REVIEW

Flexibility is a hidden axis of biomechanical diversity in fishes

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ABSTRACT

Nearly all fish have flexible bodies that bend as a result of internal muscular forces and external fluid forces that are dynamically coupled with the mechanical properties of the body. Swimming is therefore strongly influenced by the body's flexibility, yet we do not know how fish species vary in their flexibility and in their ability to modulate flexibility with muscle activity. A more fundamental problem is our lack of knowledge about how any of these differences in flexibility translate into swimming performance. Thus, flexibility represents a hidden axis of diversity among fishes that may have substantial impacts on swimming performance. Although engineers have made substantial progress in understanding these fluid–structure interactions using physical and computational models, the last biological review of these interactions and how they give rise to fish swimming was carried out more than 20 years ago. In this Review, we summarize work on passive and active body mechanics in fish, physical models of fish and bioinspired robots. We also revisit some of the first studies to explore flexural stiffness and discuss their relevance in the context of more recent work. Finally, we pose questions and suggest future directions that may help reveal important links between flexibility and swimming performance.

KEY WORDS: Body mechanics, Fins, Muscle activity, Physical models, Stiffness, Swimming

Introduction

Fishes differ dramatically in the size and shape of their bodies. Different external morphologies often correlate with different behaviors and environments, suggesting each of these morphologies provides specific functional and ecological benefits. But within this readily observable variation there is a hidden axis of biomechanical diversity: flexibility. Fish bodies bend as a result of muscular, structural, inertial and fluid forces. The amount and speed of that bending is determined by many mechanical properties, including stiffness (the resistance to bending) and damping (the resistance to the speed of bending), which we will refer to collectively as 'flexibility' or 'stiffness' (Fig. 1). The importance of flexibility to swimming has been recognized for nearly a century (Aleyev, 1977; Gray, 1933; Long and Nipper, 1996; reviewed by Long, 1998) and flexibility itself has been observed to vary among and within the bodies of different fish species (e.g. Summers and Long, 2006). Yet, flexibility is determined by the morphological and material properties of internal and external structures that can be difficult to measure.
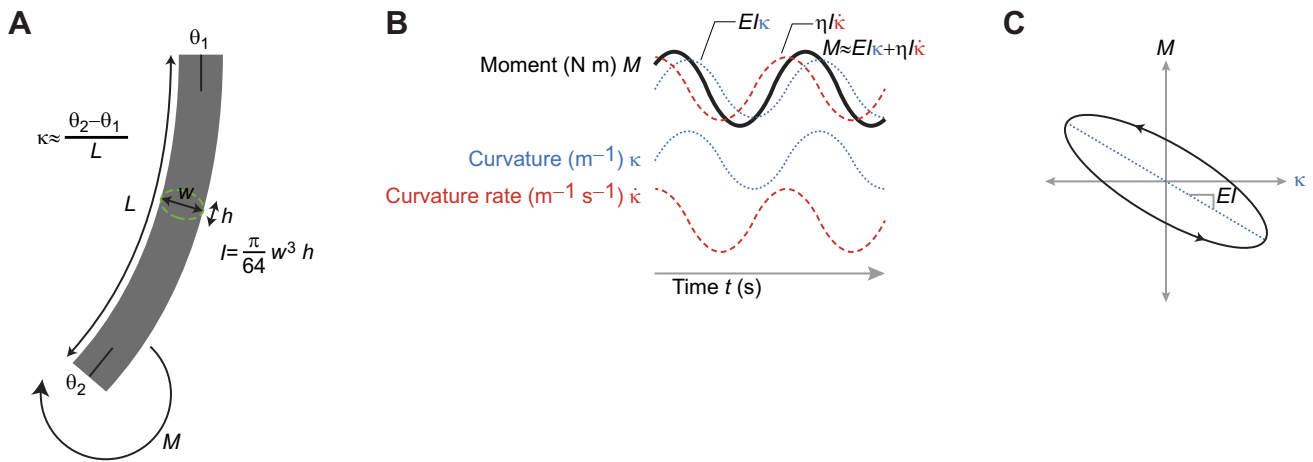
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Thus, compared with the purely morphological properties of size and shape, flexibility has not been well studied.

Our limited understanding of flexibility – including its diversity and functional implications – leaves us with many questions that are simple yet fundamental to understanding the biomechanical and locomotor diversity of fishes. Which fish species are more flexible than others? For a single species, how do stiffness and damping vary across the fish's body, and how does the resulting non-uniform flexibility influence swimming? Internally, what different anatomical and morphological features influence body flexibility? How does this diversity correlate with behavior and performance? How do these passive mechanical properties change over developmental and evolutionary time frames?

Adding to this complexity, as fish contract their muscles to bend the body and generate propulsion, the flexibility is altered relative to the passive state in which muscles were inactive. Muscles actively vary body flexibility when they forcefully shorten or forcefully resist shortening, with the body becoming more or less flexible, respectively. But we do not know whether the modulation of active body stiffness across swimming modes can be explained by general principles, or whether anatomical, ecological and phylogenetic differences give rise to a wide range of strategies. Such gaps in our knowledge highlight how little we understand the interplay between internal body mechanics and the external fluid environment, and how that interplay varies across diverse swimming modes and performance levels in fishes.

Here, we review what is known about the body mechanics of fishes, particularly stiffness, and how these properties contribute to swimming performance. First, we define stiffness and damping, and summarize some of the challenges in measuring them for fish bodies and tissues. Second, we summarize what is known about the passive stiffness in fishes. Third, we explore how fish can co-contract axial muscles to modulate body stiffness. Fourth, we discuss how models demonstrate the importance of stiffness for swimming performance and performance trade-offs, and detail some of the mechanisms by which stiffness may enhance performance. Finally, we emphasize the need for collaborative research and propose future areas of inquiry.

Defining and measuring stiffness and damping

The flexural stiffness EI (N m^2) of a homogeneous beam is described by the relationship between an applied torque or bending moment M (N m) and the resulting curvature κ (m^{-1}) (Fig. 1):

$$M = EI\,\kappa. \tag{1}$$

Curvature κ is approximately the difference in angle θ between segments of the body, divided by the distance L between those segments, or more precisely $\frac{d\theta}{dL}$ (Fig. 1A). When the curvature varies over time (Fig. 1B), as it does for a fish that bends laterally:

$$M(t) \approx EI\,\kappa(t) + \eta\,I\,\dot{\kappa}(t), \tag{2}$$

Fig. 1. Flexural stiffness measured through the bending and damping moduli. (A) A structure is bent by a moment M through curvature κ. The second moment of area I is defined by the width w and height h of the structure (assuming an oval cross-section). (B) The bending moment M, curvature κ, and curvature rate $\dot{\kappa}$, as a function of time. The bending moment has components that depend on κ and $\dot{\kappa}$. (C) A Lissajous plot, showing the moment versus curvature, where time progresses counterclockwise around the curve. The overall slope of the curve is the flexural stiffness EI. The diagram here shows a small segment of a bent structure, but in a fish, a bending moment can be applied at different locations and that the stiffness can vary based on location.

indicating that the structure resists bending (with stiffness EI) and the rate of bending (with the damping modulus ηI, with units N m² s). There is also an additional term related to the inertia of the body and the water's added mass, which usually is omitted but may become important for high-speed movements.

