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Tunable stiffness in fish robotics: mechanisms and advantages

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Abstract

One of the emerging themes of fish-inspired robotics is flexibility. Adding flexibility to the body, joints, or fins of fish-inspired robots can significantly improve thrust and/or efficiency during locomotion. However, the optimal stiffness depends on variables such as swimming speed, so there is no one “best” stiffness that maximizes efficiency in all conditions. Fish are thought to solve this problem by using muscular activity to tune their body and fin stiffness in real-time. Inspired by fish, some recent robots sport polymer actuators, adjustable leaf springs, or artificial tendons that tune stiffness mechanically. Models and water channel tests are providing a theoretical framework for stiffness-tuning strategies that devices can implement. The strategies can be thought of as analogous to car transmissions, which allow users to improve efficiency by tuning gear ratio with driving speed. We provide an overview of the latest discoveries about 1) the propulsive benefits of flexibility, particularly *tunable* flexibility, and 2) the mechanisms and strategies that fish and fish-inspired robots use to tune stiffness while swimming.

Keywords: bio-inspired robotics, fluid-structure interaction, smart materials, underwater vehicles

Introduction

One of the most immediately evident traits of fishes is that they are flexible. Thanks to a network of collagenous membranes, muscle fibers, and ligaments, fish are highly flexible in both their bodies and fins^{1–4}. Their body’s passive rigidity can be $O(1\text{ N mm}^2)$ ⁵, on par with thin sheets of rubber. Many fish species can bend their vertebral column bilaterally into a “C” shape⁶, a feat that in humans is reserved for professional contortionists.

Robots have historically been stiff in comparison. To many, the idea of a “robot” brings to mind rigid metal components, epitomized perhaps by “the robot”, the dance style in which limbs are straight and jerky. As the field of *soft robotics* matures, this perception is fading. Bio-inspired robots today often use advanced polymers or soft materials to be as flexible (or more so) than animals in nature⁷, yet a large performance gap remains.

The main challenge of adding flexibility is that there is no one “best” stiffness. One stiffness may provide maximal efficiency, while another produces the most thrust. And the best stiffness for thrust may itself depend on inputs like swimming speed. A solution found in nature is *tunable* stiffness. With situation-dependent stiffness, an animal can access the advantages of flexibility while avoiding some of its pitfalls. Tunable stiffness is behind the dexterity of octopus arms, elephant trunks, and human tongues, and there is growing evidence that fish too use active muscle tensioning to adjust their stiffness^{5,8–10}.

Before understanding why fish robots should tune stiffness, it is best to understand why fish-robots should be flexible at all. We will first review studies that explore the *role of flexibility* in fish and fish-inspired robots (Section 1). We will then review studies and models that show the *advantages of tuning stiffness* (Section 2). Lastly, we will review the known and hypothesized *mechanisms of tuning stiffness*—both in real fish (Section 3) and fish-inspired robots (Section 4). We suggest that the inclusion of tunable stiffness in the design of fish-like robotic systems is a key direction for improving the performance of aquatic robots.

1. Why be flexible?

The role of flexibility in fish-like swimming has been studied over a range of fidelities. Lower-order studies (e.g. those that abstract fishes as simply-actuated beams) offer scalable models rooted in physics, but they risk oversimplifying dynamics. Higher-order studies (e.g. those that quantify the kinematics of live fish) offer direct metrics of real swimmers, but they risk obscuring physics-based patterns in the data. Only with the full spectrum of studies has the role of flexibility begun to materialize, and there is now a considerable diversity of fish-inspired mechanical models that span the range from the simple to the complex (Fig. 1).

Some of the earliest work applying hydrodynamic theory to flexible swimmers was done by Wu¹¹. Wu used linearized potential flow equations to show that 2D flexible hydrofoils could be more efficient than rigid ones at producing thrust. Computational studies later showed that Wu's findings applied to 2D foils with finite amplitudes and deforming wakes¹², and to 3D foils¹³. Several theoretical^{14–19} and experimental^{20–26} studies have since confirmed that adding flexibility can improve a hydrofoil's thrust and/or efficiency.

Real fish are more complicated than hydrofoils: they are complex networks of muscle, cartilage, bone, skin, and organs²⁷. They use heterogeneous materials, such as bony rays connected by collagen fibers²⁸, and their stiffness is nonuniform, often varying within a single fin²⁹. Nevertheless, even the complex musculature of vertebrates can exhibit simple spring-like behavior^{30,31}. When comparing fish to comparably stiff hydrofoils, one will often find similar swimming speeds, patterns of curvature, and Reynolds and Strouhal numbers³². Models with increasing fidelity (e.g. silicone casts of sunfish bodies³³ or robotic sunfish pectoral fins³⁴) continue to find that flexibility can increase thrust and/or efficiency.

From this spectrum of flexibility studies, two physical explanations have emerged to explain how flexibility improves thrust and/or efficiency: 1) flexibility leverages the phenomenon of *resonance* to maximize fin/body amplitude, and 2) flexibility *tunes aerodynamic variables* like camber and angle-of-attack to maximize the thrust-to-drag ratio.

Theory 1: Flexibility leverages resonance

The idea that resonance improves efficiency relies on fish and fish-robots acting like harmonic oscillators. The concept, first proposed by Blight¹⁰, is that fish will deform most easily when actuated at their resonant frequency. At sub-resonant frequencies, energy is wasted on needless deformation; at super-resonant frequencies, energy is wasted on needless lateral accelerations; at resonance, the energy converted to useful work is maximized³¹. There is evidence that some scallops actuate at the resonant frequency of their shell-hinge system³⁵, and that some jellyfish save 30% of their energy costs by actuating at the resonant frequency of their bells³⁶.

Several reduced-order studies have supported this theory about resonance. As stiffness is varied, simulated^{24,37} and experimental^{22,38} hydrofoils can pass through a series of local maxima in speed and/or efficiency. This kind of multi-modal response is typical of harmonic oscillators. In some setups, performance and amplitude peak at the same conditions, confirming that resonance plays an important role^{22,23,39–42}. In robotic and computational fluid dynamics (CFD) simulations of lampreys, for example,

actuating at resonance increased stride length with only a small increase in wake energy, suggesting resonance plays a role in maximizing efficiency^{43,44}.

Theory 2: Flexibility tunes aerodynamics

Other studies suggest a smaller role for resonance. Peaks in the amplitude of a flexible foil do not always correspond to peaks in thrust and efficiency^{45–47}. As a result, the efficiency of bio-inspired propulsors may peak at just a fraction of the resonant frequency: 0.33⁴⁸, 0.4⁴⁹, 0.4–0.5⁵⁰, 0.4–0.7⁵¹, or 0.5–0.6⁵². In these cases, efficiency must be governed by more than just resonance.

Here is an explanation that avoids resonance: flexible propulsors deform in ways that—regardless of amplitude—optimize thrust-to-drag, i.e. they are more “aerodynamic”. For example, flexibility creates a passive phase offset between a forcing and its response. This phase offset could reduce the effective angle of attack at the leading edge of a fin¹⁶, which is a critical parameter for efficiency because it affects leading edge vortices (LEVs) and hence leading edge suction^{53,54}. Flexibility affects not just phasing, but also the temporal evolution of flexible shapes more generally, and these changes can reorient forces in ways that boost thrust and reduce drag^{16,50,52,55}.

A key step toward reconciling these two theories came recently, when resonant peaks in efficiency were proven to be absent from inviscid models⁴⁵. This discovery explains why resonance-driven efficiency maxima do not show up in potential flow models^{24,56,57} but do show up in water channel experiments^{22,23,38,40,58} and models that add resistive drag^{38,41,45,58}. The role of resonance will therefore depend on whether/how viscous forces are modelled. Still, even viscous studies find differing degrees of resonance, so unexplained discrepancies remain.

However, there is no reason that Theories 1 and 2 cannot both be correct. The two theories are also highly interconnected, because a propulsor’s resonance and general shape are both functions of its midline kinematics. Efficiency in aquatic propulsion is probably governed by a combination of these two theories. This view helps to explain why global efficiency maxima are often affected by both resonance and aerodynamics. Heaving flexible foils, for example, peak in efficiency when driven at resonance *and* a moderate Strouhal number (0.2–0.4)⁴⁰. Pitching flexible foils peak in efficiency when driven at structural resonance *and* wake resonance⁵⁹.

Most likely, the relative importance of Theories 1 and 2 depends on physical inputs to the system. Many of the studies that downplay resonance are from the Micro Aerial Vehicle literature^{48–50,52}, so the importance of resonance may be linked to mass ratio or Reynolds number. Indeed, peaks in efficiency are highly sensitive to drag^{45,57}. Resonance may also be more important for carangiform and thunniform fishes than it is for more flexible anguilliform swimmers, because the dynamics of sufficiently flexible foils can be dominated by fluttering modes^{45,46}. Efforts to refine the role of flexibility are ongoing.

