FIG. 7 Still frame a largemouth bass (*Micropterus salmoides*) leaping out of the water to successfully capture a mealworm suspended approximately 20 cm above the surface. Image taken by Erik Axlid.

due to shifts in feeding strategy or result incidentally from the comparatively low density and viscosity (and therefore drag) of air. Larger gape sizes, for example, may increase the volume engulfed and minimize the accuracy necessary to capture the prey (Lowry et al., 2005). This was corroborated by Higham et al. (2007) in which the authors found that gape size and ram speed were positively correlated among cichlid species and proposed that larger mouths may offset the reduced accuracy that occurs when feeding at high speeds.

The second challenge associated with aerial and terrestrial feeding lies in transporting prey once it has been captured. Tetrapods accomplish this by using tongue-based transport, supported by modifications to the hyobranchial apparatus, but fishes do not have the benefit of this evolutionary novelty (Herrel and Aerts, 2004; Reilly and Lauder, 1990; Van Wassenbergh, 2019). Instead, most fishes manipulate prey within the mouth cavity using intra-oral water currents, which are generated through movements of cranial and hyobranchial bones

(Alexander, 1969; Bemis and Lauder, 1986; Reilly and Lauder, 1990). However, as is the case during ingestion of the prey, air flows generated by the fish buccal apparatus during terrestrial and aerial feeding are too weak to transport food (Heiss et al., 2018; Herrel and Aerts, 2004; Van Wassenbergh, 2019). Therefore, nearly all fishes must return to the water to swallow or otherwise process their prey (Van Wassenbergh, 2019). The mudskippers (Gobiidae: Oxudercinae) represent the single known exception to this rule, and while they cannot swallow without water, they retain water in the buccopharyngeal cavity during terrestrial excursions which can be used to transport food into the esophagus while remaining on land (Michel et al., 2015).

4 Flow

The field of fish swimming biomechanics was formed from the fundamental advances provided by studies of locomotion through still water, where there is an absence of flow (Gray, 1933, Gray, 1953, Bainbridge, 1958, Lighthill, 1971, Webb, 1975). However, fishes are commonly exposed to flow in nature, often varying dramatically across space and time. Fish locomotion in complex flows has attracted interest from across disciplines, from conservation and ecology to fluid dynamics and robotics (Anderson et al., 1998; Enders et al., 2003; Fausch 1993; Heggenes 2002; Higham et al. 2015; Liao et al., 2003a; McLaughlin and Noakes 1998; Odeh et al., 2002; Pavlov et al., 2000; Shuler et al., 1994; Smith and Brannon 2005; Triantafyllou et al., 2002). In this section, we review the types of flow experiences by fishes in nature, how fish swim and capture prey in these different flows, the energetic benefits and costs to swimming in flowing environments, and how the integration of functional systems might be altered when complex flow is considered.

4.1 Types of flow experienced by fishes in nature

Fishes are less constrained by the force of gravity than terrestrial vertebrates owing to the greater denser and viscosity of water versus air. Because water does not stay still for long in nature, these same properties make fishes suspended in water susceptible to the effects of flows arising from abiotic and biotic sources. Gravity-induced water flow over elevation (i.e. rivers and streams), lunar-driven changes in tidal cycle, Coriolis forces and temperature differences, and waves in shallow water (caused by wind) all lead to water movement. Depending on their strength and scale, these three-dimensional flows have the potential to substantially alter fish swimming and feeding kinematics and behavior.

Fish locomotion is impacted by flows, which can span the spectrum of laminar to turbulent. Turbulence and turbulence intensity (e.g., the standard deviation of the flow velocity divided by the mean flow velocity) has been used to describe complex flows that fish swim through (Kirkbride 1993; Warhaft 2002; Enders et al., 2003; Odeh et al., 2002). Natural flows are often unsteady, varying with respect to time for a given point in space, and viscous, where velocity gradients may not lead to the formation of vortices. Flows can perturb the body, causing shape deformations or rotational movements depending on the direction of force (e.g., perpendicular or parallel to the body, corresponding to normal or shear strain, respectively, Liao, 2007).

