

Volume 226 (11) June 2023

Journal of Experimental Biology

100
YEARS OF
DISCOVERY



COMMENTARY

A fundamental propulsive mechanism employed by swimmers and flyers throughout the animal kingdom

John H. Costello^{1,*}, Sean P. Colin², Brad J. Gemmell³, John O. Dabiri⁴ and Eva A. Kanso⁵

ABSTRACT

Even casual observations of a crow in flight or a shark swimming demonstrate that animal propulsive structures bend in patterned sequences during movement. Detailed engineering studies using controlled models in combination with analysis of flows left in the wakes of moving animals or objects have largely confirmed that flexibility can confer speed and efficiency advantages. These studies have generally focused on the material properties of propulsive structures (propulsors). However, recent developments provide a different perspective on the operation of nature's flexible propulsors, which we consider in this Commentary. First, we discuss how comparative animal mechanics have demonstrated that natural propulsors constructed with very different material properties bend with remarkably similar kinematic patterns. This suggests that ordering principles beyond basic material properties govern natural propulsor bending. Second, we consider advances in hydrodynamic measurements demonstrating suction forces that dramatically enhance overall thrust produced by natural bending patterns. This is a previously unrecognized source of thrust production at bending surfaces that may dominate total thrust production. Together, these advances provide a new mechanistic perspective on bending by animal propulsors operating in fluids – either water or air. This shift in perspective offers new opportunities for understanding animal motion as well as new avenues for investigation into engineered designs of vehicles operating in fluids.

KEYWORDS: Body bending, Movement in fluids, Propulsor flexibility

Introduction: a contemporary perspective on the development of flexible propulsor models

The efficiency with which animals move through fluids, both air and water, evolved over many millions of years and is not easily replicated by even the most advanced engineered designs (Chin et al., 2017; Zhu et al., 2019). However, early investigators successfully used moving plates and foils (see Glossary) to generate an essential framework for understanding biological propulsion (Lighthill, 1975; Pennycuik, 1975; Blake, 1983; Videler, 1993; Dudley, 2000; Alexander, 2003; Smits, 2019). By outlining biological propulsion within the context of planar structures

moving in fluid flows, this early work capitalized on the broad expertise of physicists and engineers who studied fluid–structure problems (Shelley and Zhang, 2011). By necessity, the study of plates and foils, as well as live animals, primarily utilized wake structures to evaluate thrust generation of both swimmers (Lauder, 2015) and flyers (Bomphrey, 2012). This has been the method of choice because, until recently, there was no way to directly resolve flows and, ultimately, forces generated along body–fluid interfaces as an object moves through a fluid. Quantification of the energy imparted to wakes produced behind animals provides a record from which to reconstruct the effects of force generation (Dickinson et al., 2000). Such reconstructions can be considered as analogous to using ‘footprints’ to describe terrestrial animal movement (Müller et al., 1997; Gries et al., 1999; Zhang, 2017). Much early work on propulsion focused on rigid panels or foils (reviewed in Triantafyllou et al., 2004); however, a growing consensus based on empirical (Bozkurtas et al., 2006; Heathcote et al., 2008; Toomey and Eldredge, 2008; Thiria and Godoy-Diana, 2010; Ramananarivo et al., 2011; Dewey et al., 2013; Quinn et al., 2015), modeling (Alben et al., 2002; Mittal et al., 2006; Alben, 2008, 2009; Michelin and Llewellyn Smith, 2009; Kim and Gharib, 2011; Jing and Kanso, 2012) and computational (Mittal, 2004; Vanella et al., 2009; Young et al., 2009; Le et al., 2010; Kang et al., 2011; Hoover et al., 2018) studies supports the view that flexible structures can, under favorable conditions, yield increased propulsive performance (extensively reviewed by Smits, 2019).

But what are those favorable conditions under which flexibility enhances propulsive performance? Flexibility alone is insufficient to enhance performance because some flexible propulsors perform unfavorably compared with rigid structures (Liu and Bose, 1997; Heathcote et al., 2008; Eldredge et al., 2010; Tangorra et al., 2010; Hang et al., 2022). In order to tease out the favorable trait combinations enabling higher performance, a range of material traits such as modulus of elasticity (see Glossary; Heathcote et al., 2008; Kang et al., 2011; Kancharala and Philen, 2016; Tytell et al., 2018), flexural stiffness (see Glossary; Combes and Daniel, 2001, 2003; Tangorra et al., 2010; Lauder et al., 2011; Lauder, 2015) or fluid–structure resonance interactions (see Glossary; Moored et al., 2012; Dewey et al., 2013; Moored et al., 2014; Quinn et al., 2014, 2015; Tytell et al., 2016; Hoover et al., 2018; Smits, 2019; Floryan and Rowley, 2020) have been described as key variables acting on the propulsor to determine propulsive performance – over its full length (Miao and Ho, 2006; Kang et al., 2011), over a limited portion (Villanueva et al., 2011; Colin et al., 2012; Vincent et al., 2020; Hang et al., 2022) or at joints (Eldredge et al., 2008; Wilson and Eldredge, 2011). Fine control of these variables can be achieved by taking advantage of controlled laboratory conditions with tunable artificial propulsors. This work greatly advanced our understanding and provided an extensive literature relating material traits to flexible propulsor performance. Yet, the mechanistic understanding of critical processes that occur at

¹Providence College, Biology Department, Providence, RI 02918-0001, USA.

²Department of Marine Biology and Environmental Science, Roger Williams University, Bristol, RI 02809, USA. ³Department of Integrative Biology, University of South Florida, Tampa, FL 33620, USA. ⁴Graduate Aerospace Laboratories and Department of Mechanical and Civil Engineering, California Institute of Technology, Pasadena, CA 91125, USA. ⁵Aerospace and Mechanical Engineering, University of Southern California, Los Angeles, CA 90089, USA.

*Author for correspondence (costello@providence.edu)

 J.H.C., 0000-0002-6967-3145; S.P.C., 0000-0003-4463-5588; J.O.D., 0000-0002-6722-9008; E.A.K., 0000-0003-0336-585X

Glossary

Antiphase bending

Movement of two body parts on either side of a bend in opposite directions. For example, when the portion of a propulsor that adjoins the main body moves downward but, simultaneously, the distal tip on the opposite side of the bending joint moves upwards. Passive bending is when the body bending occurs due to external fluid forces acting on the propulsor tip or due to the inertia of the propulsor. Active bending entails internally directed body motions that are phased to external flow.