2. Why tune flexibility?

Adding flexibility does not always improve performance. Making an oscillating hydrofoil more flexible may actually decrease its propulsive efficiency^{22,60–62}. When a propulsor is too flexible, actuation energy can be wasted on deformation rather than transmitted to the surrounding fluid. The resulting kinematics may even become chaotic²². An analogy from solid mechanics would be an overly-loosened shock absorber on a bicycle.

Different performance metrics are also affected by flexibility in different ways. For lamprey-like robots, one stiffness may maximize acceleration while another maximizes steady swimming speed⁶³. For bluegill-inspired robotic fin rays, one stiffness may maximize thrust while another maximizes lift⁶⁴. For tuna-inspired hydrofoils,

one stiffness may maximize thrust while another maximizes efficiency⁶⁰. The stiffness that optimizes performance depends on how “performance” is defined.

Even within a single performance metric, the optimal flexibility can be situation-dependent. The magnitude of the incoming flow speed, for example, can determine whether a foil made more flexible becomes more or less efficient²². Consider the pectoral joint in Behbahani and Tan’s fish-robot capable of rowing motions⁶⁵. For low fin-beat frequencies, a more flexible joint led to higher speeds, but for high fin-beat frequencies, the trend was reversed. Dolphin-like⁶⁶ and tuna-like⁶⁷ robots exhibit similar trends: certain joint stiffnesses are more efficient at some speeds than others.

To make sense of these competing effects of flexibility, biomechanists and roboticists have used reduced-order models. The models offer a framework for understanding *why* tuning stiffness may be helpful, and also *when* and *how* tuning should be implemented. We will review two models that have been put forth. Each offers a different set of insights about the role that tuning stiffness plays in fish-like locomotion.

Model 1: A hydrofoil segmented by a torsional spring

Perhaps the simplest model of a flexible fin is to take an otherwise rigid hydrofoil and add a torsional spring partway along its length (Fig. 2A-D). The modelled efficiency of a foil with an internal spring can be nearly 5 times that of a purely rigid foil⁶⁸. The “flexibility” of the hydrofoil is contained in one variable: the stiffness of the spring. Several studies have considered this one-spring model^{48,57,68–70}. Simple actuations can then be applied, and the resulting kinematics can be studied easily. For example, Moore⁵⁷ pointed out that for small amplitudes and inviscid flow, this system has an exact solution when the spring is at the leading edge.

Despite the model’s simplicity, it demonstrates both theories about flexibility mentioned in Section 1. Consider, for example, the case where the spring’s position is fixed and heave oscillations are prescribed at the leading edge. As stiffness changes, the amplitude of the trailing edge passes through a local maximum, i.e. resonance (Fig. 2A), and the effective angle of attack passes through a local minimum (Fig. 2B). The stiffness of the spring affects both the resonant (Theory 1) and aerodynamic (Theory 2) properties of the system, and no one stiffness optimizes both.

Changing the streamwise position of the torsional spring, i.e. the flexion ratio (ℓ_1/ℓ), also affects the system’s dynamics. In the model, stiffness is infinite everywhere except at the torsional spring, so increasing flexion ratio redistributes stiffness toward the leading edge. Nonuniform distributions of flexibility can lead to faster swimming speeds and/or higher efficiencies^{62,71–76}. Biomimetic fins with stiffness distributions modelled after pumpkinseed sunfish were 26% more efficient than comparably (but uniformly) flexible NACA0012 airfoils⁷⁶. These studies tend to show that concentrating stiffness near the leading edge is better for performance^{70,72,73,77}.

As in the case of tuning spring *strength*, the importance of tuning spring *position* can be seen in the context of both resonance and aerodynamics. Here, it is the distribution of stiffness that is tuned: the value of the flexion ratio (ℓ_1/ℓ) affects both the amplitude of the trailing edge (Fig. 2C) and the angle of attack of the leading edge (Fig. 2D). These variables are maximized/minimized at some intermediate flexion ratio (~0.55-0.65). Interestingly, a wide range of fish—and even birds, bats, and insects—have flexion ratios in the 0.56-0.74 range⁷⁸.

Adding springs leads to increasingly complex distributions of stiffness. By adding a second spring to their model, Zeyghami and Moored⁶⁸ found that they could benefit thrust and efficiency simultaneously.

Another study modelled a trapezoidal fin as six rigid elements connected by springs⁷²; another modelled the backbone of a blue marlin as 23 rigid vertebrae connected by springs¹. In Fig. 2, we chose one spring to illustrate that the importance of tuning stiffness (both in terms of strength and distribution) persists even in the simplest possible model of a flexible foil.

Model 2: An elastic hydrofoil

In the limit of a continuous distribution of an infinite number of linear springs, the hydrofoil model becomes a linearly elastic beam. Now the dynamics of the hydrofoil are governed by elastic beam theory, and the system again has exact solutions in some loading scenarios. Using beam theory to understand swimming dynamics has been successful across a wide range of theoretical^{24,37,41,49,79–81} and experimental^{20,23,25,40,82–85} studies. It has also contributed to the design of actual swimming robots^{86,87}.

A key advantage of modeling a foil as an elastic beam is that it offers a framework for considering intrinsic flexibility and shape simultaneously. The response of a beam/foil is dictated not just by its intrinsic flexibility (quantified by its elastic modulus E), nor by its shape (quantified by its cross-sectional moment of area I_A), but rather by their product, the flexural rigidity EI_A . A beam with constant rectangular cross-section has $EI_A = E(1/12)s\delta^3(1 - \nu^2)^{-1}$, where s and δ are the span and thickness of the beam, and ν is the Poisson’s ratio⁸⁸. One could then predict, for example, that doubling this foil’s thickness or octupling its elastic modulus will have the same effect on its dynamic response to loading.

Tuning the flexural rigidity in Model 2 has similar effects as tuning the spring stiffness in Model 1. As flexural rigidity increases, trailing edge amplitude passes through a local maximum, i.e. resonance (Fig. 2E), and trailing edge amplitude passes through a local minimum (Fig. 2F). The flexural rigidity affects both the resonance (Theory 1) and aerodynamic (Theory 2) properties of the system, and no one flexural rigidity optimizes both. Note that unlike the one-spring model, the elastic foil model will exhibit an infinite number of higher-order resonant modes as $EI_A \rightarrow 0$, but only the first mode is shown in Fig. 2E,D.

The sample beam solutions shown (Fig. 2E,F) assume that the fluid only applies added mass and linear damping forces to the beam. More advanced beam-like swimming models add streamwise variation in flexural rigidity⁸⁹, a viscoelastic damping term³⁸, an internal tension term^{14,16,19,24,37}, or a linearized pressure drop across the trailing edge^{24,37,38,41,45}. See Valdivia y Alvarado⁹⁰ for a comprehensive list of shear, inertia, and fluid-forcing terms and a discussion of the conditions meriting their neglect. In some cases, exact solutions can be found even with higher-order terms added by assuming quadratic rigidity variation⁸⁹ or quartic beam deflection⁴¹.

Elastic foil models can be further advanced by adding nonlinear forcing terms. With these terms included, resonant peaks can broaden and weaken with increasing heave amplitudes⁹¹. Even these nonlinear models are only “weakly nonlinear”³⁸, because less predictable nonlinearities can be introduced by the wake⁹². Experiments confirm that forcing amplitude affects resonance for heaving flexible foils⁵⁸. Real flexible joints, such as intervertebral joints in marlin, can also exhibit amplitude-dependent elasticity¹. In Fig. 2, we chose a linear model with as few terms as possible to illustrate that the importance of tuning stiffness persists even in the simplest version of elastic beam theory.

Both Models 1 and 2 reveal the importance of tuning stiffness. First, they reveal that certain performance metrics (e.g. trailing edge amplitude and effective angle of attack) respond differently to flexibility. A roboticist may therefore want to change flexibility as performance goals shift. More importantly, they reveal that even

within one metric (say, trailing edge amplitude), the optimal stiffness depends on other variables such as frequency. Resonance in Model 1 occurs not at a particular value of spring stiffness k , but rather at a particular value of the dimensionless ratio $k/(I_1 f^2)$ (Fig. 2A,C). Resonance in Model 2 occurs not at a particular value of beam rigidity EI_A , but rather at a particular value of the dimensionless ratio $EI_A/(\mu \ell^4 f^2)$ (Fig. 2E).

These dimensionless ratios, which represent a ratio of elastic forces to hydrodynamic forces, go by a variety of names: “effective flexibility/stiffness”^{23,49,59,68,83,93}, “dimensionless rigidity/stiffness/frequency”^{20,24,37,38,41,79,81}, “elastoinertial number”^{25,52}, etc. The ratios shine light on the patterns lurking in these abstract models, but they also provide actionable stiffness-tuning strategies. For example, to maintain a constant value of $k/(I_1 f^2)$ —perhaps one that leads to resonance—stiffness should be tuned to scale with frequency squared. This result was used to program a tuna-like robot that saves energy by tuning its own tail stiffness in realtime⁶⁷.