The flexural stiffness EI consists of two terms: the elastic modulus E (in N m⁻² or Pa; also referred to as Young's modulus) that characterizes the contribution of the material to the stiffness; and the second moment of area I (in m⁴) that characterizes the contribution of the cross-sectional shape to stiffness. For objects with an oval cross section, a close approximation to that of a fish, the second moment of area is:

$$I = \frac{\pi}{64} w^3 h, \qquad (3)$$

where w is the width of the body (perpendicular to the bending axis) and h is its height (parallel to the axis) (Fig. 1A). Just as flexural stiffness is the product of E and I, flexural damping ηI is the product of a material property (η) and the same shape parameter (I).

Beam theory, from which these equations derive, assumes a structure is made of the same material throughout; however, fish are clearly not homogeneous. The second moment of area I only approximates body shape effects, and E and η, where they are known, represent composite average material properties of the diverse structures in a fish (Fig. 2). Yet, several studies have shown that these approximations are surprisingly accurate for fish during simple lateral bending (Coughlin et al., 1996; Katz et al., 1999; Long et al., 2002a), simple dorsal bending (Jimenez et al., 2021) and even during complex biplanar bending (Jimenez and Camp, In Review).

For homogeneous materials like plastics or metals, E and η are often fairly constant as the curvature κ increases. In contrast, many biological materials, such as those that compose fish bodies and fins, become stiffer at higher curvature (Nowroozi and Brainerd, 2012). Thus, there may be a different effective stiffness or damping when the bending body is straight compared with when it is highly curved at the end of a tail beat. These complexities are beyond the scope of this review; we refer readers to the large amplitude
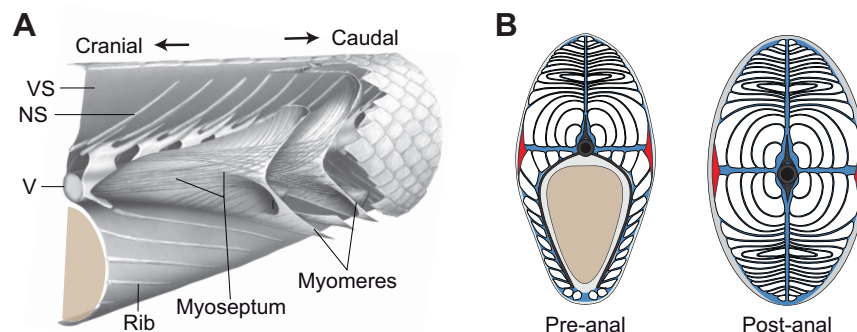
Fig. 2. Fish bodies are complex heterogeneous structures. (A) Axial anatomy of longnose gar (*Lepisosteus osseus*; modified from Gemballa and Röder, 2004), oblique view. Vertebrae are separated by intervertebral joints and are linked by connective tissue, ligaments, and bony processes. Muscle segments (myomeres) are separated by collagenous sheets (myosepta). Each myomere attaches to other structures via myosepta, with lateral attachments to the integument and medial attachments to structures including the vertebrae, the vertical and horizontal septa and the peritoneum (Vogel and Gemballa, 2000; Westneat et al., 1993). A vertical septum composed of cross-woven collagen fibers encloses both the neural spines of the vertebral column and the pterygiophores of the fins. (B) Cross-sectional views of a fish at different axial positions, illustrating differences in the relative composition of muscle. Colors: red, slow-twitch muscle; white, fast-twitch muscle; blue, connective tissue – primarily myosepta; gray, bone; brown, viscera. VS, vertical septum; NS, neural spine; V, vertebra.

oscillatory bending framework (Ewoldt et al., 2008; Porter et al., 2016).

Challenges with measuring mechanical properties

Stiffness is a difficult property to measure for theoretical and methodological reasons. First is the challenge of deciding which structures are relevant. Fish bodies are composite structures made up of many different biological tissues with varying material and structural properties, whose individual properties may differ from the properties of their composite (Fig. 2; Table 1). Second is the challenge of selecting an appropriate technique. Many techniques have been used to measure the mechanical properties of various structures and structural groups, ranging from static tests on isolated skin and muscle to dynamic oscillatory tests of whole fishes being bent with synchronous muscle stimulation.

In practice, measuring the stiffness of a whole fish or parts of it is challenging. The hydrated, heterogeneous, and hierarchical structure of fish bodies means that any measurement of EI depends first and foremost on the condition of the fish. Is the fish anesthetized, freshly dead, purchased fresh or thawed? In addition, the internal temperature and temperature gradient of the fish and the laboratory's ambient temperature and relative humidity alter the measurements: warmer specimens or tissues within a specimen may have a lower EI than cooler ones; a rapidly desiccating fin or excised vertebral column will become stiffer as it dehydrates. Testing at a temperature other than that at which the fish lives may shift the measured EI out of an ecologically valid range.

In order to bend a whole fish, a fin or a portion of fish's body, the specimen must be gripped firmly to avoid slippage during the application of motion and moment. Different modes of gripping – pressure pads, adhesive pads or indirect attachment to skeletal elements – alter in different ways the internal stress field of the body, which, in turn, alters the EI. Finally, the easiest tests to perform, static or quasi-static tests, are the least physiologically valid because they allow the moment M at a given curvature κ to equilibrate; a mechanical situation never seen during continuous swimming. Moreover, static tests, lacking movement, cannot estimate damping η, which is proportional to the rate of change of curvature κ. For these reasons, dynamic oscillatory tests are preferred but they have their own drawbacks, including inertial noise generated by the flexing of the specimen or vibrations of the testing platform. These must either be accounted for or mitigated in the design of the testing device or measured directly.

Passive mechanics of fish bodies

The elastic modulus, E, ranges over several orders of magnitude for biological structures across different species (Table 1). E is a size- and shape-independent material property that facilitates the detection of changes to the properties of tissues within and among species. Depending on the species and body region, the stiffness of the fish body ranges from 0.005 MPa to 19 MPa, indicating that fish bodies are similar to polymer rubbers in their stiffness (e.g. silicone and nitrile). Yet, fish with the same elastic modulus do not necessarily have the same internal anatomy. Differences could arise

Table 1. Summary of measurements of the mechanical properties of fish bodies and tissues