Flexural stiffness

A measure of material deformability that includes both the elastic modulus of the material and the geometrical arrangement of the material in the structure. For example, the flexural stiffness is different for two objects of the same absolute mass and modulus of elasticity but arranged as a solid rod versus a hollow tube.

Fluid–structure resonance

Interactions between the frequency and magnitude of fluid patterns, such as vortices, and the frequency response patterns of solid objects, such as airfoils in flow. Propulsive efficiency is thought to reach optima when the frequency of fluid oscillations matches the natural frequency of the solid structure comprising a propulsor.

Foil

A solid object shaped so that when placed in a moving fluid at a suitable angle of attack, lift (force generated perpendicular to the fluid flow) is generated. If the fluid is a gas, the foil is called an airfoil or aerofoil, and if the fluid is water, the foil is called a hydrofoil.

Metachronal waves

A wave of movement produced by the sequential motion of structures along a surface such as cilia on a cell surface or multiple limbs of a millipede.

Modulus of elasticity

A unit of measurement of an object's or substance's resistance to being deformed elastically (i.e. non-permanently) when a stress is applied to it.

Particle image velocimetry (PIV)

A technique to quantify fluid motion around aquatic organisms. A two-dimensional laser sheet illuminates reflective particles added to the water. The particles are assumed to faithfully track water motion, and particle velocities derived by correlating successive particle image patterns are used to evaluate flow characteristics.

Reynolds number (Re)

A dimensionless number used to estimate the relative ratio of viscous to inertial forces in a fluid. For animal motion, a typical definition is $Re = UL/\nu$, where U is the flow velocity, L is the characteristic length (for example, body diameter perpendicular to the flow) and ν is the kinematic viscosity of the fluid. When $Re \ll 1$, viscosity dominates and when $Re \gg 1$, inertia dominates.

Steady-state motion

Motion by a body that does not vary over the observed time period.

Strouhal number (St)

A dimensionless number describing oscillating flows. For animal motion, a typical definition is $St = fA/U$, where f is the frequency of vortex shedding, A is the peak-to-peak oscillation amplitude (for example, of a wing or fin beat) and U is the flow velocity. Animal propulsors such as bird wings or fish fins achieve highest propulsive efficiency in the $0.2 < St < 0.4$ range.

Vortex sheet model

A modeling approach used in fluid dynamics to quantify flow patterns across a surface in which there is a discontinuity in fluid velocity, such as with vortex flows.

bending surfaces and influence propulsor performance is also limited by the use of artificial structures that imperfectly resemble natural movements and by reliance on fluid 'footprints' in wakes.

Our aim here is to emphasize that two important developments – the recognition of widespread patterns among animals moving in fluids, coupled with recently developed fluid dynamic methods – provide a new perspective on the subject of propulsor bending. We first discuss patterns of flexion that are pervasive among animal

propulsors. This is followed by hydrodynamic analyses of model species that have revealed the importance of suction forces operating along surfaces that influence the high performance of natural propulsors. Lastly, we compare model predictions for optimizing the location and extent of flexible structures with empirical patterns found among animals that fly and swim. We use these to demonstrate both the selective importance and the highly predictable nature of these patterns. We hope that the perspective presented in this Commentary will contribute to our understanding of animal designs while enabling application of these evolutionary lessons to engineered structures.

A revised perspective: comparative animal kinematics indicate a deeper story

Our studies with living organisms selected over evolutionary time scales have allowed us to address some of the important mechanisms affecting flexible propulsor performance. Comparative studies of live animals moving in fluids indicate that material traits are subordinate to kinematic traits of animal propulsors (Lucas et al., 2014). Comparison of movement by 59 animal species from diverse taxa demonstrates clear, replicable patterns of spanwise propulsor bending during steady motion. These patterns are similar over a broad range of animal sizes, fluid media and taxonomic groups (Fig. 1). The position of propulsor bending is documented as the flexion ratio (i.e. the length from the propulsor base to the flexion point of bending relative to the total propulsor length, indicated by the bending icon in Fig. 1D). Additionally, the maximum extent of propulsor bending is measured as the maximum flexion angle (referred to simply as flexion angle, indicated by the bending icon in Fig. 1E). Both flexion ratio and angle vary only within constrained ranges (Fig. 1). The two variables form a discrete set of combinations, or a 'morphospace' (Raup and Michelson, 1965; McGhee, 1999; Costello et al., 2008), within the range of potentially available combinations.

The reason for this remarkable consistency of bending patterns across animal sizes, fluid media or taxonomic groups is not obvious from a traditional materials-oriented perspective. For example, during steady motion, the tail flukes of a humpback whale bend in a proportionately similar location and to a similar maximum angle to the wings of a wasp or the wing-foot of a molluscan pteropod (Fig. 1A–C). These are examples of common bending patterns that are consistent across groups with exoskeletons (insects), endoskeletons (birds, bats, fish, cetaceans) or hydrostatic skeletons (mollusks). The propulsors may be actuated (birds, bats, fish, cetaceans, mollusks) or passive (insects) (Fig. 1D,E). The material compositions of these propulsors vary dramatically (e.g. chitin, feathers, bones, microtubules) among taxa (Lucas et al., 2014). The propulsors may act individually or in concert within metachronal waves (see Glossary; Colin et al., 2020). Although these bending patterns characterize propulsors of the largest swimmers, such as whale flukes (Lucas et al., 2014), they also characterize the millimeter-scale ciliary ctene rows of ctenophores (Colin et al., 2020). A phylogenetically corrected analysis of variance indicates that there are no significant differences in bending patterns between distantly related taxonomic groups, animals of different sizes or even animals operating in air versus water (Fig. 1F–H).