Lastly, note that while we have focused on propulsive benefits, tunable stiffness may have more exotic benefits beyond increasing thrust or efficiency. Flexibility affects how hydrofoils interact with solid boundaries^{94,95}, so tunable stiffness could perhaps assist with near-boundary control. The flexibility of a foil’s trailing edge affects the swirling strength of wake vortices, so tuning stiffness could be used to inhibit/enhance cross-stream dispersion⁹⁶. Flexible structures are also less likely to damage their environments, so tunable stiffness could be used as a safety mechanism⁷. There are clearly many reasons for swimmers to tune stiffness. But how can a swimmer tune its own stiffness while swimming?

3. Potential biological mechanisms of stiffness alteration and tuning

Virtually every component of the locomotor system in fishes has some degree of flexibility and undergoes both bending and longitudinal strain during swimming^{97–103}. Undulatory motion of the fish body results in an obvious wave of bending that progresses from head to tail during forward locomotion^{104–106}. Even stiff skeletal elements can experience 2% strains during movement in sharks, suggesting that the entire vertebral column (vertebrae and intervertebral joints together) may exhibit spring-like behavior, with total strains approaching 12% during maneuvering⁹⁷.

Fish are not, however, uniformly flexible. Fish bodies have non-uniform cross-sectional areas: they are thickest approximately one-quarter body length back from the head, then taper to a thin tail region^{106–108}. This change in cross-sectional area is accompanied by changes in the relative proportion of muscular and skeletal elements, which further complicates the distribution of stiffness along the body. While some data exist on the flexural stiffness of passive fish bodies^{5,33,109,110}, not much is known about how material properties of the fish body change quantitatively from head to tail, nor how the relative proportions of muscle, connective tissue, and skeletal elements affect body stiffness.

So, what is known about fish stiffness and how it compares to the simple flexible systems that have been used to model fish undulatory propulsion? McHenry et al.³³ estimated that sunfish body flexural stiffness (EI) varies from approximately 1×10^{-3} N m² near the head to 1×10^{-6} N m² near the tail. Other researchers^{5,109} have estimated EI values that range from 3×10^{-4} N m² to 1.8×10^{-4} N m² and suggested that during locomotion, body flexural stiffness may increase two to threefold due to body muscle activation. Naughton et al.¹¹¹ reported body stiffness values of 0.5 to 0.9 Nmm⁻¹ for the body and 0.05 to 0.4 Nmm⁻¹ for the tail region in four species of elongate fishes. Shelton et al.³² used flexible foil materials with EI values of 3.3×10^{-5} N m² and 9.9×10^{-4} N m² as simple models of undulatory swimming, and suggested that these values reflect, approximately, *in vivo* body stiffness values.

Realtime adjustments to fish body and fin stiffness are most likely mediated by changes in muscle activation. The organization of fish body musculature uses a two-gear system^{99,112–117}: so-called “red” fibers that extend

longitudinally and power slow-speed swimming, and so-called “white” fibers that are W-shaped and power high-speed movements like rapid accelerations or maneuvers (Fig. 3A,B). In most fishes, red fibers are located along the lateral body margin, but in many tuna-like species they are deeper beneath the skin and have complex attachments to tendons that connect in turn to the vertebral column and tail^{118–120}. Both red and white fibers are segmentally arranged into blocks called myomeres and separated by connective tissue called myosepts, and it is the sequential activation of these myomeric blocks down the body that generates propulsive waves.

There are many challenges to conducting experimental analyses of muscle function and body stiffness in freely-swimming fishes, so it is hard to test the hypothesis that fish actively alter stiffness. There are, however, a few stiffness-tuning mechanisms that have been proposed and studied to some degree.

Mechanism 1: Antagonistic body muscle contraction

As muscles on opposite sides of the body change the extent of their co-contraction, there will be a concomitant change in stiffness of that body region^{8,121}. Simultaneous antagonistic actuation implies that at times, muscles will do “negative work”, i.e. absorb energy rather than transfer it to the surroundings. Negative work is thought to be done by the red fibers of largemouth bass¹²² and carp¹²³, and the white fibers of sculpin¹²⁴ and saithe¹²⁵. Negative work requires extra energy, but the energetic benefits of altering stiffness may be worth the costs^{8,10}. In lampreys, for example, negative work can stiffen the tail, and more anterior muscles can make up for the losses with additional positive work⁶³. It has been hypothesized that lampreys use appropriately-timed antagonistic muscle contractions to modulate their effective stiffness by about two-fold¹¹⁰, thereby tuning their passive dynamics to maximize acceleration or speed⁶³.

Antagonistic muscle actuation can be recorded directly using electromyography. For example, when largemouth bass swim at high speeds and transition to an unsteady burst-and-glide mode, antagonistic muscle activity has been detected between white muscles on the left and right sides of the body (Fig. 3C)¹²⁶. These data reflect coactivation of the body muscles by the nervous system, so they suggest that the fish is being stiffened by antagonistic activity, though these data do not allow quantification of the *degree* of stiffening.

Antagonistic body muscle activity also appears in some rapid C-start escape responses. Figure 3D shows recordings from *Polypterus* during a high-speed maneuver¹²¹. In the initial bending phase, there was muscle electrical activity on the left side of the body (the side toward which the fish body is bending), but also activity on the right side of the body. During the second phase of the escape response, there was little activity on the left side, but even stronger activity on the right side, corresponding to the body bending in the opposite direction. These data suggest that antagonistic muscle activity during the escape response might be involved in tuning body stiffness, although Tytell and Lauder¹²¹ could not detect any correlation between the extent of antagonistic activity and the body kinematic wave speed, so the effect of antagonistic muscle activation on locomotor performance remains unknown.

Fish are likely capable of regionally controlling where stiffness is altered along the body, because fish can recruit myomeres independently, and they may not recruit all regions of a single myomere simultaneously¹²⁶. For example, white muscle myomeres usually have thinner regions extending anteriorly both above and below the vertebral column (Fig. 3A,B)^{127–129}, and each myomere can span several vertebrae. In largemouth bass, myomeres each span 7-10 vertebrae, or nearly 20 % of the body length¹³⁰. The complex folding of white body muscle suggests that fish can control where stiffness is

altered both along the anterior-posterior axis and along the dorsoventral axis, perhaps to initiate a maneuver or to modulate the amount of force generated at any one location.

Mechanism 2: Antagonistic fin actuation

Fins are also important elements of the functional design of fishes and are used in a diversity of ways during both rectilinear propulsion and maneuvering^{105,131}. Fins are not simply passive elements attached to a bending body—they have their own intrinsic musculature and skeletal elements that allow complex three dimensional movement^{132,133}. Fish fin rays can be actuated at their base by up to four distinct muscles, and each ray has a bilaminar design in which two half-rays (hemitrichs) slide past each other in response to antagonistic muscle activity (Fig. 4A)^{4,29,84}.

Antagonistic actuation at the bases of fin rays can vary the effective stiffness of a fin. A linear elasticity model, validated against simply-loaded bluegill sunfish pectoral fins, shows that actuating the bases of pectoral fin rays can vary stiffness by an order of magnitude⁸⁴. Figure 4B shows the right pectoral fin of a bluegill sunfish executing a maneuver. In the absence of active control of fin rays, the fin would curve away from incident flow, but instead the fin is concave *toward* the free-stream flow. Electrical recordings in sunfish pectoral fin musculature verify that antagonistic muscle activity takes place (Fig. 4C)¹³³.

Antagonistic actuation may also play a role in stiffening the caudal fin or tail. The caudal fin contains several segmented fin rays which receive tendons from body musculature (Fig. 4D). There is a considerable diversity of attachment patterns in fishes, but in high-performance scombrid fishes (tunas and relatives), two prominent dorsal and ventral lateral tendons extend posteriorly to splay out over the heads of fin rays in the upper and lower tail lobes of the tail^{134–136}. These tendons can be robust and at least indicate the potential for fish to actively control tail conformation^{137,138} and stiffness. For example, muscle activity was found to increase in the caudal fin of bluegill sunfish at high speeds, “suggesting stiffening of the tail fin against imposed hydrodynamic loads”¹³⁹.

Given the potential importance of antagonistic muscle activity, there is surprisingly little evidence to support this stiffness-tuning mechanism. One reason for the lack of examples could be that experiments must be done in freely moving (and often uncooperative) fishes. A successful test requires multiple successful electrode implantations, simultaneous high-speed video over a range of swimming conditions, and post-mortem confirmation of electrode placement. Low-speed locomotion often exhibits little or no antagonistic muscle activity, and high-speed locomotion can destabilize electrode arrays. Considerable care needs to be taken to ensure that any “antagonistic” muscle activity is not actually the result of electrical crosstalk among channels.