4.2 Biomechanics of swimming in flow

To know how fishes swim in flow, it is useful first to understand how fishes swim in the absence of flow. Body and caudal fin swimmers, a mode of locomotion that represents the vast majority of fishes, pass a body wave from head to tail that travels faster than the forward speed of the fish (Gray, 1933). This undulatory wave is generated by the sequential contraction of axial muscles, alternating from on either side of the body. The movement of the body generates vortices that are shed in the downstream wake that resemble a toroid or vortex ring (Lauder and Drucker 2002; Müller et al., 1997; Shadwick et al., 1999; Webb, 1975) Rosen (1959). Undulatory swimming through still water is thought to be similar to swimming in uniform flow. With the advent of swim tunnel respirometers, the energetics of a continually swimming fish could be measured (Blazka (1960) and Brett (1964)), providing a crucial link between swimming velocity and its associated metabolic cost.

4.3 Benefits and costs to swimming in flow

The relative benefits or costs of swimming in flow depends on the nature of the flow. For fishes swimming against uniform flows to remain in the same location in the Earth frame of reference, known as holding station, the cost of swimming is thought to be similar to that of swimming through still water at an equivalent velocity. Indeed, the literature of experimental fish swimming biomechanics in flow tanks implicitly assumes this.

Unsteady flows present a more complex environment, one that generates a greater diversity of behavioral responses in fishes beyond rheotaxis. Unsteady flows that display chaotic and wide fluctuations in velocity can require more energy for fish to swim through, while flows that are more predictable can decrease the cost of swimming. Additionally, vortical flows need to be at an appropriate size relative to the length of the fish to exact a behavioral response. One can imagine relatively small (plankton wakes) or large (ocean gyres) vortices having no effect on the body swimming kinematics of a migrating tuna. The ability to maintain stability in three-dimensional flows, either actively with powered movements or passively using with intrinsic compliance of the body and fins, plays a key role in whether fish will seek out or avoid turbulence, as it influences the energetic costs of locomotion and feeding (Masashige and Liao, 2011, Johansen et al. 2020, Gibbs et al. 2024).

Fish can seek hydrodynamics benefits in at least two ways when they swim in flow (Fig. 8). The first is by exploiting regions of reduced flow (flow

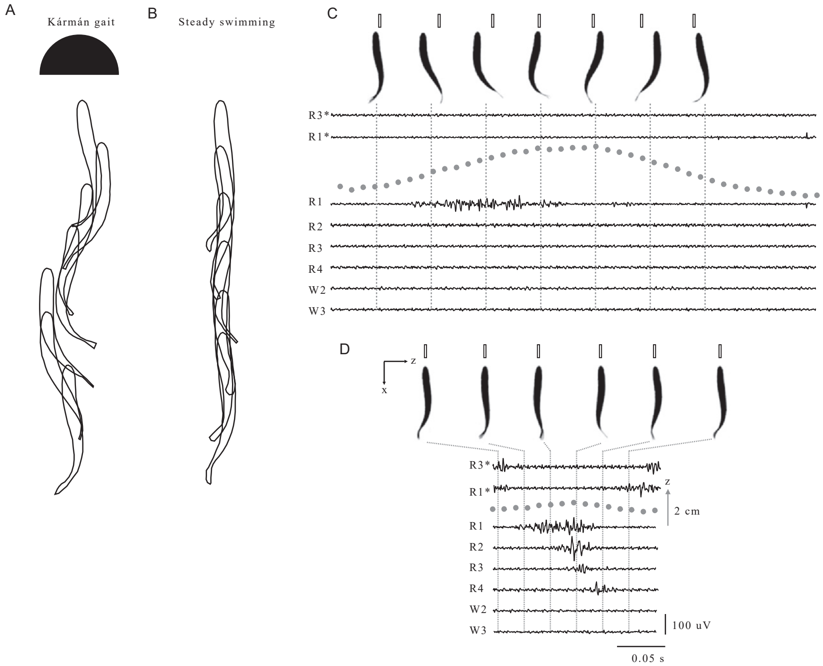

FIG. 8 Swimming fish can recapture energy from vortical flows in their environment. (A) A trout positioned behind a stationary D-section cylinder in flow adopts a novel gait, called the Kármán Gait, that exhibits substantial deviations in body kinematics compared to (B) fish swimming steadily in uniform flows at the same velocity. (C) Electromyography reveal a propagating wave of red R but not white (W) axial muscle activity during steady swimming. (D) During Kármán Gaiting, all muscle activity stops except for axial muscles close to the head.

refuging). The second is by harnessing the energy of environmental vortices from stationary structures in flow (rocks, large woody debris, coral branches) or from the wake of other fish, as when schooling.