The fact that there are wide disparities in material composition yet constrained bending patterns across such a wide range of species indicates that kinematics, particularly bending position and extent, have been converged upon by multiple disparate animal lineages. For this reason, we argue that material traits provide the necessary

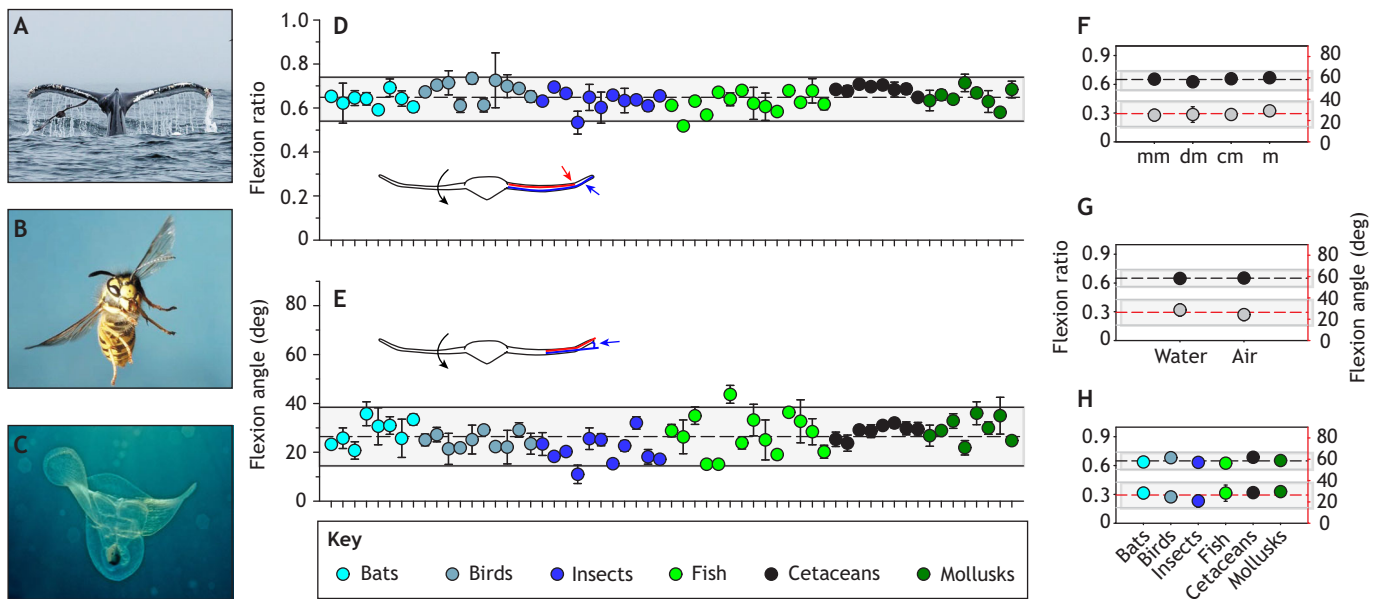


Fig. 1. Widespread convergence upon similar propulsor bending patterns among animals that move through fluids. (A–C) Examples of bending patterns: (A) flukes of a humpback whale (a cetacean; CC-BY 2.0; www.flickr.com/photos/mikebaird/9492198090/), (B) wings of a wasp (CC BY NC ND 2.0; www.flickr.com/photos/fotoopa_hs/2353552495/) and (C) wing-foot of a pelagic mollusk (photo credit: David Wrobel). (D,E) Distribution of bending patterns across a range of animal groups. Data points represent mean values of individual species and error bars indicate ± 1 s.d. from the species mean. Where not visible, error bars are encompassed by the data point. Inset diagrams illustrate the location of bending, or flexion ratio (D) and maximum flexion angle during bending (E). Dashed lines represent mean values and shaded regions show the 95% confidence intervals for all species combined ($N=59$, flexion ratio mean=0.65, flexion angle mean=26.5 deg). (F–H) Black data points represent mean values for (F) size classes or (G) fluid medium, whereas gray data points represent mean flexion angle for (F) size classes or (G) fluid medium, and error bars indicate ± 1 s.d. Where not visible, error bars are encompassed by the data point. Black dashed lines represent mean flexion ratio, with 95% confidence intervals (as in D); red dashed lines represent mean flexion angle, with 95% confidence intervals (as in E). There are no significant differences in bending patterns between diverse animal sizes (millimeters, decimeters, centimeters and meters), fluid medium (air and water) or major animal taxonomic categories for the 59 species. All points represent conditions of steady propulsion as detailed in the phylogenetic analysis by Lucas et al. (2014).

starting conditions but are not sufficient to explain patterns of flexible propulsion across the animal kingdom. Instead, a variety of materials are sufficiently flexible to operate as effective propulsors, as long as they remain within a constrained kinematic range. From this perspective, natural selection has acted at the level of mechanical kinematics to organize a wide array of biological materials according to a constrained set of guidelines. Accordingly, examination of bending kinematics using animal models, rather than solely relying on engineered propulsors in laboratories, provides critical insight into the contribution of flexibility to natural propulsion.

The deeper story explained with novel hydrodynamic methods

What selective advantage could be of such general applicability and magnitude to produce convergence upon the limited range of kinematic patterns discussed above? To answer this question, a new suite of hydrodynamic tools was developed that could measure fluid–structure interactions at the location of propulsor bending. New tools were necessary because conventional wake analysis cannot discern dynamic interactions along a bending propulsor surface. By definition, wake analysis documents the net result of propulsor motion at a distance from the animal itself – the residual fluid ‘footprint’ of a propulsive stroke. This footprint is left downstream of the animal after the propulsive oscillation is completed. Consequently, fluid dynamic processes occurring along the propulsor itself during bending are essentially invisible to conventional wake analysis. In order to quantitatively understand

propulsor–fluid interactions, a different set of methods is needed that allow us to dynamically measure force production along the full length of a propulsor surface during bending events. This new approach relies on particle image velocimetry (PIV; see Glossary) which has long been a tool for measuring fluid flows (Spedding et al., 1984; Willert and Gharib, 1991; Adrian, 2005). PIV provides velocity data (Fig. 2B) used by a new algorithm to determine dynamic changes in pressure fields during propulsor bending (Dabiri et al., 2014; Fig. 2C). Evaluation of pressure differences across propulsor surfaces then provides estimates of force application along the full surfaces of moving propulsors (Gemmell et al., 2015; Fig. 2D). These dynamic force measurements closely resemble measurements made by conventional force and torque transducers, thus providing a hydrodynamically based, non-invasive, validated method to empirically quantify force generation throughout full bending cycles of propulsor oscillations (Lucas et al., 2017). The development of these methods has allowed quantitative distinction of fluid forces that act to both push and pull a propulsor during its power stroke (Gemmell et al., 2015, 2016; Colin et al., 2020) and led to the unexpected finding that extensive negative pressure regions on the leeside of an advancing propulsor are critical components determining the benefits of naturally bending propulsors. Pulling forces arising from the enhanced negative pressure regions on the leeside of an advancing propulsor – termed suction forces – are an important mechanistic feature for understanding why nature’s propulsors bend.