Mechanism 3: Fin shape alteration

Changing the shape of a fin also affects stiffness, because a fin’s second moment of area contributes to its flexural rigidity. Fish have fine control over a fin’s shape^{132,133}. Some caudal fins have up to 50 muscle bundles for controlling shape in addition to the myotomal muscle fibers that generate the primary bending motion of the body^{140–147}. These shape changes alter stiffness: “cupping” a sunfish-inspired robotic caudal fin increased its stiffness and led to higher thrust⁶⁴. Reconstructions of mackerel pectoral fins suggest that cupping can increase stiffness by 3-7 times¹⁴⁸. And changes in fin curvature during rapid maneuvers have been suggested to reflect alterations in fin stiffness as a means to resist fluid loading^{149,150}.

Changes in fin shape can also be as simple as a change in area, a technique fish often use to enhance performance⁹. As bluegill sunfish swim faster, they decrease the surface area of their median dorsal and anal fins¹⁵¹ while increasing the area of their caudal fin¹³⁹. They may also increase the area of dorsal/anal fins immediately prior to maneuvers^{151,152}. By modulating total surface area and the location of area increase along the body, fish change the way they respond to fluid loading.

Mechanism 4: Pressure-driven stiffness alteration in skin

One last feature of fish functional design that could impact stiffness and possibly contribute to stiffness tuning is the skin. Fish skin has been implicated in body stiffness control, due both to the cross-helical pattern of collagen fibers that lie underneath the scales (a form of passive stiffness)^{153–156} and to a proposed pressure-driven stiffening that occurs as a result of body muscle activity pressurizing the body cavity (a form of active stiffness)^{157,158}. Measurements of pressure inside the fish body during locomotion show that as fish myotomal musculature contracts, the pressure increases, which is thought to increase the strain on cross-helical skin fibers as they resist radial expansion. Wainwright et al.¹⁵⁷ recorded pressures during rapid swimming that were 15x higher than resting body pressures. These authors suggested that fish skin could act like an external tendon that uses cyclical strain cycles to increase the mechanical advantage of myotomal musculature and exert a force on the tail that increases thrust.

There are many challenges to analyzing the role of stiffness-tuning in freely-swimming fishes. And yet, there is a clear-cut theoretical expectation that altering the stiffness of propulsive surfaces should increase locomotor performance. One path forward is to turn to robotic fish-like platforms in which the cost of swimming and thrust can be directly measured and in which stiffness can be experimentally altered in a controlled manner to assess the effects on thrust and efficiency.

4. Robotic mechanisms that tune stiffness

Fish-inspired robots have become increasingly flexible over the past couple of decades. A seminal example is MIT’s 1996 RoboTuna¹⁵⁹, whose hull was a thin layer of flexible foam covered by a spandex sock. Since then, dozens of fish-like robots have used flexible components. Some use rigid frames but flexible skin-like coverings and/or fin membranes^{160–167}; some have rigid components connected by flexible joints that mimic vertebrae^{168–170}. Others have entirely flexible components, such as silicone bodies or tails^{86,171–179}. Thanks to advances in soft actuators, at least one prototype has been made almost entirely of flexible components⁸⁷.

Tunable stiffness is a newer concept that only a few fish-like robots have implemented. The simplest examples are robots designed with interchangeable flexible parts. There have been, for example, robotic tadpoles with interchangeable tails of varying stiffness¹⁸⁰ or robotic peduncles made with interchangeable springs at the peduncle joint⁵⁵. Other fish-like robots adjust stiffness using nylon⁴³ or steel¹⁸¹ tail inserts, extra vertebrae¹⁸², extra joints¹⁸³, or the tension in the cables of tensegrity structures^{184,185}. In all of these examples, stiffness is tuned in between trials, i.e. *offline*. For roboticists wanting a stiffness that adapts to changing conditions, tuning must be done while swimming, i.e. *online*.

Online stiffness-tuning is new to robotic fish but rather common in other subfields of robotics. Some walking robots, for example, tune the stiffness of their leg joints in realtime¹⁸⁶. To facilitate cross-field comparisons, we will therefore use established categories of stiffness tuning^{7,186} as we review mechanisms thus far implemented in robotic fish:

Antagonistically-Controlled Stiffness

Mechanisms that tune stiffness *antagonistically* do so by pulling in two directions on the same structural component. Because stiffness is essentially “resistance to deformation”, the dual actuation effectively stiffens the structure. For example, two springs pulling on the same rotational joint will increase its effective torsional stiffness¹⁸⁷. This concept is the robotic analogue of antagonistic muscle actuation, so it is the most bio-inspired of the tuning mechanisms, at least based on the little that is known about stiffness-tuning in fish. Antagonistic actuators can be packaged into small, self-contained, adjustable-stiffness rotary actuators^{188,189}, and springs are just one option—the actuators could also be dielectric elastomers¹⁹⁰ or soft pneumatic actuators⁷.

One feature that makes antagonistically-controlled stiffness appealing is that—as in real fish—the same antagonistic actuators can both actuate a fin and actively stiffen it (Fig. 4A). Tangorra et al.¹⁹¹, for example, showed how conducting polymer actuators could both actuate and actively stiffen robotic fins simultaneously (Fig. 5A). Similar fin-stiffening strategies have been demonstrated with other smart materials, like flexible matrix composite (FMC) actuators (which employ pressure-driven elastomers)⁸², and macro fiber composite (MFC) actuators (which employ piezoelectric fibers)¹⁹² (Fig. 5B). In the case of FMC actuators, which can increase stiffness by up to 56 times¹⁹³, the authors tuned stiffness based on actuation frequency in order to maintain constant thrust.

Because antagonistic actuators work against each other, they at times perform negative work on the structure they control. As in real fish, this costs the robot energy, but the advantages of tuned flexibility may outweigh those costs. A recent study of antagonistic stiffening by Jusufi et al.⁴⁷ proves this point. The authors used pneumatically-actuated, silicone-based elastomers to pull antagonistically on two sides of a flexible panel (Fig. 5C). The actuators were driven over a range of amplitudes and phases, and thrust was maximized when there was some level of bilateral co-contraction. Optimal performance occurred at a condition where some negative work was done on the panel.

Antagonistic stiffening has also been attempted several times in octopus-inspired robots. The layout is quite different than fish-like robots, but the stiffening is similar enough to merit a brief discussion. Octopi use antagonistic muscle pairs to stiffen their arms: transverse muscles elongate arms, longitudinal muscles contract arms, and both actuated together stiffen the arm. Laschi et al.¹⁹⁴ proposed an artificial muscle layout based on this strategy, and the idea was later implemented using a pneumatic bladder (to elongate arms) and artificial tendons (to contract arms)¹⁹⁵. The concept has since been miniaturized using shape-memory alloys (SMAs) and deployed in a self-contained 8-armed robot¹⁹⁶.

Structurally-Controlled Stiffness:

Mechanisms that tune stiffness *structurally* do so by changing the geometry of elastic elements. A classic demonstration of structurally-controlled stiffness is curling a slice of pizza to prevent it from drooping. Cross-sections of the curved pizza have a higher second moment of area, resulting in a higher flexural rigidity and thus a higher resistance to bending. This concept explains how a fin can be stiffened by 3-7 times by “cupping”¹⁴⁸, a technique that has been recreated in robotic caudal fins⁶⁴.

Another simple way to structurally-control stiffness is to change the length of a bending element. An actuator can, for example, change the length of a leaf spring¹⁹⁷ or helical spring¹⁹⁸ attached to a load. This strategy has been used to stiffen robotic fins. In one case, an extendible rigid plate was used to

adjust the active length of a flexible panel (Fig. 5D)¹⁹⁹. The adjustable stiffness joint was shown to be more efficient compared with a uniform stiffness control. In another case, a tendon through the center of a beam was used to compress the beam (Fig. 5E)²⁰⁰. This mechanism was later tested in a robotic dolphin fluke²⁰¹.

Mechanically-Controlled Stiffness

Mechanisms that tune stiffness *mechanically* do so by changing the pre-tension of elastic elements. For example, if a mechanical arm is connected to a body via a pin joint *and* a spring, then tuning the pre-tension on the spring will tune the effective stiffness of the pin joint²⁰². This mechanism can be miniaturized to fit into a self-contained joint, e.g. a torsional joint with a controllable spindle that compresses internal springs²⁰³. In some ways, mechanically-controlled stiffness is a robotic analog to the hypothesized intermuscular pressure modulation of fish²⁰⁴. In that case, pressure increases the pre-tension of connective tissues, rendering a muscle effectively stiffer.