Species and reference	Location Description	Location Position (L_b)	E (MPa)	EI (N L_b^2)	Change in E when $\kappa\uparrow$	Change in E when $f\uparrow$	Change in E when $\rightarrow$ post.	η (kPa s)	I (L^4)	L_b (mm)	N	Method
Whole body												
Anguilla rostrata[1]	Mid-caudal	0.7	0.59	2.3×10^{-3}				12	4.91×10^4	280	3	Dynamic bending
Carassius auratus[2]	Midbody	0.48	0.047	0.058	=	=	↓		3.43×10^7	190		Dynamic bending
Ichthyomyzon unicuspis[3]	Midbody	0.55	0.088	3.1×10^{-3}				0.22	7.13×10^5	260	6	LAOB
Lepisosteus osseus[4]			0.75	0.15					4.48×10^5	663	3	Bending
Micropterus salmoides[5]	Midbody	0.43	3.8	12					3.50×10^7	300	1	Dynamic bending
Morone saxatilis[6]	Midbody	0.41	0.057	1.4	↑				1.56×10^8	400		
Myxine glutinosa[7]	Midbody	0.37	0.29	2.2×10^{-3}	=	↑			5.10×10^4	379	4	Dynamic bending
Skin												
Anguilla rostrata[9]	Midbody	0.17	9.1							525	2	Tensile
Anguilla rostrata[8]			6.9							395	10	Tensile
Apodichthys flavidus[10]	Posterior	0.75	28								4	Tensile
Carassius auratus[2]			1.8							186	4	Tensile
Eptatretus stoutii[10]	Posterior	0.75	53								5	Tensile
Katsuwonus pelamis[11]	Midbody		34							470	4	Tensile
Leiostomus xanthurus[11]	Midbody		9.4							185	5	Tensile
Lutjanus campechanus[12]	Midlateral	0.61	4.7		↑		↑			268	5	Tensile
Morone saxatilis[13]	Midbody dorsal	0.50	440								3	Tensile
Oncorhynchus kisutch[12]	Midlateral	0.56	1.6		↑		↑			650	5	Tensile
Petromyzon marinus[10]	Posterior	0.75	21								5	Tensile
Trachinotus carolinus[12]	Midlateral	0.54	8.4		↑		↑			292	5	Tensile
Muscle												
Carassius auratus[2]			1.1							186	4	Tensile
Vertebral column												
Makaira nigricans[14]	Joint 11		1.1	0.04	↑	↓	↑	13	2.98×10^4	1092	6	Dynamic bending
Morone saxatilis[15]	Abdominal		23	1.4×10^{-3}	↑	=	↑↓		522	346	5	Dynamic bending
Squalus acanthias[16]	Precaudal		0.59	1.2×10^{-4}	↑	↑		4.2	351	772	3	LAOB

[1]Long, 1998; [2]Zhou et al., 2011; [3]Tytell et al., 2018; [4]Long et al., 1996; [5]Long and Nipper, 1996; [6]Szewciw et al., 2017; [7]Long et al., 2002b; [8]Danos, 2005; [9]Hebrank, 1980; [10]Clark et al., 2016; [11]Hebrank and Hebrank, 1986; [12]Kenaley et al., 2018; [13]Szewciw and Barthelat, 2017; [14]Puri et al., 2017; [15]Aiello et al., 2018; [16]Taft et al., 2018; [14]Long, 1992; [15]Nowroozi and Brainerd, 2012; [15]Porter et al., 2016.

$\kappa\uparrow$, increasing curvature; $f\uparrow$, increasing frequency. $\rightarrow$ post., more posterior locations; L_b, body length; LAOB, large-amplitude oscillatory bending. ↑, increases; =, stays the same; ↓, decreases; ↑↓, increases and then decreases; L_b, body length; LAOB, large-amplitude oscillatory bending; EI and I are normalized by the fish's body length L_b.

from the elastic modulus of internal structures (e.g. stiffer tendons) or the relative proportions of stiff and flexible structures (e.g. bigger bones), or both. This complexity highlights the challenges of correlating the elastic modulus with function across simple tissues, composite structures and whole bodies.

The spatial distribution of mass within the transverse bending plane, or second moment of area I, also contributes to flexural stiffness. Thus, whole-body stiffness can vary simply because of shape or size differences in the internal or external anatomy. Assuming the same size and material composition, a wide fish will be stiffer than a narrow fish because more of its mass is distributed away from the neutral axis of bending. And, assuming the same body shape and internal geometric configuration, a fish with more tendon will have a greater body stiffness because tendon is generally stiffer (higher E) than other soft tissues such as muscle.

Not only do fish bodies differ in average stiffness, but the stiffness and second moment of area also vary along the body, and the pattern of this variation is different among species. These patterns were most systematically (though somewhat idiosyncratically) described by Aleyev in the 1960s and 1970s (Aleyev, 1977). His results cannot be converted into standard engineering units, but they do demonstrate that fish differ substantially in their effective bending modulus E. Aleyev reported two shape parameters (his G and Q parameters) that together allowed us to estimate the second moment of area I. He marked five points along the body of a freshly euthanized fish when it was straight, then bent the bodies through a 45 deg angle and reported the straight-line distance between the points (his 'E' parameter, not to be confused with the elastic modulus E). Regions of the body that flex more thus had a smaller value of 'E' than other regions. A simple numerical analysis allowed us to estimate curvature based on Aleyev's 'E', and since the bending moment was constant, we could then estimate the relative flexural stiffness EI of the different segments (Fig. 3). Details of the analysis are provided on Zenodo (doi:10.5281/zenodo.7630071).

We have chosen three example species (Fig. 3), the garfish *Belone belone* (a pelagic needlefish unrelated to freshwater gars), the Atlantic mackerel *Scomber scombrus*, and the great barracuda *Sphyraena barracuda*. *Belone belone* has a much lower EI than the other two, even though its second moment of area I is much lower, because its body tissues are much stiffer (higher E). In contrast, the mackerel and the barracuda have similar EI values, but the mackerel has a much higher I and lower E than the barracuda (see also Fig. S1 for other species).

Thus, body stiffness requires direct mechanical measurements like these and cannot be deduced from the morphology of the body alone. It is for this reason that we consider flexibility a hidden axis of variation – it is not visible. We must give a caveat to the data reported here in Fig. 3 and Table 1. They represent our best attempt to make measurements comparable across a wide range of measurement types, experimental protocols, species sampling, and tissue sampling (Table 1). As such, we do not suggest they be used in formal comparative analysis for making quantitative functional interpretations. Nevertheless, we include them for several reasons: (1) to provide an accessible reference for future studies; (2) to outline the challenges with measuring stiffness; (3) to illustrate the myriad factors that determine stiffness of the whole fish body; and (4) to highlight areas of interspecific variation that require further study. Table 1 also highlights the need to standardize the quality and consistency of measurements with the aim of conducting more rigorous phylogenetic and comparative analyses (see 'Future directions'). Importantly, they provide a valuable range of morphological and mechanical parameters to be used in developing physical and computational models for exploring the link between stiffness and swimming performance.

Fish can modulate whole-body flexibility

Fish muscle activity, and sensorimotor feedback more broadly, both produces the bending pattern for swimming, but also modulates the flexibility of the body (Long, 1998; Long and Nipper, 1996; Tytell et al., 2018). Fish produce complex and varied spatiotemporal patterns of muscle activity. Owing to the neuronal circuitry of their axial muscles (Bello-Rojas et al., 2019; Fetcho and Faber, 1988; McLean et al., 2007), fish can independently activate myomeres, allowing differential control in the cranio-caudal direction (Altringham and Ellerby, 1999; Wardle and Videler, 1993; Wardle et al., 1995) and different regions within each myomere, allowing differential control in the dorso-ventral direction (Ellerby and Altringham, 2001; Jayne and Lauder, 1995; Jimenez and Brainerd, 2020, 2021). Sensorimotor feedback could also lead to changes in effective body stiffness. Fish sense the deformation of their bodies (Grillner et al., 1984; Massarelli et al., 2017; Picton et al., 2021) and this proprioceptive sensory information is used to modulate the activity of spinal interneurons that drive muscle activity (Grillner and El Manira, 2020; Viana Di Prisco et al., 1990). If the effective gain of that modulation increases, that would also increase the effective body stiffness.