Fish have evolved behaviors to conserve energy in dynamic aquatic environments (Fig. 9). One such behavior is the Kármán gait, a distinctive swimming pattern that allows fish to maintain position behind stationary objects like cylinders by synchronizing their movements with the swirling eddies in the wake. More specifically, a von Kármán vortex street is established behind cylinders and other bluff bodies, in which a repeating pattern of vortices is created by the unsteady separation of flow. Kármán gaiting enables fish to exploit the energy of the surrounding fluid, reducing their own energy expenditure. When the ratio of body length is about twice that of the cylinder diameter, fish can shut down red muscle activity along most or all of the body (Liao, 2004, Beal, 2006). Under these specific conditions, the vortices can "swim" the fish passively through passive interactions of the flow and a flexible body (e.g., not by active muscle contractions). Fish do not only

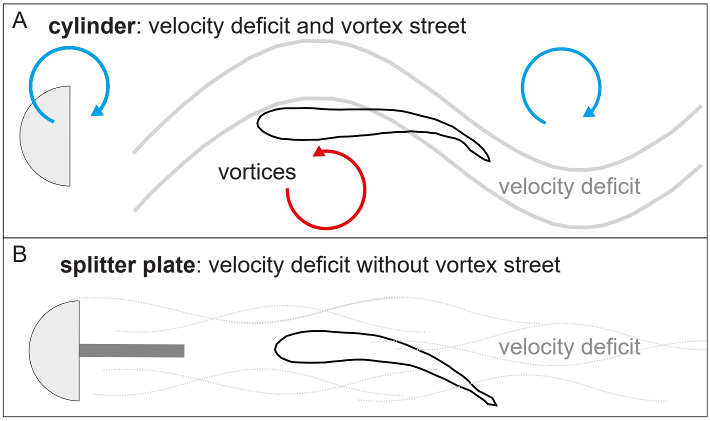

FIG. 9 Fish exploiting a vortex street versus swimming in reduced flow (a velocity deficit). A. A vortex street shed behind a cylinder contains vortices and a velocity deficit, as the two are inseparable. B. A splitter plate behind a cylinder generates a velocity deficit, which for this example is a region of reduced flow without large, discrete vortices.

Kármán gait around a cylinder, but they can also entrain just downstream and to the side of the cylinder as well as swim in the high-pressure bow wake region in front of the cylinder (Taguchi and Liao, 2011). Both Kármán gaiting and entraining trout consume 50% less oxygen as compared to those swimming in uniform flow. Energetics savings depend heavily on flow speed, which in turn dictates the strength of shed vortices from a bluff body, its periodicity and turbulence levels. For example, when flows are too slow or fast, trout do not Kármán gait because the vortex street is not strong enough, or it becomes too turbulent to maintain stability, respectively. Instead, fish choose to occupy other regions around the cylinder. Note that the most energetically favorable regions around a cylinder change with flow speed, suggesting that in nature fish may be constantly shifting habitats to save energy.

Laboratory experiments with multiple cylinders illustrate how more complex structures such as coral branches or large woody debris may influence fish swimming biomechanics and energetics (Stewart et al., 2016; Sparks et al., 2024; Fig. 10). In complex habitats, the spacing of cylinders is critical in promoting station-holding behavior and eliciting changes in swimming kinematics. Whereas true turbulence has been shown to increase the cost of locomotion (Enders et al., 2003; Hinch and Rand 1998; Pavlov et al., 2000; Pavlov et al., 1982; Webb 1998), powerful opportunities exist for understanding how fish can save energy in complex yet repeatable flows created in the laboratory.

Across species, the flow conditions experienced in nature have been linked to both morphology and performance. Among wrasses (family Labridae) occupying reef sites at Lizard Island, northern Great Barrier Reef, high wave energy habitats were characterized by labrids with high pectoral fin aspect