Mechanically-controlled stiffness has been implemented in four fish-like robots. The first, TenFiBot²⁰⁵, uses springs with adjustable pre-tensions in a mechanism the authors call a mechanically adjustable compliance and controllable equilibrium position actuator (MACCEPA) (Fig. 5F). The second is a robot with a pre-tensioned internal spring that modulates the effective stiffness of a silicone tail²⁰⁶ (online tuning was hypothesized but not demonstrated; Fig. 5G). The third is a tethered four-joint robot in which the final three joints each have a pre-tensioned spring for tuning stiffness²⁰⁷ (Fig. 5H). The fourth is a tethered tuna-like robot with a pre-tensioned internal spring connected to the peduncle⁶⁷ (Fig. 5I).

Intrinsic Rigidity Tuning

A robot could, in theory, change its stiffness by changing the *intrinsic* material properties of its elastic elements. Until recently, this strategy has been hypothetical, but it has become more viable with the advent of smart materials. Intrinsic rigidity tuning has been attempted once in fish-like propulsion. The authors, Behbahani and Tan²⁰⁸, used an electrorheological fluid-filled beam as a fin (Fig. 5J). As the electric field applied to the fluid changed from 0 to 1800 kV/m, the natural frequency of the fin increased by almost 40%. Other methods of intrinsic rigidity tuning include granular jamming and transition-based softening⁷, but there is no evidence that real fish use these types of material-based active stiffening.

5. Future Directions

Implementing tunable stiffness in next generation robots

When a theoretical understanding of stiffness tuning is applied to a fish-like robot, the result can be an immediate improvement in efficiency. Consider, for example, the Tunabot²⁰⁹, whose swimming performance depends on the stiffness of its peduncle (Fig. 6A). By modeling the caudal fin as a thin airfoil attached to a tendon-inspired spring, one can make sense of the stiffness-dependent performance of the Tunabot (Fig. 6B). Then, by building a tuna-like robot whose peduncle has a mechanically-controlled stiffness, one can drastically improve performance (Fig. 6C). Not only is the resulting robot more efficient, but also it can reach a wider range of speeds.

As benefits of tuning stiffness become clearer, more fish-like robots may start implementing stiffness-tuning mechanisms. Only a small handful of fish-like robot prototypes have attempted tuning stiffness—most of them in lab settings. Some of the more successful attempts have used antagonistically-

controlled or mechanically-controlled stiffness, but there are a variety of other mechanisms from the robotics literature^{7,186} that have yet to be attempted in fish-like robots (e.g. granular jamming).

The stiffness model shown in Figure 6 suggests that the benefits of tuning increase with size and frequency⁶⁷, so tuning may be especially important to future generations of fish-like robots that are larger and faster. However, these benefits can only be accessed if these faster robots can tune stiffness over increasingly wide ranges, so they will require robust tuning mechanisms. Large fish-like robots may therefore need to rely on tuning mechanisms that have no clear maximum stiffness, such as mechanically-controlled stiffness, rather than mechanisms that are constrained by material properties, such as intrinsic rigidity tuning. These hypotheses are based on a model developed for thunniform locomotion⁶⁷; it is unknown how tuning benefits scale to other types of swimming, such as rajiform (stingray-like) locomotion. Effective models of tunable stiffness could be particularly helpful when designing controllers, such as model-based precision controllers that have been tested in soft robotics applications^{210,211}.

Passive stiffness tuning

Another promising direction that has so far received little attention is “passive stiffness tuning”. The tuning mechanisms we have discussed are “active” in that a nervous system or controller actively adjusts stiffness based on swimming conditions. However, elements with nonlinear stiffness could in theory offer “passive tuning”, e.g. an element could automatically get stiffer at higher speeds simply because it is experiencing higher loads. If the increased stiffness were energetically favorable, this setup would offer a form of automatic stiffness control²¹².

There is some evidence that passive stiffness tuning occurs in aquatic animals. A model of lampreys showed that negative work emerged at higher frequencies without sensory input, and that the higher effective stiffness led to higher efficiency⁶³. The vertebral column of dogfish sharks exhibits nonlinear stiffness: it stiffens automatically at higher frequencies, a feature the authors compare to a continuously variable transmission (CVT)²¹³. It would be of interest to see if other, non-elasmobranch, fish species with different backbone materials and anatomies show similar properties. The line between passive and active stiffness tuning can be blurry, because a backbone with naturally occurring frequency-dependent stiffness could be functionally identical to a backbone that is actively made to have frequency-dependent stiffness. In these cases, more formal treatments of stiffness may be helpful, such as decoupling stiffness matrices into passive and active elements²¹⁴.

Robo-inspired Biology

While stiffness tuning strategies are poised to improve fish-like robotics, they can also offer insights into new studies of live fish locomotion. This learning will require challenging new experiments. Testing stiffness-related hypotheses in living fishes requires invasive surgery to implant transducers and electrodes into fish, appropriate and cooperative model fish species with anatomy conducive to *in vivo* stiffness measurements, flow tanks to control swimming speed in instrumented fish, simultaneous measurement of the energetic cost of swimming, and some good fortune so that fish maintain functioning instrumentation as they swim post-surgically at different speeds in a metabolic chamber. And even with a successful experimental protocol of this kind, there is the question of an appropriate control: how does one make a comparison between these data and swimming in live fish that lack stiffness adjustments?

One experimental option that we suggest is implanting small tendon buckles onto tail tendons, then measuring how muscle activation changes with speed. The study of Shadwick and Syme²¹⁵ and the previous work of Knower¹³⁵ provide examples of this method and show that tendon buckles allow *in vivo* measurement of tendon forces. To address the issue of an appropriate control, new studies would ideally use experimental alterations of body stiffness, such as scale removal¹⁵⁵ or muscle deactivation via botulinum toxin. The latter option, which has the advantage of converting active elements to passive elements, has been used in a study of fish jaw muscles²¹⁶. We suggest that particular emphasis be placed on studying antagonistic musculature. Data on antagonistic muscle activity, estimated muscle fiber length changes using sonomicrometry^{101,128,215,217}, combined with *in vitro* studies of muscle length-tension relationships, could help in understanding how much bilateral force is being applied to the spinal column and fins, and if (and how) bilateral force production changes with swimming speed.

Despite the sparse biological evidence of stiffness tuning, there are clear reasons to believe that changes in stiffness play an important role in the locomotor dynamics of fishes^{5,33,67,218}. These reasons can be argued based on anatomical data from fish, comparative data from walking and flying animals, as well as theoretical and computational models^{135,215,219}. Biological hypotheses can also be tested on fish-like robotic platforms where stiffness can be tuned with swimming speed^{205,208}. This concept highlights the interplay between biology and robotics. Biology can inspire robotic models of stiffness tuning, and these models can help us further understand the biological mechanisms on which they were based.

6. Conclusion

We believe that a closed loop of “bio-inspired robotics” and “robo-inspired biology”²²⁰ will be critical to our understanding of aquatic stiffness tuning in the years ahead. Fish vastly outperform even the most advanced swimming robots²²¹, and our limited understanding of flexibility is thought to be a key contributor to this gap²²². Fish-like robots have typically used a fixed stiffness—often one chosen based on rules of thumb. Based on recent discoveries, we suggest that future studies of flexibility in fish and robots should consider stiffness as a constantly-shifting variable. To keep pace with real fish, bio-inspired robots may need to adapt their stiffness based on realtime performance goals and swimming conditions. Such robotic platforms may even outperform biological systems, which may have limitations on their ability to actively tune stiffness.