Fish directly modulate their body stiffness by varying the timing and intensity of muscle activity on opposite sides of the body. Co-activation, in which muscles on opposite sides of the body are active at similar times, involves active shortening (concentric) on the flexing side with simultaneous active lengthening (eccentric) on the side that resists flexion, increasing flexural stiffness (Altringham and Ellerby, 1999; Long, 1998; Wardle et al., 1995; Tytell et al., 2018). As eccentric muscles experience enhanced force production (Altringham et al., 1993) they are especially effective at resisting body bending and, therefore, increasing body stiffness. Co-activation has been observed for left–right pairs of red and white muscle fibers during various swimming behaviors and are likely to be used to modulate body stiffness (Jimenez and Brainerd, 2021; Schwalbe et al., 2019; Tytell and Lauder, 2002; Westneat et al., 1998).

During steady swimming, eccentric red and white muscle activity can be found in the caudal regions of fish species with different body shapes and swimming styles, suggesting the underlying importance of stiffening the posterior body (Wardle et al., 1995). During the escape response, or fast-start, eccentric white muscle activity is found in anterior (Jimenez and Brainerd, 2021) and midbody regions (Westneat et al., 1998), serving to enhance power production but also likely increasing body stiffness (James and Johnston, 1998). How exactly bilateral co-activation may impact local body stiffness is determined by, among many other factors, timing (Long, 1998; Tytell et al., 2018), asymmetry of left–right muscle activation intensity (Jimenez and Brainerd, 2021), intrinsic muscle physiology (Johnston et al., 1990) and strain-activation characteristics of the behavior (Rome et al., 1992; Askew and Marsh, 1997).

Although *in vitro* muscle fiber mechanics and *in vivo* muscle activation patterns during swimming have been studied extensively, little is known about how fish use their muscles to modulate body stiffness and how their body stiffness changes during swimming. Similarly, although sensorimotor feedback has been widely examined, we do not know how fish use sensory information to modulate muscle activity and whole-body mechanics. Even less is known about how regional changes in body stiffness
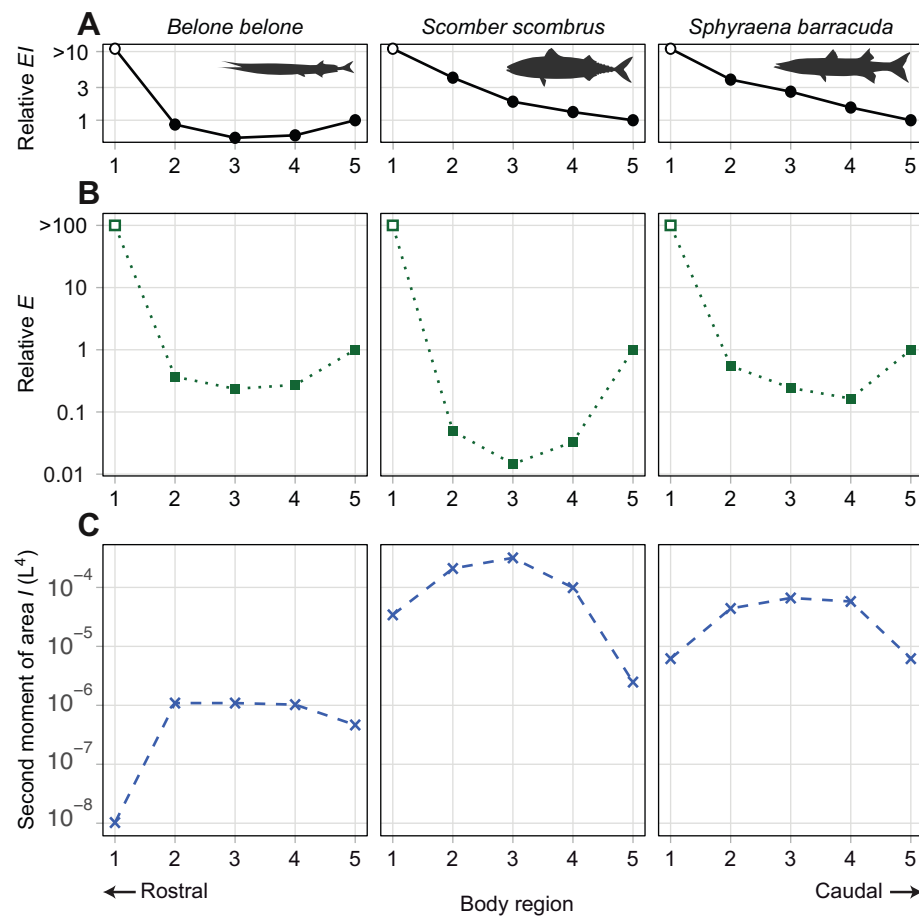
Fig. 3. Passive stiffness varies along the body of fishes (based on data from Aleyev, 1977). (A) Bending modulus EI relative to the caudal segment modulus. (B) Stiffness E relative to the caudal segment's stiffness. (C) Second moment of area of the body. Open points indicate a bending modulus more than 10× the caudal segment or a stiffness more than 100× the caudal segment. Aleyev measured I for several fish species at five equidistant positions along the body (body region 1–5), from approximately the tip of the lower jaw to the last caudal vertebrae. He also measured an index of flexibility, related to curvature, which we have converted to a flexural stiffness EI relative to the stiffness of the caudal segment, thus allowing a comparison of flexibility and cross-sectional shape along the body. The full data set and analysis scripts used to produce Fig. 3 are available in Zenodo (doi:10.5281/zenodo.7630071).

might impact performance during distinct swimming modes such as steady swimming, swimming steadily at different speeds and accelerating from a standstill. To understand the effects of variable body stiffness on swimming performance, it is important to quantify the stiffness of a fish as it contracts the axial muscles to swim.

Muscle activity is the primary determinant of body mechanics
Whole-body work loops demonstrate that muscular activity is the primary determinant of body mechanics. Even though passive stiffness varies across the body of individual fish and among different species (Table 1), muscle activity can change both stiffness and damping much more. The experimental protocol typically involves euthanizing and pithing a fish, then mounting it onto an apparatus where the whole body is oscillated at precise angles with synchronized torque measurements (Long and Nipper, 1996). As the body is oscillated at any combination of sinusoidal frequencies and amplitudes, the muscle can be stimulated with any desired activation parameters. Measurements of active body stiffness vary greatly depending on stimulation parameters (Fig. 4); therefore, knowledge of the *in vivo* kinematics and muscle strain-activation patterns are needed for interpreting muscle function (Rome et al., 1992). Simulating the *in vivo* kinematics and muscle activation of fish at different swimming speeds allows the researcher to estimate changes to body mechanics at different speeds of steady swimming, and perhaps even during unsteady swimming behaviors (Schwalbe et al., 2019).