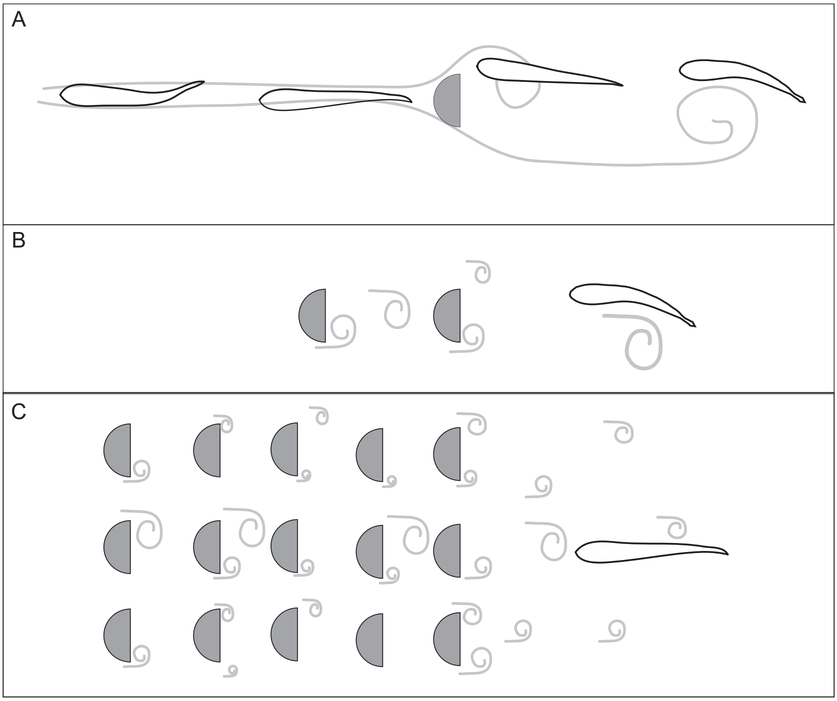

FIG. 10 The study of fish swimming around cylinders provides a repeatable approach to understanding how fish relate to vortices. Fish adopt different swimming kinematics and energy-saving behaviors when associating with single cylinders (A). The wake behind tandem (B) or multiple cylinders (C) that are spatially separated can elucidate how fish relate to more complex flows by approximating the hydrodynamic signatures behind vegetation or fish schools. *This figure has been redrawn from the following sources: Liao et al., 2003a, 2003b; Stewart et al., 2016; Sparks et al., 2024.*

ratios (Fulton et al., 2001). High-aspect ratio fins are used by these fishes to achieve high sustained swimming speeds (Wainwright et al., 2002). Fishes with lower aspect ratio pectoral fins typically occupy low wave energy (deeper) habitats and are generally slower swimmers. In a follow-up study, Fulton and Bellwood (2004) examined the relationship between swimming performance, wave exposure, and the distribution patterns of labrids on temperate rocky reefs. Again, swimming speed was strongly correlated with fin shape (Fulton and Bellwood, 2004). However, temperate labrid fishes appear to successfully occupy wave-exposed habitats using enhanced swimming ability through increased body size, rather than high-aspect ratio pectoral fins. The lack of very high-aspect ratio finned species in the temperature regions might indicate a phylogenetic constraint (Fulton and Bellwood, 2004). Other than for labrid fishes, studies examining the link between flow environment, morphology, and swimming performance are lacking. In addition, we know little about how feeding performance and morphology might relate to flow conditions.

4.4 Waterfall climbing

An extreme environment that exists at the interface of aquatic and aerial environments are waterfalls. Three species of goby from Hawai'i can ascend waterfalls, although their kinematics and performance differ (Blob et al., 2006). One species is an inching climber (*Sicyopterus stimpsoni*) and the net climbing speed of this species remains constant across substrates of varying coarseness. They remain attached to the substrate using oral and pelvic sucking disks, and the roughness of the substrate likely impairs their ability to attach. Blob et al. (2006) found that this species spends more time moving on coarser surfaces, accommodating the decrease in attachment ability.

In contrast, the other two species of waterfall climbers in Hawai'i (*Awaous guamensis and Lentipes concolor*) are powerburst climbers and exhibit increases in speed as the coarseness of the substrate increases (Blob et al., 2006). These species push off using their pectoral fins and it is likely that slipping is reduced on coarser surfaces, enhancing their ability to progress upwards. More about waterfall climbing in gobies can be found in another chapter (Maie et al., 2025).