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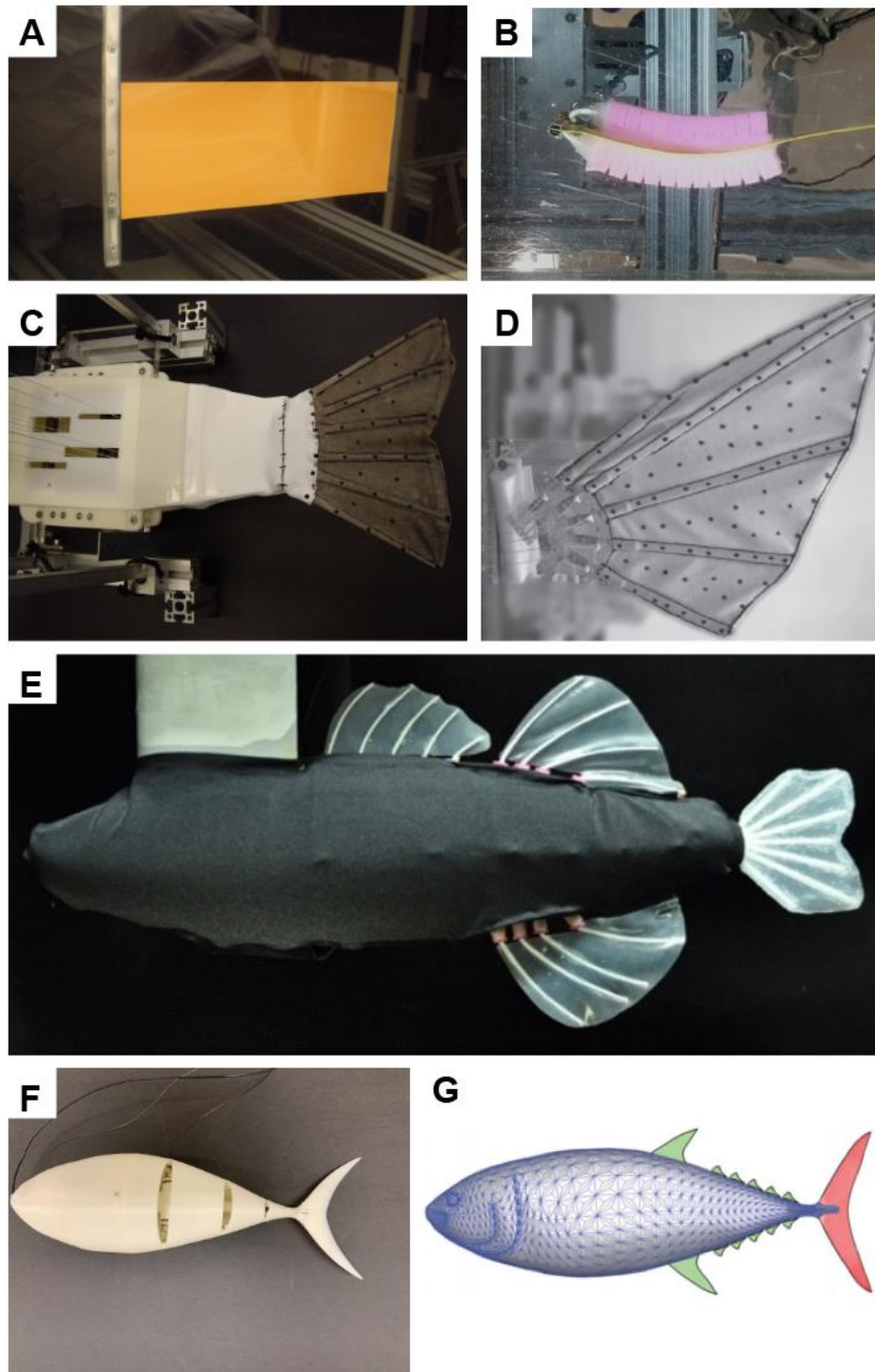


Figure 1. Flexibility studies use models that range in complexity. **A:** A simple rectangular plastic foil actuated at the leading edge in pitch and heave (see Saadat et al.²²³). **B:** Soft robotic fish-inspired model using antagonistic pneumatic actuators (see Jusufi et al.²²⁴). **C:** Robotic fish caudal fin with individually-controlled fin rays attached to a rigid body (from Esposito et al.⁶⁴). **D:** Robotic fish pectoral fin (from Tangorra et al.³⁴). **E:** Pneumatically-controlled dorsal, anal, and caudal fins attached to an undulating body for analyses of acceleration performance (see Wen et al.²²⁵). **F:** Tuna-inspired robot with flexible joints capable of high-frequency locomotion (see White et al.¹⁸³). **G:** Three-dimensional reconstruction of a bluefin tuna used in immersed boundary simulations of the surrounding flow (from Zhong et al.²²⁶).

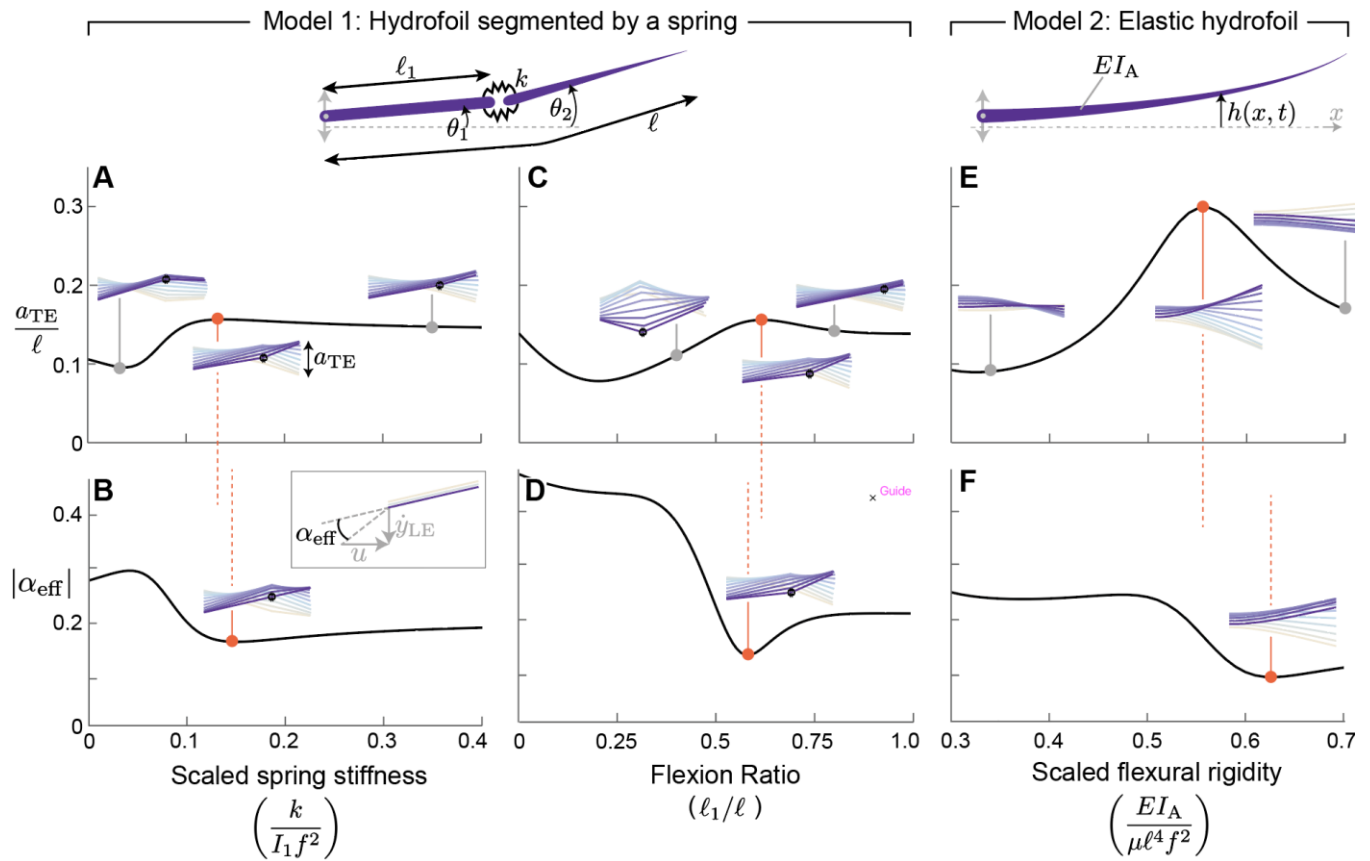


Figure 2. Two common flexible hydrofoil models highlight the importance of stiffness tuning. A-D:

Flexible foil is modeled as a hydrofoil segmented by a linear torsional spring heaved at the leading edge. Here, the pitch angles of the two hydrofoil segments (θ_1 and θ_2) are governed by the coupled equations $I_1 \ddot{\theta}_1 = k(\theta_2 - \theta_1) - \zeta_1 \dot{\theta}_1 + \tau_i$ and $I_2 \ddot{\theta}_2 = -k(\theta_2 - \theta_1) - \zeta_2 \dot{\theta}_1$, where k is the torsional spring constant, τ_i is an inertial torque imposed by the heaving leading edge, and ζ_i and I_i are the i 'th segment's damping coefficient and effective pitch moment of inertia, assumed to be proportional to the length of the segment and the length of the segment squared, respectively. **E-F:** Flexible foil is modeled as a linearly elastic beam heaved at the leading edge. Here, the deflection of the beam ($h(x, t)$) is governed by elastic beam theory: $\mu h_{tt} = -EI_A h_{xxxx} - \zeta h_t$, where subscripts denote partial derivatives and μ , E , I_A , and ζ are the beam's effective mass per length, elastic modulus, cross-sectional second moment of area, and damping coefficient. **A**, **C**, and **E** show trailing edge amplitude (a_{TE}); **B**, **D**, and **F** show maximum effective angle of attack (α_{eff}), as defined in the insert (u , incoming flow; h_{LE} , deflection at the leading edge). See, e.g., Moore⁵⁷, Zeyghami & Moored⁶⁸, or Floryan & Rowley⁴⁵ for derivations, additional terms, and more details.