When inactive, all of the axial musculature contributes only ∼25% of passive body stiffness (Summers and Long, 2006). In

contrast, stimulating axial muscle in the silver lamprey (*Ichthyomyzon unicuspis*) increases body stiffness between 10 and 100% from the passive state (Tytell et al., 2018). Stimulating the white musculature of American eels (*Anguilla rostrata*), which makes up the majority of their cross-section, increases body stiffness up to 300% (Long, 1998). These increases in stiffness are caused by co-contractions of the left–right muscle pairs, where eccentric muscle contractions on one side of the body resist and absorb the work produced by the muscle on the opposite side. However, muscle activity can also reduce body stiffness, particularly when muscle is stimulated strictly during the concentric phase (Long, 1998; Tytell et al., 2018). Thus, muscle activity is often the primary determinant of body stiffness.

Increasing body stiffness comes at a cost: the stiffer the body becomes, the more muscular work it takes to bend the body, thereby increasing the energetic cost of bending (Fig. 4). As eccentric muscles absorb work to stiffen the body, bending can become mechanically inefficient as the amount of concentric muscular power that gets transferred to the surrounding fluid is reduced (Hess and Videler, 1984). Thus, there is a trade-off between two important variables: body stiffness and muscle power output. Computational and physical models of stiffness show that although flexural stiffness and power are important, they are not in and of themselves optima for undulatory swimming. Instead, various combinations of stiffness and power can theoretically optimize different performance metrics such as acceleration, efficiency and peak velocity (Tytell et al., 2018). In order to optimize specific performance outcomes, fish may need to adjust how they balance body stiffness and muscle power, although the details of this balancing act are yet to be determined.
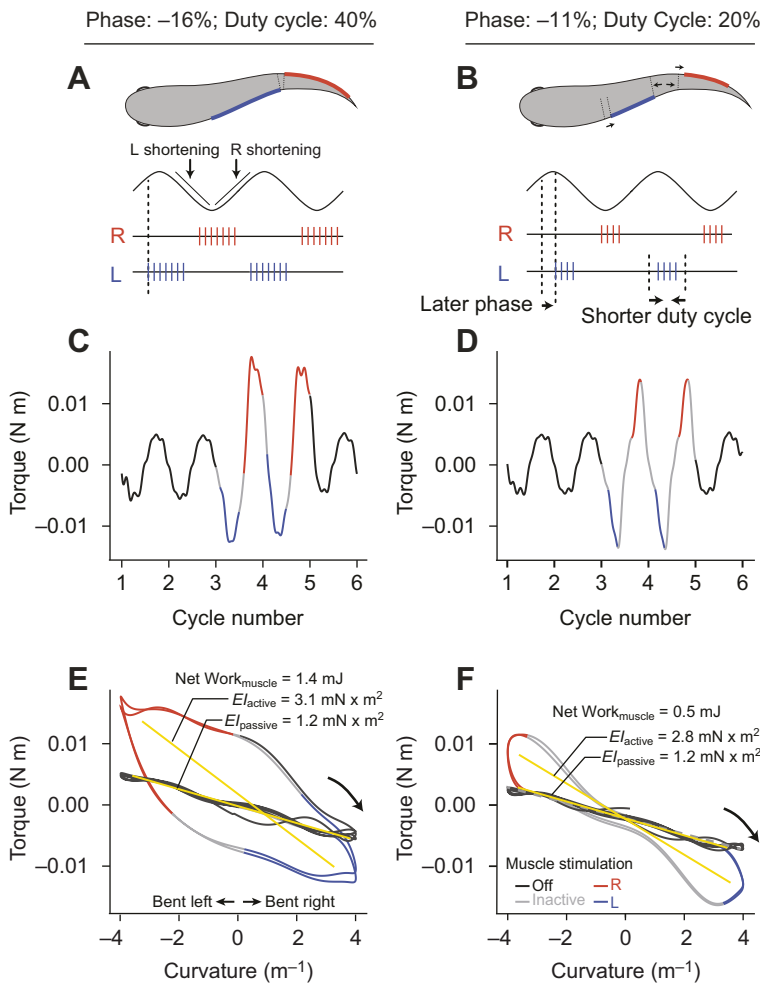
Fig. 4. Stimulation conditions affect net muscle work and active body stiffness. Left and right columns show different activation patterns during a whole-body work loop. Line colors throughout indicate when red muscle is stimulated on different sides of the body. (A,B) Fish can alter body stiffness by shifting the phase and/or duty cycle of muscle activity. (C,D) Sample data showing passive and active torques during a whole-body work loop. (E,F) Work loops showing torque over local body curvature during the bending cycle, with arrows indicating the time course of the work loop. Average mechanical data for sample trials are noted, including values for passive and active stiffness, which are shown as yellow lines. Data are from a 2 cm body segment at 65% total length in a scup (*Stenotomus chrysops*) with bending cycles at 4 Hz and 4 m^{-1}.

## Models reveal the functional significance of flexibility

Modeling systems approximate biological structures and enable us to focus on specific questions that are difficult to answer with live animals. Particularly, physical models (experimental systems) paired with appropriate sensors provide a wealth of information that is usually inaccessible with live fishes. For example, load cells incorporated into a model may directly measure swimming forces and torques, and high-speed videography and flow imaging (e.g. particle image velocimetry) provide kinematic and fluid mechanical data with repeatability and precision that is nearly impossible with live fishes. So, physical models have been invaluable in linking bending and stiffness with specific swimming performance outcomes. Alongside, computational models are used to explore conditions that are difficult to physically construct, but they have only rarely explicitly explored the impacts of flexibility for fish swimming (e.g. Tytell et al., 2010). Recent comprehensive reviews of flexible physical and computational models, their performance and fluid mechanics in an engineering context have been provided by Smits (2019), Wu et al. (2020) and Wang et al. (2022). We focus on physical modeling studies and reference a select few computational studies to support their conclusions on key ideas pertaining to fishes.

Most fish-like models fall into two broad categories: those with chordwise bending along an axis parallel to the flow (Fig. 5A), similar to the axial bending of a fish's posterior body and caudal fin (Fig. 5C,D) or those with spanwise bending along an axis perpendicular to the flow (Fig. 5B). Spanwise bending models are most typically used to investigate movement of pectoral fins but can also represent the active spanwise bending (i.e. conformation changes) of the caudal fin exhibited in many swimming fishes (e.g. Fig. 5D) (Esposito et al., 2012; Flammang and Lauder, 2009). To demonstrate that stiffness likely has functional significance for body/caudal fin locomotion by fishes, we focus in this section on models with chordwise, passive flexibility: those where bending is purely a function of stiffness.

Rectangular panels or hydrofoils are the most common passively flexible models. In addition to being simple to construct, these models are advantageous for their ability to isolate specific material or structural characteristics. Dominating the literature are studies of rectangular panels made of plastic or rubber sheets with uniform flexural stiffness across their structure or of hydrofoils made of rigid or flexible material.