Suction forces merit closer attention in order to understand their connection to propulsor bending. Suction force depends upon

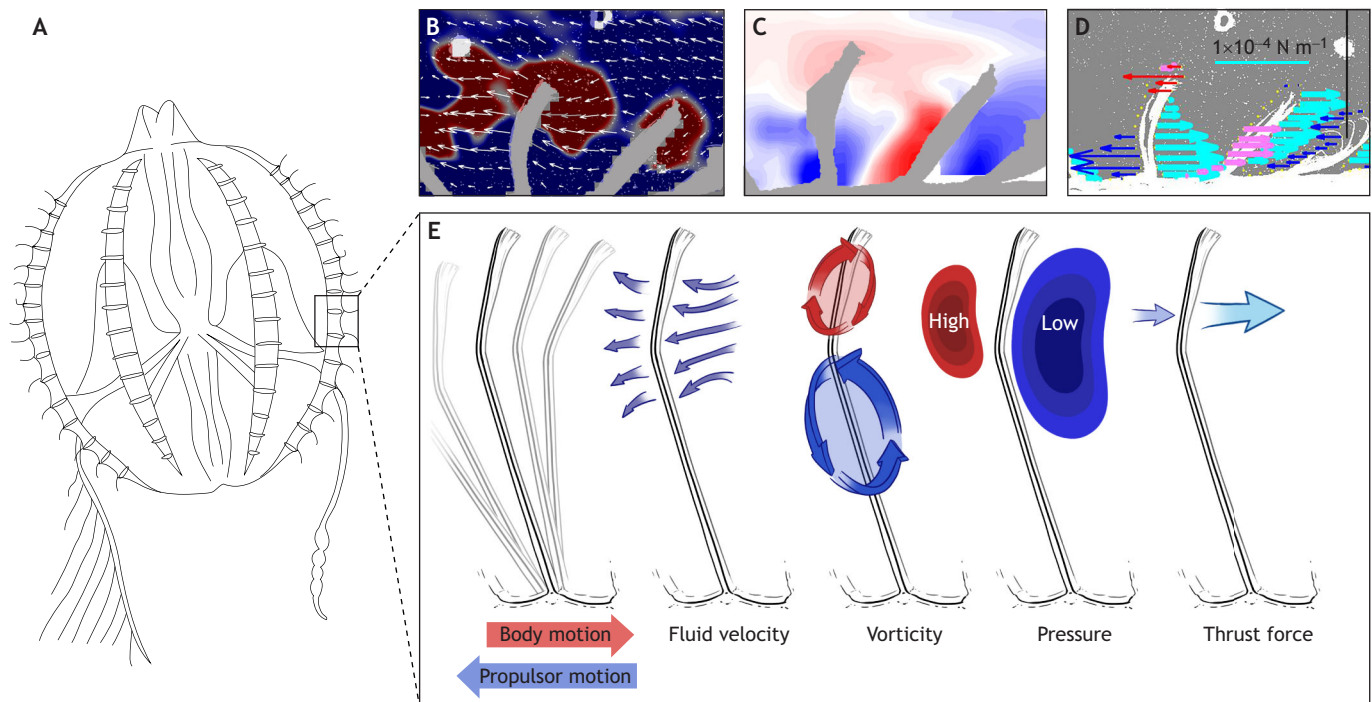


Fig. 2. Mechanics of performance enhancement by bending propulsors exemplified by cteno motion. For the ctenophore *Pleurobrachia bachei* (A), the hydrodynamic basis of force production was determined by (B) vector and vorticity fields measured using particle image velocimetry (PIV) of cteno motion, (C) pressure fields based on velocity vectors and (D) force measurements based on pressure differences measured along the length of the propulsor surface (data from Colin et al., 2020). (E) Conceptual relationship between (left to right) propulsor position during a movement cycle, fluid velocity patterns, vorticity development, pressure gradients and components of total force production including ‘push’ and ‘pull’ components acting on the propulsor and, consequently, the animal body. Although illustrated as separate components, all of these processes are interdependent and occur synergistically.

pressure gradients established at the site of bending by a propulsor. Bending by a structure involves rotation of adjoining structural sections around a central inflexion point along the propulsor (Fig. 2E). Vorticity (Ω) of the fluid adjacent to the moving body parts (no-slip fluid; White and Majdalani, 2006) increases twice as rapidly as the angular velocity (ω) of the structure ($\Omega=2\omega$). Natural propulsor components bending around an inflexion point move with opposite phase relationships relative to each other – termed antiphase bending (Hang et al., 2022) – so that as the propulsor base moves in one direction, the tip section on the opposing side of the inflexion point moves in the opposite direction (Fig. 2E). This type of bending during propulsor motion creates the systematic flexion evident in natural propulsor motion. However, it also creates vorticity of opposite rotational directions on either side of the inflexion point along the lee surface of the propulsor as it moves through the fluid (Fig. 2E). The angular velocity of propulsor motion controls the vorticity, and the angle of the bend controls the relative positions of the opposite-spin vorticity surrounding the bend (Gemmell et al., 2016).

Spatial positioning of opposite-spin vorticity (Costello et al., 2019) is an essential element underlying the force production advantages of bending propulsors. Vortex production along leading surfaces of oscillating propulsors has been described extensively because of its critical contribution to pressure differences that determine lift production for flight (Ellington et al., 1996; Dickinson et al., 1999; Birch and Dickinson, 2001; Sane, 2003; Birch et al., 2004; Videler et al., 2004; Warrick et al., 2005; Shyy and Liu, 2007; Lentink et al., 2009; Bomphrey et al., 2009). Leading edge vorticity is of a single rotational sense but, in contrast, bending along a propulsor generates counter-rotating vorticity moving in the