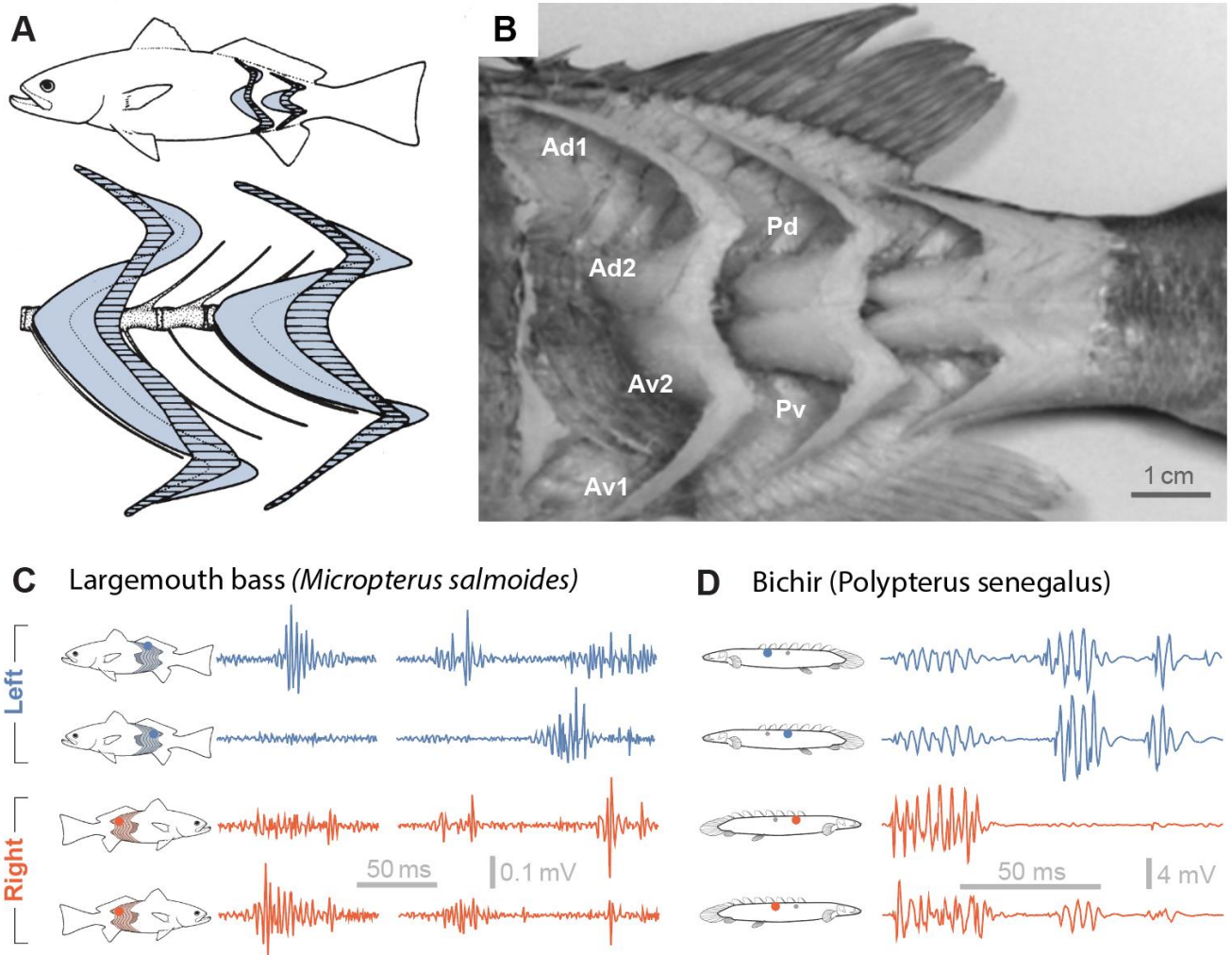


Figure 3. Stiffness control in body musculature. **A:** White myotomal segmental muscle arrangement in diagrammatic form. **B:** A largemouth bass (*Micropterus salmoides*) dissection reveals the W-shape of body myomeres with anteriorly-pointing regions (dorsal, Ad1 & Ad2; ventral, Av1 & Av2) and posteriorly-pointing deep regions (dorsal, Pd; ventral, Pv). From Jayne & Lauder²²⁷. **C:** Varying degrees of antagonistic body muscle activity in largemouth bass during slow (left) and fast (right) swimming. See Jayne & Lauder¹²⁶. **D:** Varying degrees of antagonistic body muscle activity in bichir (*Polypterus senegalus*) during the first 50 ms of an escape maneuver. See Tytell & Lauder¹²¹.

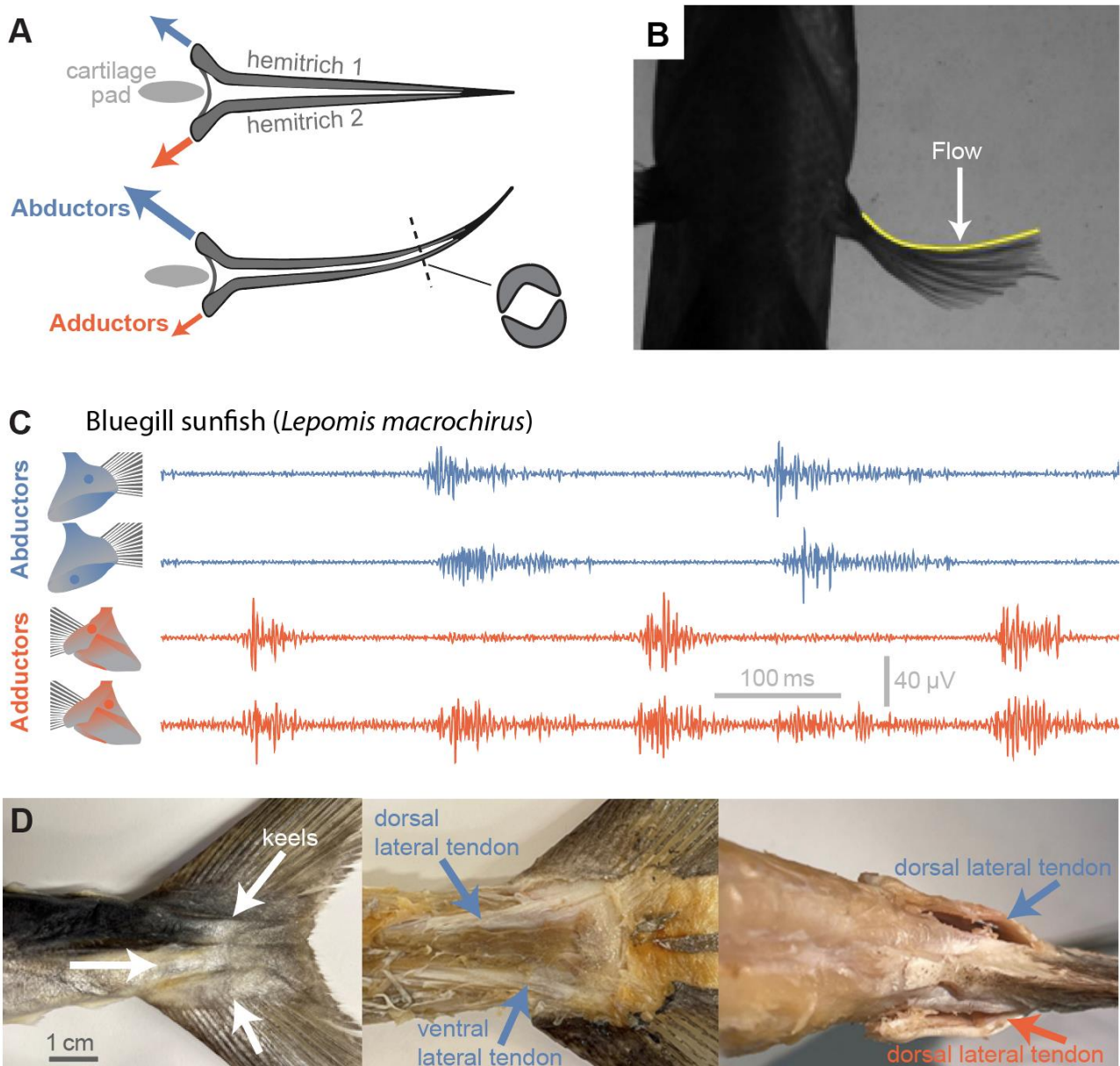


Figure 4. Stiffness control in fins. **A:** Schematic anatomy of a fish fin ray to show its bilaminar structure and muscle attachment points. Antagonistic motion can stiffen fin (top) and/or bend fin (bottom). Insert: cross section of a fin ray. **B:** Right pectoral fin of a maneuvering bluegill sunfish (*Lepomis macrochirus*); the fin's leading edge (outlined in yellow) curves into the incoming flow. From Lauder et al.⁴. **C:** Electrical recordings from pectoral fin muscles in bluegill sunfish. At first, adductor muscles are active while abductor muscles are not; then, during a rapid maneuver, both are active. See Lauder et al.¹³³. **D:** Tail and caudal tendon anatomy in spanish mackerel (*Scomberomorus maculatus*). Left: caudal peduncle region with finlets and three external horizontal keels (white arrows). Middle: Superficial dissection shows dorsal and ventral lateral tendons which splay out to attach to fin rays in the upper and lower tail lobes. Right: Viewed from above, a dissection exposes two lateral dorsal tendons, one on each side.