Over the past decade, researchers have begun using 'near-rectangular' physical models that more closely resemble the fish body. These models are all variations on the rectangular panel or hydrofoil and include rectangular models with non-uniform stiffness (e.g. Cleaver et al., 2014; Han et al., 2022; Leroy-Calatayud et al., 2022; Lucas et al., 2015; Riggs et al., 2010; Vincent et al., 2020), panels cut into tail shapes (e.g. Feilich and Lauder, 2015; Rosic et al., 2017) or at the most complex, panels with both non-uniform stiffness and a tail-like shape (Kancharala and Philen, 2016; Luo et al., 2020).
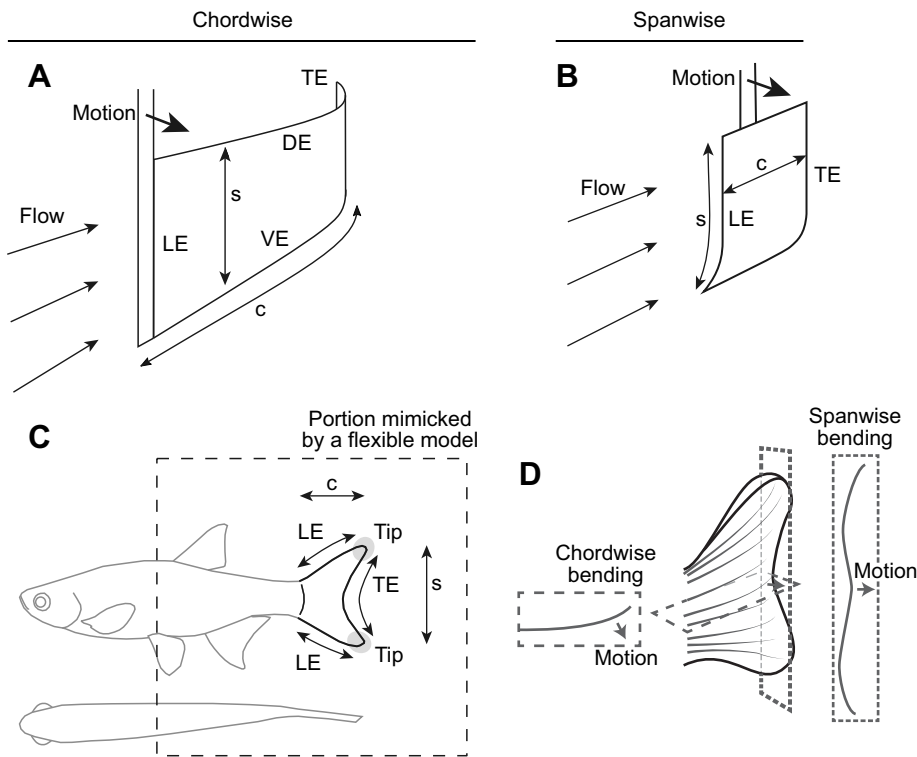
Fig. 5. Configurations of chordwise and spanwise bending panel models.
(A) Chordwise and (B) spanwise bending. (C) Comparable region of the caudal fin. (D) Caudal fin demonstrating simultaneous chordwise and spanwise bending. Note that the fin actively cups into the flow along the spanwise axis, where the passive foil in B is bending in the opposite direction, with the tip lagging behind the rest of the model. c, chord; DE, dorsal edge; LE, leading edge; s, span; TE, trailing edge; VE, ventral edge.

Panel stiffness modulates swimming performance

Modeling studies have demonstrated that certain stiffnesses can dramatically boost swimming performance. Improvements of up to 150–200% have been reported for performance metrics such as thrust, hydromechanical efficiency [Froude efficiency, or the proportion of the total input energy that goes into thrust, which is not well defined for self-propelled bodies like fish (see Schultz and Webb, 2002; Tytell, 2007)], self-propelled speed (the speed where thrust and drag balance during a given actuation regime) and cost of transport (energetic cost of motion at the self-propelled speed, where efficiency is undefined) (Dewey et al., 2013; Han et al., 2022; Kancharala and Philen, 2014, 2016; Leroy-Calatayud et al., 2022; Lucas et al., 2015; Luo et al., 2020; Quinn et al., 2014; Riggs et al., 2010; Rosic et al., 2017; Shelton et al., 2014).

But it has also become clear that the effects of stiffness on performance are complex, following nonlinear patterns. Some studies have identified conditions in which peak efficiency decreased or increased only modestly (2–30%) (Cleaver et al., 2014; Iverson et al., 2019; Katz and Weihs, 1978; Vincent et al., 2020). Even those reporting large performance enhancements indicate that these improvements are highly dependent on model configuration, actuation parameters and performance metrics. Notably, thrust and efficiency are rarely maximized simultaneously, irrespective of model type (Katz and Weihs, 1978; Lucas et al., 2015; Rosic et al., 2017; Shelton et al., 2014). This suggests that fishes would benefit from being able to tune stiffness depending on swimming needs – maximizing thrust delivery during an acceleration or turn versus maximizing efficiency for traversal of long distances.

The relationship between non-uniform stiffness and performance has become a growing topic of interest. Many animal propulsors have a flexible tip that experiences substantial bending starting between 50 and 75% of the propulsor's span (for wings) or chord (for fish-like bodies) (Lucas et al., 2014). In fact, this pattern is also shown in Aleyev's data, where most fish species are the most flexible in the caudal two segments, or 60–80% of body length (Fig. 3). Using simple physical models with non-uniform chordwise stiffness (stiffer anterior, less stiff posterior), several investigators have demonstrated that this pattern of stiffness enhances propulsive thrust or efficiency over that produced during uniform bending (Han et al., 2022; Kancharala and Philen, 2016; Leroy-Calatayud et al., 2022; Lucas et al., 2015; Luo et al., 2020; Vincent et al., 2020). These findings support the hypothesis that this stiffness pattern is mechanically advantageous and has arisen through natural selection, but a more controlled comparative study would be required to fully evaluate this claim for fishes.

Mechanisms by which flexible models enhance performance

Modeling studies identify three major mechanisms through which flexibility modifies swimming performance: flow control, wake formation, and mechanical resonance. The first mechanism is through control of flow along the flexible structure. The bending of a flexible structure may align the body more favorably in the flow such that forces produced along its surface have a larger thrust and smaller lateral component, increasing efficiency (e.g. Iverson et al., 2019; Kancharala and Philen, 2014, 2016; Katz and Weihs, 1978; Lucas et al., 2020, 2015; Ramananarivo et al., 2011; Tangorra et al., 2010). This effect only works in a narrow range: too much bending will lead to separation at the peaks of the bending waveform (Quinn et al., 2015; Ramananarivo et al., 2011).

The second mechanism is through formation of the wake. Chiefly, an appropriate degree of flexibility aids in directing flow off the trailing edge into the wake in a way that maximizes the momentum of the time-averaged, downstream-oriented jet, resulting in greater thrust and efficiency (Cleaver et al., 2014; Huera-Huarte and Gharib, 2017; Leroy-Calatayud et al., 2022). Such flexibility also reduces parasitic drag by minimizing or delaying the formation of vortices around the tips or trailing edge (Iverson et al., 2019; Vincent et al., 2020).