4.5 Predator-prey interactions in flow

It is often convenient to separate behaviors to better study them. However, in nature animals typically have a goal to accomplish, such as capturing prey, and many different mechanical systems must interact and integrate to ensure success (Higham, 2007b). For example, suction feeding, the most common mode of prey capture among fishes, relies on the rapid expansion of the buccal cavity in order to generate a negative pressure relative to the fluid outside the mouth (Lauder, 1980, Muller et al., 1982, Day et al., 2005, Higham et al., 2006b). This pressure gradient draws in the water from around the mouth. However, the area of water that is impacted is typically restricted to one mouth diameter away from the mouth aperture (Day et al., 2015), forcing the fish predator to be very close to the prey when the strike is initiated. Indeed, striking milliseconds too early (Shirazi and Higham, 2024) can erase the effectiveness of suction, causing a failed capture attempt. This constraint means the locomotor system must accurately bring the mouth to the correct location relative to the prey. In light of this, feeding and locomotion, two historically different disciplines, can be considered one integrated behavior where insight into each is essential to fully understand prey capture (Rice and Westneat, 2005, Higham, 2007b, Kane and Higham, 2011, Kane and Higham, 2015, Kane et al., 2019, Olsen et al., 2019, Kane and Higham, 2020). Additionally, there are muscles in fishes used for both locomotion and feeding (Thys, 1997, Camp and Brainerd, 2014). In largemouth bass, the hypaxial and epaxial muscle used in suction expansion extend almost halfway down the body (Camp and Brainerd, 2014). A traditionally examined feeding muscle, the sternohyoid, acts as a ligament by transmitting hypaxial shortening to the hyoid during ventral expansion (Camp and Brainerd, 2014). This highlights the discovery of underlying mechanisms by studying both locomotor and feeding muscles simultaneously. Ultimately, there are both integration and potential trade-offs where one function may be enhanced at the expense of another.

Integration is essential for successful prey capture in most fishes, but the influence of varying flow conditions on the integration of functional systems is unclear. This is a major gap in our understanding of prey capture in fishes. As noted by Higham et al. (2015), turbulent water may alter the position of the prey in unpredictable ways, which could lead to decreased capture success for visual predators. In addition, turbulent flow has the potential to disrupt the ability of the lateral line sensory system to detect prey-induced hydrodynamic disturbances in the water, limiting the ability to detect prey using this sensory system. There are a number of alternative strategies that predators could employ in the face of turbulent flow. Swimming faster, for example, would increase the fish's momentum and energy, making them better capable of damping and correcting displacements caused by turbulent flow (Webb and Cotel, 2010). This would, however, result in a potential trade-off as faster predatory speeds often reduce the strike accuracy of the predator (Higham et al., 2006a, Higham 2007a, 2007b, Higham et al., 2007).

Although few observations exist for fish feeding in flow, the flow conditions in the environment can influence feeding strategy, performance, and diet (Finelli et al., 2009). Recent work has illustrated that fish can combine prediction and self-motion in flowing water to generate successful attacks on evasive prey (Martin et al., 2024). The ecology of a species is also likely to influence its ability to feed in flow. For example, a study from Belize found that two species of coral reef blennies were vertically separated in that roughhead blennies (*Acanthemblemaria aspera*) live in shelters that are deeper and are associated with topographically low features compared to spinyhead blennies (*A. spinosa*). The latter also feeds more in the water column, suggesting a preference for zooplankton over benthic prey, and also suggests that this species is more effective at swimming and foraging under more energetic conditions (Finelli et al., 2009). Given that calanoid copepods are not able to escape as effectively in turbulent flow, *A. spinosa* may be better at exploiting this food resource at locations of higher flow. Support for this was found by Clarke et al. (2005) in that *A. spinosa* (compared to *A. aspera*) had a slower initial approach to prey and a lower proportion of approaches that resulted in a strike in turbulent water (Clarke et al., 2005). Interestingly, both species exhibited a decrease in success when attempting to capture a passive prey item (*Artemia* sp.) in turbulent water, whereas both exhibited an increase in success when attacking an evasive prey (*Acartia tonsa*). This suggests that turbulence interferes with the hydrodynamic sensing of the approaching predator (Clarke et al., 2005).