same direction as the entire propulsor but with opposite spin on either side of the bend (Fig. 2). The dynamic geometry of the bend – the bend kinematics – places opposite-spin vorticity in close proximity. This proximity is important because, at the opposite-spin interface, fluid is accelerated, creating relatively high velocities and negative pressure in the fluid on the suction side (Fig. 2E) of an advancing, bent propulsor (Fu and Liu, 2015; Gemmell et al., 2016; Costello et al., 2019). By bending the propulsor tip backwards, towards the propulsor base, a bent propulsor directs tip vorticity closer to opposite-spin vorticity regions along the propulsor span so that a large negative-pressure region is formed on the suction side of an advancing, bent propulsor. The opposite-spin vorticity generating these pressure gradients is positioned more closely for a greater portion of the power stroke of a bent antiphase propulsor compared with a rigid propulsor (Colin et al., 2020). The high-velocity, negative-pressure regions on the suction side contribute forces which ‘pull’ on the propulsor as it moves forward and act in concert with the lower-velocity, high-pressure regions on the leading side of the propulsor which ‘push’ against the propulsor as it advances through the fluid (Fig. 2E). Together, these push and pull forces resist forward motion of the propulsor as drag. It is this equal and opposite response of the fluid to propulsor motion that provides thrust for movement of the animal body to which the propulsor is attached. By augmenting low-pressure regions during a propulsor’s power stroke, flexible propulsors can generate higher thrust forces than rigid paddles (Smits, 2019). Rigid propulsors also produce high–low pressure gradients across the propulsor; however, they exhibit different hydrodynamic structures from flexible propulsors (Hussong et al., 2011; Ford et al., 2019) and do not generate such strong negative-pressure fields associated with counter-rotating

vorticity on the suction side of a propulsor (Hu, 2009; Suryadi and Obi, 2011; Colin et al., 2012; Nakata and Liu, 2012). The development of new hydrodynamic methods for evaluating pressure patterns along moving animal surfaces has enabled recognition of the important role played by the high-velocity, negative-pressure regions occurring on the suction side of an advancing, bent propulsor. That recognition has been critical for understanding the propulsive advantages of flexible propulsors. These recent results emphasize a relatively under-studied component – extensive negative-pressure regions on the suction side of advancing propulsors – to deepen our understanding of why flexible propulsors are so widespread in nature.

Forces generated during bending can dominate thrust forces during swimming

How important to overall movement are the advantages provided by natural propulsor bending? Comparative analyses of swimming animals in steady-state motion (see Glossary) indicate that pressure differences at propulsor bends can be dominant contributors to net propulsive thrust by those propulsors (Fig. 3A–C). Members of multiple animal taxa – lampreys, medusae, polychaetes, decapod crustaceans and ctenophores – all generate more forward thrust through the ‘pull’ of suction effects than the ‘push’ of high-pressure paddling (Gemmell et al., 2015; Gemmell et al., 2016; Colin et al., 2020). In some cases, the pull forces exceed those pushing against the propulsor by an order of magnitude (Fig. 3D; Colin et al., 2020).

Although the potential advantages of propulsor bending are substantial, they are also strongly constrained by kinematic limitations of bending location and angle. This is because the location and extent of bending along a propulsor strongly affect the speed and efficiency of propulsion. Fluid–structure interactions demonstrated by a vortex sheet model (see Glossary) indicate that active antiphase bending (see Glossary) results in lower power requirements and more efficient overall propulsion. Speed advantages are maximal relative to a rigid propulsor when the bend deflects 30–60 deg and is located at 60–80% of the distance from propulsor base to tip (Fig. 3E). Efficiency of movement is greatest for similar bending locations but with a slightly lower optimal deflection range (25–50 deg) (Hang et al., 2022).

Empirically measured biological data closely match the kinematic constraints on flexion ratio and angle for enhanced efficiency predicted by fluid dynamic modeling of bending propulsors. We expect the biological data to coincide more closely with the efficiency maximum than the speed maximum because the empirical bending patterns measured thus far (Lucas et al., 2014; Colin et al., 2020) were collected from animals during steady-state motion and would favor efficiency relative to overall speed. Although presently unexplored, animals often vary propulsive modes or gaits (Dickinson et al., 2000), and they are likely to be capable of shifting the bend location and magnitude in order to transition between efficiency and speed maxima (Zhong et al., 2021; Hang et al., 2022). Overall, the advantages of force enhancement through suction forces and optimization of both speed and efficiency provide valuable incentives for natural selection to repeatedly converge upon biological bending patterns. The substantial gains in propulsive speed and efficiency that accompany preferred bending kinematics require relatively minor changes in tip configuration (20–40 deg) during propulsor oscillation. Given the relatively simple configuration changes required to generate high propulsive advantages and their resemblance to passive bending of flexible materials (Vincent et al., 2020; Hang et al., 2022), perhaps it is unsurprising that similar

bending patterns evolved independently across such a wide diversity of organisms (Lucas et al., 2014; Colin et al., 2020).

Bending kinematics belong to a group of interactions with versatile applications for biological and engineered systems

The advantages of bending propulsive structures have been applied with great versatility across the animal kingdom. Animals exploit a range of highly constrained bending kinematics across a variety of propulsive structures, fluid media and modes of propulsion. Legs, wings, fins and ctenophore rows all employ similar hydrodynamic mechanics to amplify force production (Fig. 4). Of course, this list is not exhaustive, and species may use these mechanics for a variety of different structures simultaneously. For example, humpback whales exhibit whole-body bending patterns simultaneously with bending of fluke elements (Fig. 1) and pectoral fins – all within typical constraints. This set of constrained bending kinematics is seen wherever animals use biological propulsors to propel themselves through fluids.

Although such widespread use of these kinematic constraints may at first seem unlikely, bending kinematic patterns can be viewed as simply adding to a growing list of fluid–structure patterns widely employed by natural swimmers and flyers. For example, swimmers of diverse lineages that use elongate fins have converged upon specific propulsor wave patterns optimized for efficient propulsion (Bale et al., 2015). Perhaps most instructively, the frequency–amplitude relationships of oscillating animal appendages such as fins or wings fall within a limited range of Strouhal numbers (St ; see Glossary; Taylor et al., 2003, Rohr and Fish, 2004) tuned for efficient propulsion (Triantafyllou et al., 1993; Read et al., 2003; Triantafyllou et al., 2004; Schouveiler et al., 2005; Eloy, 2012; Floryan et al., 2019). Animal propulsors of varying designs, materials and sizes functioning in both liquids and air operate within this highly constrained St range. For both kinematic patterns and St range, their convergence across species is based in fluid-dynamic foundations that operate in both air and water over a broad range of material compositions and sizes. The observed limits to these patterns are consequences of the constrained range of motions that give rise to those specific fluid-dynamic benefits. The advantages are bounded by these constraints, and natural selection appears to have repeatedly converged upon the same propulsive solutions across a wide diversity of animals. Incorporating bending force production into animal swimming and flight models might help us to clarify the mechanics that underlie the remarkable effectiveness of animal propulsion.