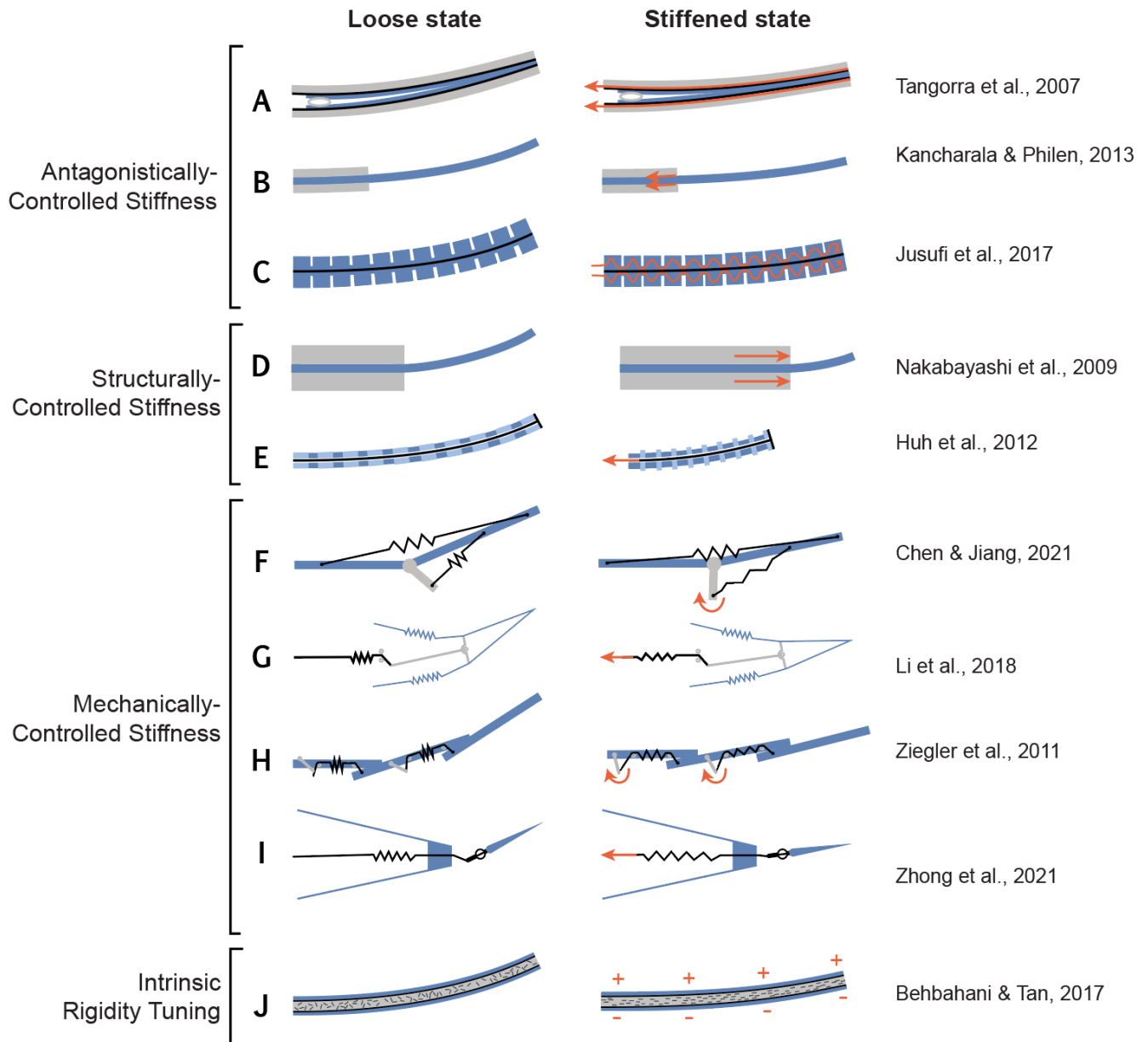


Figure 5. Stiffness control in robotic fish. Schematics illustrate the basic mechanisms of stiffness-tuning that have been tested or proposed in fish-like robotics. To antagonistically control stiffness, robots tune the co-actuation of two actuators, one on each side of a propulsor. To structurally control stiffness, robots tune the shape or length of a propulsor. To mechanically control stiffness, robots tune the pretension of internal elastic elements of a propulsor. To apply intrinsic rigidity tuning, robots make use of smart materials that change stiffness, e.g., in the presence of an electric field.

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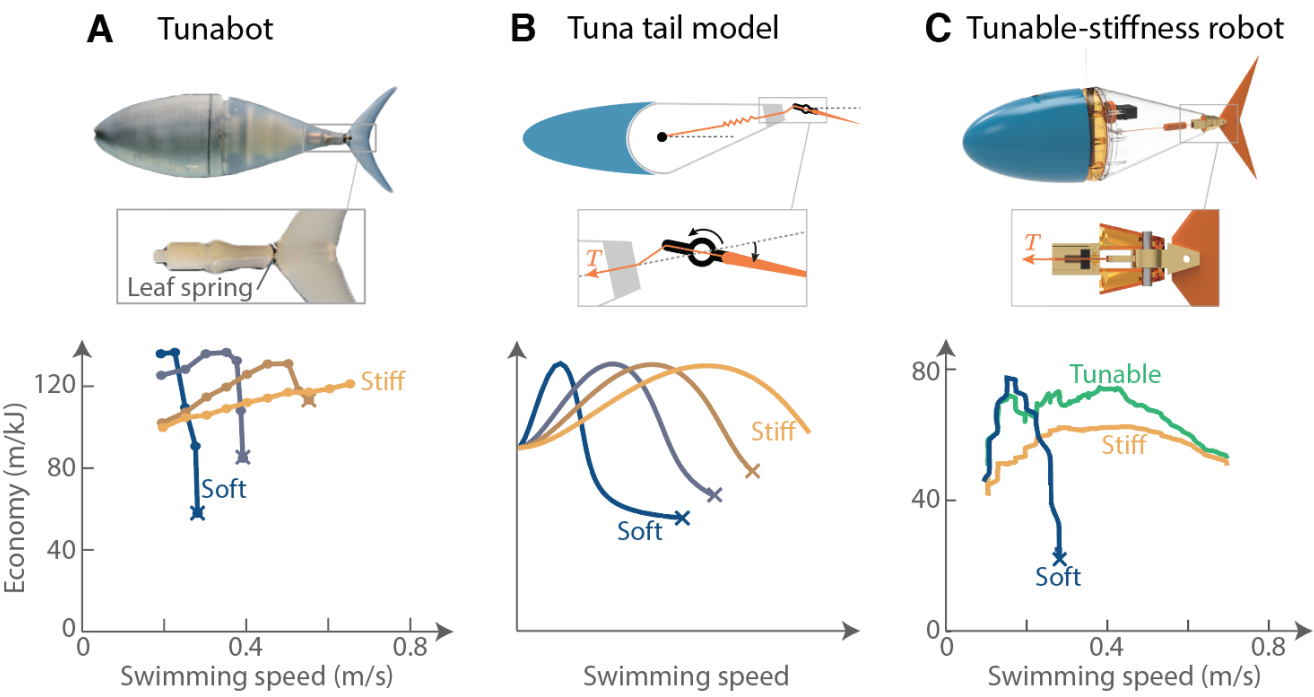


Figure 6. Tunable stiffness allows high efficiencies throughout multi-speed missions. **A:** The stiffness of the peduncle in the “Tunabot”²⁰⁹ is dictated by a leaf spring. Stiffer peduncles can reach higher speeds (X’s indicate speed limits given stiffness), but looser peduncles are more efficient at low frequencies. **B:** A model of tuna tail dynamics⁶⁷ recreates the qualitative features of the stiffness-dependent economy curves of the Tunabot. The model uses dimensionless variables and can be fit to any size, so tick marks and units were omitted. **C:** A robot with a variable-stiffness peduncle (the “AutoTuna”⁶⁷) outperforms the same robot with fixed-stiffness peduncles; by tuning the spring tension T based on swimming speed, the robot is able to reach a wide range of speeds while maintaining high efficiency (Top row images from Zhong et al.⁶⁷).

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