One of the first steps in determining the impact of flowing conditions on predator-prey interactions is quantifying the flow itself. Because of the complexity of turbulent flows, measuring and recreating them in a laboratory setting has been challenging. Measuring flow conditions in nature could involve cantilever-style drag-sphere flow probes with strain gauges (Gaylord, 1999, Johansen, 2014), particle image velocimetry (PIV) (Lacey et al., 2012), acoustic Doppler velocimeters (Garcia et al., 2005), acoustic Doppler profilers (Finelli et al. 2009), or injection of dye (Fig. 5B in Higham et al., 2015). Recent advances regarding the use of PIV to measure environmental turbulence has made this affordable and accessible (Jones and Cotel, 2024). Using the intensity, periodicity, orientation, and scale (IPOS) framework put forth by Lacey et al. (2012), which focuses on measuring the turbulence's intensity, periodicity, orientation, and scale, one can measure and recreate flows to determine the extent to which predator-prey interactions are altered in the face of varying flow conditions.

The energetics of feeding and locomotion can also be greatly informed by respirometry (Fig. 11). Station-holding behind a cylinder in flow is less costly than swimming in uniform flow at the equivalent velocities (Liao, 2003a). However, feeding is more costly when behind a cylinder compared to uniform flow. Station-holding trout feeding on artificial, drifting prey in a flow tank

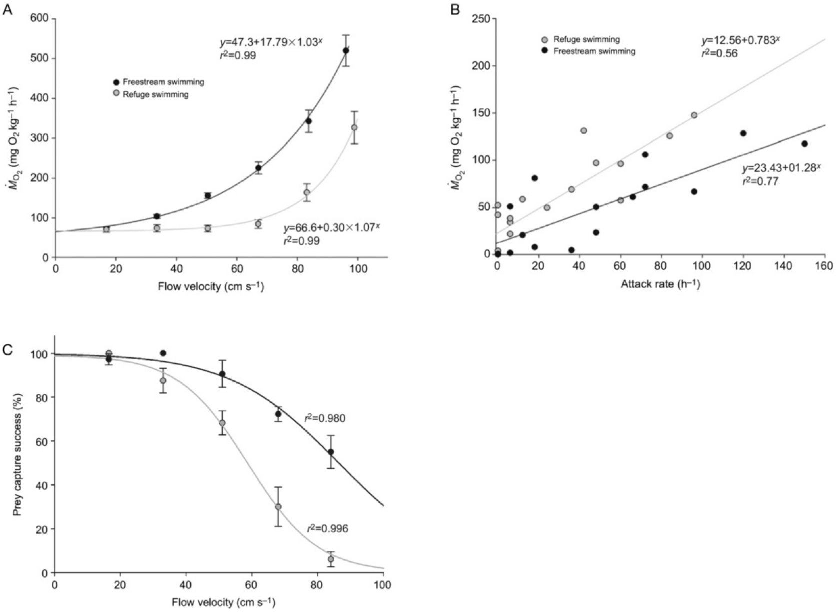

FIG. 11 Energetic tradeoffs in the cost of feeding and swimming. (A) Rate of oxygen consumption (MO_2) of rainbow trout swimming in uniform flow is greater than compared to refuging behind a cylinder. As flow increases, the FS cost increases more quickly compared to cylinder refuging (which is similar across flow speeds until higher speeds 68 cm/s). (B) While the percentage of attacks is the same for refuging and FS, the cost of attacking prey is 64 % greater during refuging (C). This likely reflects the energetic challenges of transitioning in and out of the vortex street. Note that at high flows, capture success decreases for both flow scenarios. *Figure from Johansen et al., 2020 (with permission).*

respirometer reveal a higher oxygen consumption rate compared to when feeding in uniform flow (Johanssen, 2011), likely due to increased stability and control costs. Additionally, prey capture success is lower when the fish is behind the cylinder, given the unpredictable nature of the turbulent streamlines that the food is following. This energetics perspective is useful to understand ecological behaviors in the field: in terms of oxygen consumption, it is better for a fish to feed in uniform flows, such as on insect hatches in pools (Regal, 1992) and hold station behind rocks and large woody debris for most of the day when holding station in flow (Gibson, 1978; Keenleyside, 1962). With the diversity of fish forms and the broad ranges of each of these environmental variables, research efforts should include *in situ* investigations and efforts to disentangle interacting evolutionary drivers that control fish swimming and feeding biomechanics.