It is encouraging that the propulsive solutions discussed above – evolved through natural selection over hundreds of millions of years – are accessible for contemporary human design. For example, vehicles that generate thrust using oscillating propulsors operate at maximum propulsive efficiency when their kinematics are tuned to coincide with the St range characterizing animals in fluids (Aditya and Malolan, 2007; Quinn et al., 2015). Similarly, we expect that application of the advantages inherent in natural design patterns will benefit engineered flexible propulsors. Even simple, passively bending vehicles travel further when they incorporate flexibility corresponding to the preferred range of bending (Colin et al., 2012; Lucas et al., 2017; Vincent et al., 2020).

Conclusions and the pathway forward

Although the propulsor bending patterns discussed in this Commentary are pervasive among animals moving in fluids, we are only starting to understand this phenomenon. To further understanding, we encourage interested readers to investigate the

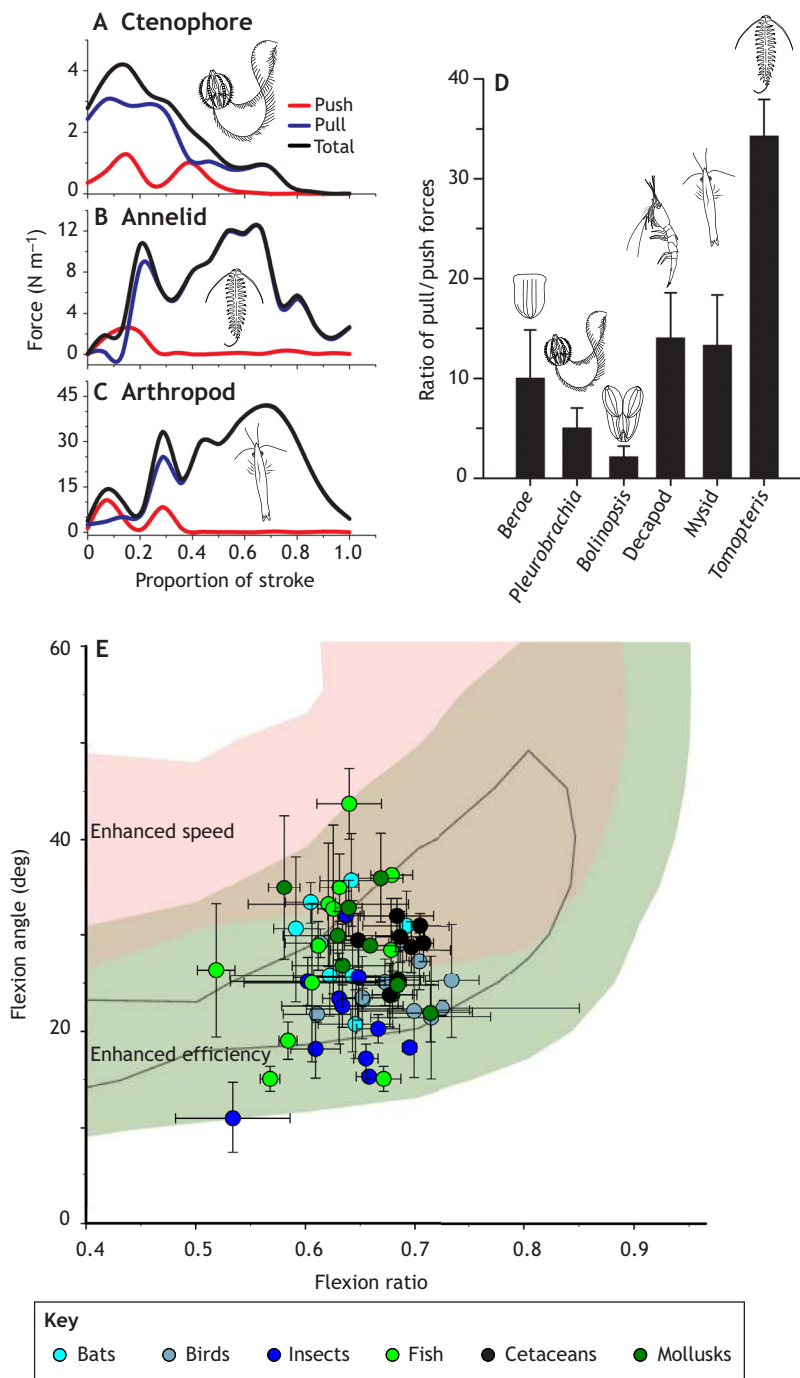


Fig. 3. Effects of bending kinematics demonstrated by experimental and model results. (A–C) Representative time series of pull, push and total forces summed around the limb/ctene of (A) the ctenophore *Pleurobrachia bachei*, (B) the polychaete annelid *Tomopteris* sp. and (C) an unidentified larval decapod arthropod (from Colin et al., 2020). All the time series show that push forces are initially high at the beginning of the power stroke but then pull forces dominate the total force acting on the limb/ctene for the rest of the power stroke. (D) The ratio of the pull/push forces (averaged over the power stroke) for a range of ctenophores (*Beroe*, *Pleurobrachia*, *Bolinopsis*) and arthropods (unidentified decapod larvae and mysid shrimp), and an annelid (*Tomopteris*). In all cases, pull forces due to propulsor bending dominate thrust production during the power stroke (Colin et al., 2020). (E) Comparison of propulsor flexion parameters and regions of optimal performance based on fluid dynamic model predictions (from Hang et al., 2022). The pink region corresponds to 200% enhancement in propulsive speed, and the green region corresponds to 300% enhancement in propulsive efficiency, both compared with the same total length rigidly flapping with no flexion. Overlap of the two regions is indicated in beige. The contour black line encloses a region of 600% enhancement in efficiency. Colored data points represent empirical measurements of organism bending patterns from Lucas et al. (2014) superimposed on the model of Hang et al. (2022).