The final mechanism is through resonance, a physical phenomenon where an amplitude is magnified by moving a

structure at specific frequency. Flexible structures can experience structural resonance, where the oscillation frequency matches the structure's natural frequency and causes the structure to experience heightened deformation (Dewey et al., 2013; Han et al., 2022; Moored et al., 2012, 2014; Paraz et al., 2014; Quinn et al., 2014, 2015; Tytell et al., 2016). This increases the amplitude of trailing-edge oscillation and classical analytical models link increased trailing-edge amplitude to increased thrust production (Blake, 1983; Katz and Weihs, 1978; Lighthill, 1975; Yates, 1983). The resonant frequency inherent to the structure may not be the same as the resonant frequency underwater, as damping effects of the water resist the curvature of the body and fins (McMillen and Holmes, 2006; Ramananarivo et al., 2011) and added mass effects mean that a body in a fluid must accelerate not only its own mass but also the mass of some of the fluid around it (reviewed in Smits, 2019). Both rigid and flexible structures oscillating in a fluid environment can also experience wake resonance, where the oscillation frequency promotes the efficient transfer of downstream momentum into the structure's wake, enhancing thrust and efficiency (Moored et al., 2012, 2014; Smits, 2019; Triantafyllou et al., 1993). Optimal thrust and efficiency are achieved when structural and wake resonance frequencies align (Moored et al., 2014).

Related to the last two mechanisms, it is not currently clear whether efficiently producing a wake causes efficient propulsion, or whether an efficient wake is simply a by-product of efficient propulsion (Arbie et al., 2016; Eloy, 2012; Mackowski and Williamson, 2015). Accordingly, neither kinematics nor wake structures alone are good predictors of performance (Floryan et al., 2020; Luo et al., 2020; Rosic et al., 2017).

Models have been very successful in advancing our understanding of how dramatically flexibility can impact performance and of the underlying mechanics, but we caution that, while it is likely that fishes use some or all of these mechanisms, no model is a 1:1 representation of a fish, and some findings from modeling studies may be misleading or irrelevant to fish locomotion. We note three major limitations to consider during modeling investigations.

First, chordwise bending models are generally considered to mimic the posterior, thrust-producing portion of a carangiform swimmer's body (e.g. Lighthill, 1975; Lucas et al., 2015; Shelton et al., 2014) (Fig. 5C). So, findings about a panel's leading edge may not be informative for fish locomotion, since the model's leading edge represents somewhere in the middle of a fish's body. For instance, moving these panels in actuation regimes that eliminate the leading-edge vortex has been shown to maximize efficiency (Kancharala and Philen, 2016; Lucas et al., 2015; Quinn et al., 2015). But the middle of the body is not a leading edge and cannot experience a leading-edge vortex, so the applicability of these findings for fishes is not clear.

Second, these models, by design, exclude the anterior body. But a carangiform swimmer's anterior body produces approximately one-third of the body's thrust during steady swimming, so these forces are not captured by such models (Lucas et al., 2020).

Finally, and along the same line, anterior body structures may impact the flow encountered by posterior body structures. For instance, flows from the median fins or shed at the peduncle interact with those generated at the caudal fin and impact propulsive forces and efficiency, making true caudal performance difficult to predict based on a rectangular panel or hydrofoil model (Borazjani and Daghooghi, 2013; Brooks and Green, 2019; Mignano et al., 2019; Tytell et al., 2008).

Further advancing our understanding of fish flexibility and its impacts on locomotion will clearly require more complex model designs, and building up to the complexity of a fish body in a stepwise approach may be wise. The construction of simple composites has become increasingly accessible through devices like multi-material 3D printers or, more simply, embedding stiffer materials in silicone casts. In the past few years, several fish-like robotic platforms have been developed, which have been helpful for our understanding of body–fin flow interactions (Brooks and Green, 2019; Mignano et al., 2019) and solving design challenges such as producing a smooth, fish-like kinematic waveform (White et al., 2021). Thus far, these platforms have not focused on flexibility. Finally, physical models incorporating active stiffness changes or passive stiffness that changes with movement (e.g. Long et al., 2006) will be critical for fully understanding fish locomotion. Designing these more complicated models represents an ongoing challenge requiring collaboration between biologists and engineers.

Future directions

Above, we have shown that body mechanics vary substantially across the bodies of fish and among fish species. Because these mechanical properties are not readily visible, we refer to them as a hidden axis of diversity. Moreover, fish can modulate their stiffness – to the extent that muscle activation, not passive body properties, could be the primary determinant of effective body stiffness. Referring to the literature on passive physical models of swimming fish, we suggest that this diversity has functional consequences for swimming performance. However, we know very little about how body mechanics contribute to swimming performance.

To start to answer these questions, we need more data collected in comparable ways. In Table 1, we have attempted to convert data from numerous different studies with different methods into comparable units. In future studies, it is crucial that investigators include detail on: (1) the cross-section of the body or tissue, including width and height, or the second moment of area, or both; (2) the distance between clamps, used to estimate curvature; (3) the size of the whole specimen; and (4) the location on the body or tissue being tested. For bending studies, we suggest that investigators report the average flexural stiffness EI based on the slope of the torque–curvature relationship (e.g. Fig. 4E,F), along with E and I.

To achieve a deeper understanding of these effects, it is imperative to investigate the role of stiffness by integrating studies on live fishes, physical models and numerical models. Further integrating these fields would create rich opportunities to test hypotheses about the effects of stiffness on swimming. As is clear from this review, almost every question about active and passive stiffness needs more research. So, we pose six critical directions focusing on issues that have proved to be among the most technically challenging yet hold great explanatory promise.

First, what are the functional consequences of differences in passive body mechanics among individual fishes and across species? Are there any? This question may be addressed by comparing mechanical and kinematic variation across individuals of a species. For example, in Long's (1998) study, individual eels differed in their passive mechanical properties by about 40% and in Tytell's (2004) study, eels swam with body wavelengths that differed by about 30%. Since wavelength is related to curvature, it is also related to stiffness. We suggest that these individual differences in swimming kinematics may correlate with individual differences in body mechanics, and this relationship may indicate differences in functional optimizations across individuals.

Second, how are patterns of passive and active mechanical properties distributed across the phylogeny of fishes? How does this

hidden axis of variation correlate with functional or ecological diversity of fishes? A phylogenetic and systematic analysis of kinematics, body mechanics, and muscle activity is needed, one that expands beyond species typically used in fish biomechanics.

Third, do fishes take advantage of mechanical resonance? If so, in which structures? Near-rectangular, non-uniform stiffness models have performance peaks at structural and wake resonance frequencies, suggesting that resonance can be functionally meaningful in structures made up of multiple materials of different properties. But animal propulsors may operate at frequencies well below those of structural resonance, and bending waveforms in passive models have substantial contributions from higher-order harmonics along the anterior body (Ramananarivo et al., 2011; Root et al., 1999; Rosic et al., 2017), although these complex waveforms may be suppressed by live fishes through active stiffening. Alternatively, analytical models indicate that internal damping by the body's materials and external damping by the fluid are critical in forming fish-like kinematics (McMillen and Holmes, 2006; Ramananarivo et al., 2011; Tytell et al., 2010).