5 Future directions

As discussed throughout the chapter, multiple biotic and abiotic factors influence how fish swim and feed across habitats. The interactions between a fish and its physical environment, as well as with other organisms, underlies the idea of environmental niche. This information helps connect geographic distribution to variation in environmental parameters. Therefore, ecomechanics and the concept of ecological niche are closely related, and understanding the ecomechanics of fishes requires integrative investigations that recognize the complexity of the environment over space and time. Studies that mimic or take place directly in the natural environment are key areas in which to focus, and these will likely reveal adaptations that can be more thoroughly studied in the laboratory (Ding et al., 2024). This reciprocal illumination of lab and field studies is necessary to fully understand how fishes do what they do. For example, and as noted above, quantifying the flow patterns experienced by fishes in nature will then permit the reconstruction of these flows in a laboratory setting (Higham et al., 2015). As research progresses towards incorporating more ecologically-relevant factors, technological advances are providing more opportunities to quantify locomotion and feeding in nature. A primary focus has been the development of smaller and more powerful portable devices to measure fish movements in the field, facilitating studies of ecomechanics under fully natural conditions (Bauer et al., 2020). These new technologies include calibrated wireless accelerometry that can recover data on fish swimming kinematics and performance with great resolution (Brownscombe et al., 2018, Gleiss et al., 2019, Venerus et al., 2024). In using these types of devices, researchers can let fishes be fishes. In addition to wireless devices, obtaining high-speed video of fishes in nature is needed. *In situ* measurements of locomotion and predator-prey interactions have been recorded for marine fish (Domenici et al., 2014) and in Hawaiian stream fishes (Schneider et al., 2021). The latter study found that predatory fish attacking at higher angles (i.e. in the direction opposite to flow) were more successful. They suggest that feeding in the same direction as flow might limit the predator's accuracy. It is clear that complex ecological scenarios should be explored in more detail.

Although we are gaining information regarding key environmental variables, others have received less attention. For example, research investigating how habitat structure influences feeding and locomotor biomechanics has been limited. It is clear that fishes can take advantage of obstacles in a flowing environment in order to reduce energy consumption (see above). However, how fishes navigate obstacles during predator-prey interactions or in complex three-dimensional habitats (e.g., coral reefs) is poorly understood. Despite this, some research has examined the role of habitat structure on the success of predators and prey (e.g., Stunz and Minello, 2001; Johansen et al., 2020). It appears that increased structural complexity enhances the survival of prey, whereas the predator finds more success when feeding in lower complexity habitats. Whether this is generalizable is unclear, but predators specialized for feeding in complex habitats might show interesting strategies for maximizing success.

As we progress in our understanding of fish biomechanics in the real world, it is worth considering model species. Of course, the model species will depend upon the specific ecological variable of interest. In addition, those interested in extreme environments would need to utilize a species that can withstand extreme conditions. On the other hand, one might want to examine generalists that span many types of habitat to determine the mechanisms underlying this flexibility. Regardless of the question, the species ought to be tractable in nature, large enough to be outfitted with wireless devices (if that is the goal), and should be species that are understood from a natural history perspective. Some examples include sunfish and bass from the centrarchids, salmonids, large marine fishes, common coral reef fishes (e.g., wrasse), or those that are comparatively easily accessible in the deep sea. An orchestrated coordination of people working on different aspects of the same species would advance our knowledge in ways that our current approach (e.g., species are selected according to individual lab needs) cannot. Using one of these model species, a dream experiment might be to measure forces, flows, kinematics and electromyography of fish in nature for long time periods *with* detailed knowledge of their environment (e.g., currents, physical habitat, temperature, prey abundance). Using these types of datasets, we could start to predict/model ecological interactions, drivers of diversification, and constraints that are not apparently from lab studies.

Extreme environments offer powerful opportunities for future study, acting as natural experiments in which to test the effects of factors such as temperature, pressure, density, and flow on fish locomotion and feeding. Advances in technology are opening experimental opportunities in habitats that were once inaccessible, such as the deep ocean. The literature, as described above, demonstrates that *in situ* conditions must be considered when investigating fish activity, locomotion, and feeding. By assessing fish ecomechanics directly in these environments, we can better inform biologically meaningful characteristics related to swimming and feeding. Additionally, we recommend increased collaboration across the fields of fish physiology; bringing together those with expertise in fluid dynamics, physics, ecology, and specific extreme ecosystems will inform better understanding of these complex systems. Fishes are diverse and complex. For more than 530 million years, abiotic and biotic factors and physical constraints have driven the evolution of these incredible organisms. Disentangling this evolutionary story requires integrating across fields of physiology, ecology, and biomechanics to understand the planet's most diverse and abundant vertebrates, fishes.

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