following areas: (1) the quantitative details of phylogenetically controlled comparative bending analyses (Lucas et al., 2014), (2) methodology for direct measurement of forces along bodies moving in fluids (Dabiri et al., 2014; Lucas et al., 2017), (3) applications to bending bodies and suction thrust (Gemmell et al., 2015; Gemmell et al., 2016; Colin et al., 2020; Dabiri et al., 2020), (4) successful incorporation of optimal bending into engineered designs (Colin et al., 2012; Vincent et al., 2020), and (5) modeling of parameters controlling optimal propulsor bending patterns (Hang et al., 2022). These studies provide an outline of the subject but also indicate important gaps that will need to be resolved for deeper understanding. For example, our considerations have centered on organisms that use propulsors to propel their bodies through fluids. But a vast array of

organisms, such as barnacles (Trager et al., 1990), pulsing corals (Samson et al., 2019) and benthic jellyfish (Durieux et al., 2023), maximize flow past bodies that are stationary or attached to substrates. Examination of propulsor bending dynamics may be useful for understanding their fluid adaptations. Existing studies have also focused on steady-state propulsor motions, but the contribution of suction forces to complex alterations that occur during acceleration, deceleration and turning maneuvers remains unexamined. Additionally, our current understanding of suction forces applies for a variety of swimming phyla, but similar analyses of flyers such as insects, birds or bats remain to be performed. Drag-based propulsive modes play important roles for flyers as small as fruit flies (Ristroph et al., 2011), as well as birds (Chin and Lentink, 2019), and

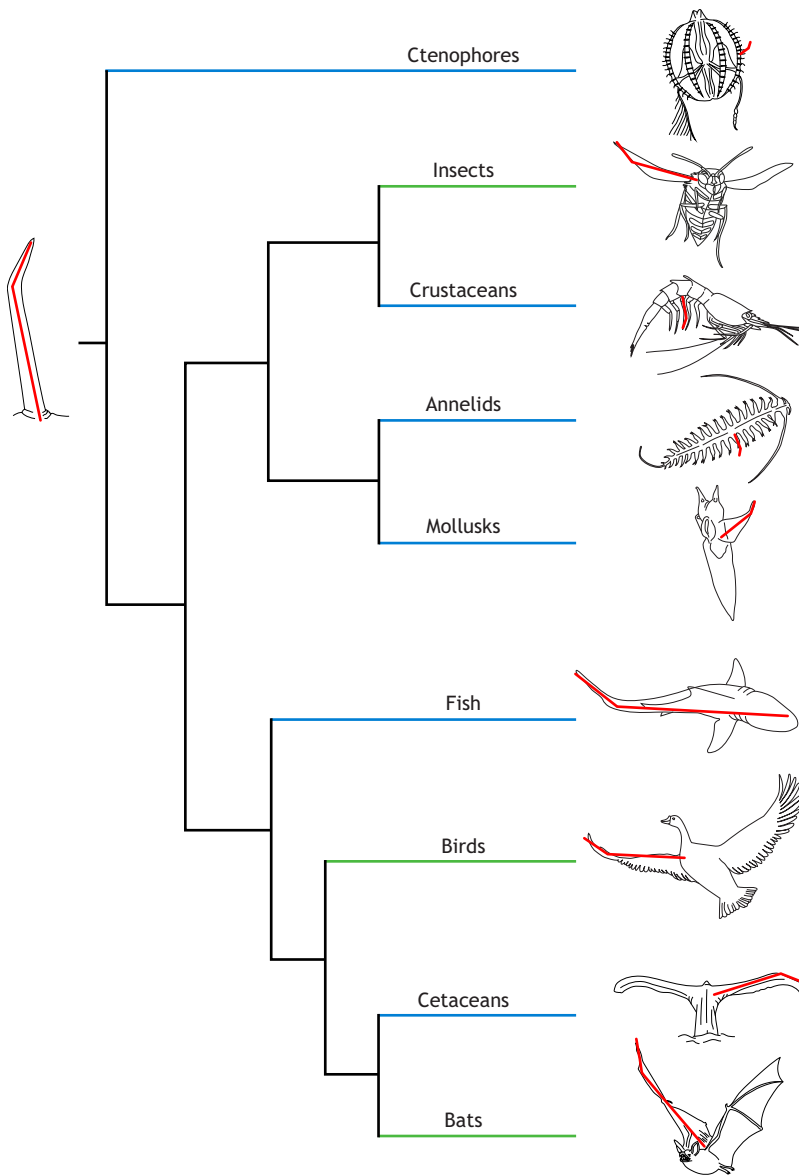


Fig. 4. Repeated convergence upon favorable propulsor bending kinematics by diverse animal lineages employing a variety of propulsors to move through fluids. The red line shows propulsor bending for each animal. Green endpoints represent lineages that fly, whereas blue represents swimming animals. Please note that the phylogenetic tree is general and used for conceptual purposes rather than actually documenting genetic distances.

outer-wing flexibility is demonstrably important for thrust and maneuverability of flyers such as bumblebees (Mountcastle and Combes, 2013; Mistick et al., 2016; Tobing et al., 2017). However, it is not presently clear how pressure gradients generated by bending integrate with other forces to influence flight performance. Knowledge in this area will be important for understanding widespread patterns of wing bending in a variety of flyers.

Importantly, the dimensional range over which bending patterns operate needs to be expanded. Although bending patterns appear to be consistent for even small propulsors (Ford et al., 2019; Colin et al., 2020), the measured cases all operate in Reynolds numbers (Re ; see Glossary) greater than 10, where vorticity interactions described in Fig. 3 are applicable. Fluid interactions are substantially different at lower Re values, and bending body components appear to be important in these viscosity-dominated systems (Lauga, 2011; Espinosa-Garcia et al., 2013; Choudhary et al., 2018). However, the reasons for bending may differ in low Re regimes, and the wide diversity of organisms operating in these regimes underscores the importance of broadening our understanding to include low and transitional Re conditions. All

of these developing research areas will benefit from more extensive application of computational fluid dynamics (CFD) models. CFD studies have provided a range of insights into the importance of propulsor flexibility for swimming efficiency (Mittal et al., 2006; Alben, 2008; Dong et al., 2010; Hang et al., 2022), and they have valuable potential to fill outstanding gaps in our understanding.

Hence, although current knowledge about common propulsor bending patterns provides a new window into the role of flexible structures, it is also part of a broader picture that includes a diverse spectrum of organism–fluid interactions. Despite current information gaps, the already-existing body of knowledge outlines exciting opportunities to advance our understanding of animal movement while providing guidelines for the translation of natural patterns to engineered designs.

Acknowledgements

We thank three reviewers for insightful improvements to this manuscript and Nick Bezio for artwork.

Competing interests

The authors declare no competing or financial interests.

Funding

We gratefully acknowledge funding support for this work from the US National Science Foundation CBET program (2100156 to S.P.C., 2100705 to J.H.C., 2019712 to J.O.D., 2100703 to B.J.G., 2100209 to E.A.K.), National Science Foundation RAISE (2034043 to E.A.K.) and US Office of Naval Research (N00014-22-1-2277 to J.H.C. and N00014-19-1-2035, N00014-22-1-2655 to E.A.K.).