Fourth, to what extent and under what conditions do fishes tune their flexibility? Tuning would enable fish to appropriately alter and regionalize body mechanics to achieve high performance in a variety of circumstances. Experimental studies hint that fishes are capable of sensing environmental conditions and responding with altered muscle activation and kinematic patterns rapidly enough to meaningfully affect performance (Lutek and Standen, 2021; Tytell and Lauder, 2002; Westneat et al., 1998). Physical and computational models that incorporate empirical measurements of body stiffness (e.g. Long et al., 2006), in conjunction with live animal studies using tools such as electromyography or the recent force calculation techniques developed by Lucas, Dabiri and colleagues (Dabiri et al., 2014; Lucas et al., 2017, 2020), may be able to resolve this question.

Fifth, how do the 3D conformation changes of the flexible body and caudal fin affect swimming capabilities? For instance, the caudal fin takes complex shapes as it actively cups into the direction of motion – a form of spanwise bending resisting deflection (Flammang and Lauder, 2009; Tytell, 2006). Models of spanwise bending of wing-like structures indicate that this bending controls propulsor performance through stabilizing or destabilizing the leading-edge vortex, depending on whether the tip of the model lags or leads the base, respectively (see Fig. 5A, in which the trailing edge lags, and Fig. 5D, where caudal cupping causes the dorsal and ventral edges to lead). Transitioning between a lagging and a leading conformation appears to modulate thrust delivery between a lower-magnitude, continuous production mode and a transient very high magnitude mode, respectively (Esposito et al., 2012; Heathcote et al., 2008; Jia et al., 2021; Wong and Rival, 2017). Intriguingly, Esposito et al.'s (2012) robotic fin model achieved its maximum thrust with a combination of a cupping (a leading spanwise bend) conformation and non-uniform (tapered) fin ray stiffness along the chordwise axis. Determining how the whole spectrum of 3D conformations taken by the body (e.g. during torsion) (Donatelli et al., 2017) and caudal fin will require models that can simultaneously bend along both axes while actively modulating stiffness.

Finally, how do the 3D conformation changes of the median and paired fins affect swimming capabilities? Fins are made up of stiffer rays connected by highly deformable membranes, and the bending of the fin may change its stiffness through coupling the rays with the stretching of the membrane between them (Nguyen et al., 2017). Similarly, although Puri et al. (2017) found no changes to overall fin flexural stiffness upon surgically disrupting caudal membranes in zebrafish, they caution that the membrane has tensile properties during swimming that they did not quantify. So, whether the coupling of membrane and fins is significant remains an open question. In addition, fins may experience dramatic conformation changes incorporating both spanwise and chordwise bending, and the impact of these shape changes are not simply the sum of fin models including chordwise and spanwise bending (Dong et al., 2010; Lauder and Madden, 2007; Mittal et al., 2006; Tangorra et al., 2010). Our understanding here is nascent; explorations of fin function with complex models incorporating multiple bending axes, elastic fin membranes and active control of individual flexible fin rays will be a fruitful direction for research.

ECR Spotlight
This article has an associated ECR Spotlight interview with Yordano Jimenez and Kelsey Lucas.

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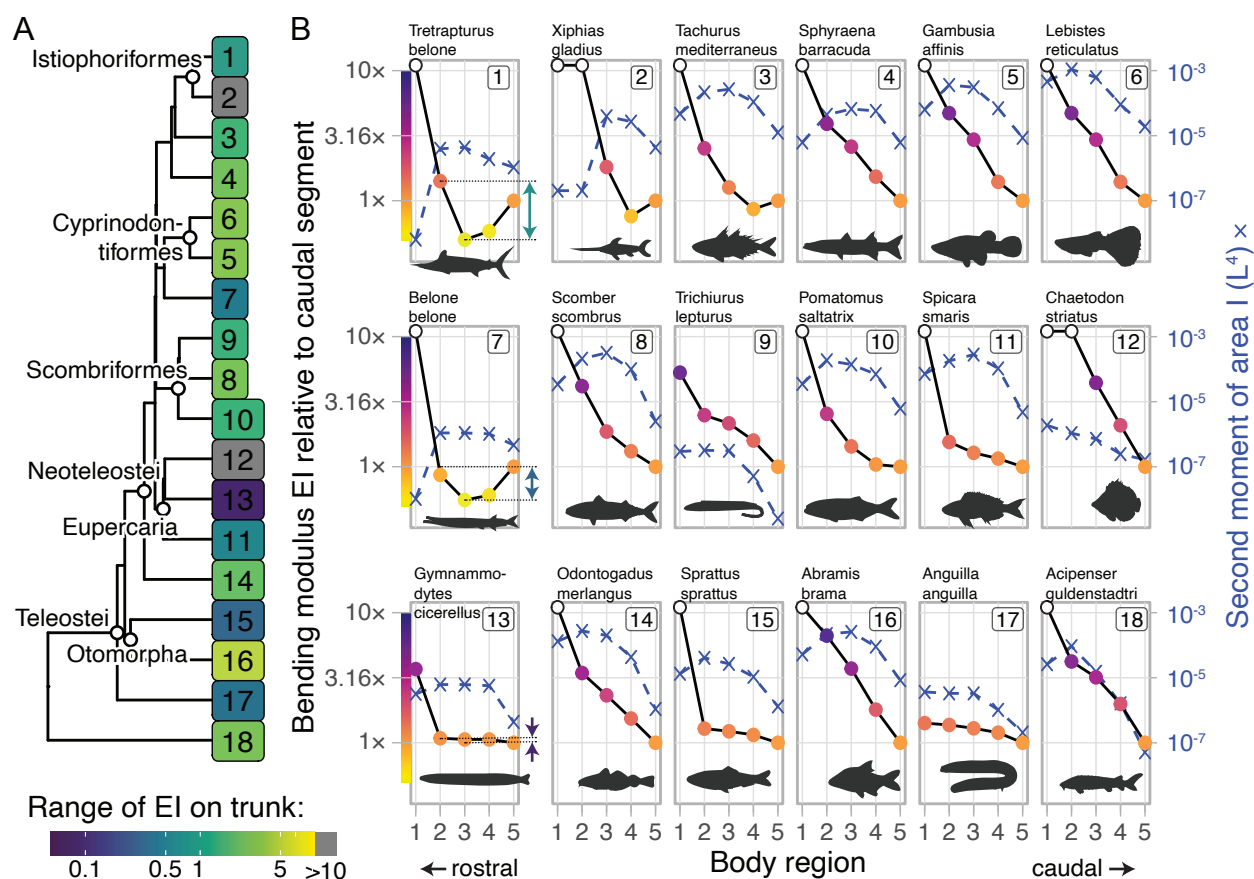
Fig. S1. The hidden axis of diversity: flexibility varies along the body of fishes (based on data from Aleyev, 1977). (A). Phylogeny of the fishes shown (from Rabosky et al., 2018), colored by the range of relative bending moduli along the body. (B). Bending modulus EI relative to the caudal segment's modulus (left axis and colored circles), and second moment of area of the body (right axis, blue crosses). Open points indicate a bending modulus more than 10x the caudal segment. Note that the scales on the left and right axes are different. In the first column, the dotted lines and double headed arrows show the range of relative moduli, which are used to color the phylogeny in panel A.