References

- Aditya, K. and Malolan, V.** (2007). Investigation of Strouhal number effect on flapping wing micro air vehicle. 45th AIAA Aerospace Sciences Meeting and Exhibit, p. 486.
- Adrian, R. J.** (2005). Twenty years of particle image velocimetry. *Exp. Fluids* **39**, 159–169. doi:10.1007/s00348-005-0991-7
- Alben, S.** (2008). Optimal flexibility of a flapping appendage in an inviscid fluid. *J. Fluid Mech.* **614**, 355–380. doi:10.1017/S0022112008003297
- Alben, S.** (2009). Simulating the dynamics of flexible bodies and vortex sheets. *J. Comput. Phys.* **228**, 2587–2603. doi:10.1016/j.jcp.2008.12.020
- Alben, S., Shelley, M. and Zhang, J.** (2002). Drag reduction through self-similar bending of a flexible body. *Nature* **420**, 479–481. doi:10.1038/nature01232
- Alexander, R. M.** (2003). *Principles of Animal Locomotion*. Princeton University Press.
- Bale, R., Neveln, I. D., Bhalla, A. P. S., Maciver, M. A. and Patankar, N. A.** (2015). Convergent evolution of mechanically optimal locomotion in aquatic invertebrates and vertebrates. *PLoS Biol.* **13**, e1002123. doi:10.1371/journal.pbio.1002123
- Birch, J. M. and Dickinson, M. H.** (2001). Spanwise flow and the attachment of the leading-edge vortex on insect wings. *Nature* **412**, 729–733. doi:10.1038/35089071
- Birch, J. M., Dickson, W. B. and Dickinson, M. H.** (2004). Force production and flow structure of the leading edge vortex on flapping wings at high and low Reynolds numbers. *J. Exp. Biol.* **207**, 1063–1072. doi:10.1242/jeb.00848
- Blake, R. W.** (1983). *Fish Locomotion*. CUP Archive.
- Bomphrey, R. J.** (2012). Advances in animal flight aerodynamics through flow measurement. *Evol. Biol.* **39**, 1–11. doi:10.1007/s11692-011-9134-7
- Bomphrey, R. J., Taylor, G. K. and Thomas, A. L. R.** (2009). Smoke visualization of free-flying bumblebees indicates independent leading-edge vortices on each wing pair. *Exp. Fluids* **46**, 811–821. doi:10.1007/s00348-009-0631-8
- Bozkurtas, M., Dong, H., Mittal, R., Madden, P. and Lauder, G.** (2006). Hydrodynamic performance of deformable fish fins and flapping foils. 44th AIAA Aerospace Sciences Meeting and Exhibit.
- Chin, D. D. and Lentink, D.** (2019). Birds repurpose the role of drag and lift to take off and land. *Nat. Commun.* **10**, 5354. doi:10.1038/s41467-019-13347-3
- Chin, D. D., Matloff, L. Y., Stowers, A. K., Tucci, E. R. and Lentink, D.** (2017). Inspiration for wing design: how forelimb specialization enables active flight in modern vertebrates. *J. R. Soc. Interface* **14**, 20170240. doi:10.1098/rsif.2017.0240
- Choudhary, P., Mandal, S. and Babu, S. B.** (2018). Locomotion of a flexible one-hinge swimmer in Stokes regime. *J. Phys. Commun.* **2**, 025009. doi:10.1088/2399-6528/aaa856
- Colin, S. P., Costello, J. H., Dabiri, J. O., Villanueva, A., Blottman, J. B., Gemmell, B. J. and Priya, S.** (2012). Biomimetic and live medusae reveal the mechanistic advantages of a flexible bell margin. *PLoS One* **7**, e48909. doi:10.1371/journal.pone.0048909
- Colin, S. P., Costello, J. H., Sutherland, K. R., Gemmell, B. J., Dabiri, J. O. and Du Clos, K. T.** (2020). The role of suction thrust in the metachronal paddles of swimming invertebrates. *Sci. Rep.* **10**, 1–8. doi:10.1038/s41598-019-56847-4
- Combes, S. and Daniel, T.** (2001). Shape, flapping and flexion: wing and fin design for forward flight. *J. Exp. Biol.* **204**, 2073–2085. doi:10.1242/jeb.204.12.2073
- Combes, S. and Daniel, T.** (2003). Flexural stiffness in insect wings II. Spatial distribution and dynamic wing bending. *J. Exp. Biol.* **206**, 2989–2997. doi:10.1242/jeb.00524
- Costello, J. H., Colin, S. P. and Dabiri, J. O.** (2008). Medusan morphospace: phylogenetic constraints, biomechanical solutions, and ecological consequences. *Invertebr. Biol.* **127**, 265–290. doi:10.1111/j.1744-7410.2008.00126.x
- Costello, J. H., Colin, S. P., Gemmell, B. J. and Dabiri, J. O.** (2019). Hydrodynamics of vortex generation during bell contraction by the hydromedusa *Eutonina indicans* (Romanes, 1876). *Biomimetics* **4**, 44. doi:10.3390/biomimetics4030044
- Dabiri, J. O., Bose, S., Gemmell, B. J., Colin, S. P. and Costello, J. H.** (2014). An algorithm to estimate unsteady and quasi-steady pressure fields from velocity field measurements. *J. Exp. Biol.* **217**, jeb092767. doi:10.1242/jeb.092767
- Dabiri, J. O., Colin, S. P., Gemmell, B. J., Lucas, K. N., Leftwich, M. C. and Costello, J. H.** (2020). Jellyfish and fish solve the challenges of turning dynamics similarly to achieve high maneuverability. *Fluids* **5**, 106. doi:10.3390/fluids5030106
- Dewey, P. A., Boschitsch, B. M., Moored, K. W., Stone, H. A. and Smits, A. J.** (2013). Scaling laws for the thrust production of flexible pitching panels. *J. Fluid Mech.* **732**, 29–46. doi:10.1017/jfm.2013.384
- Dickinson, M. H., Lehmann, F.-O. and Sane, S. P.** (1999). Wing rotation and the aerodynamic basis of insect flight. *Science* **284**, 1954–1960. doi:10.1126/science.284.5422.1954
- Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M., Kram, R. and Lehman, S.** (2000). How animals move: an integrative view. *Science* **288**, 100–106. doi:10.1126/science.288.5463.100
- Dong, H., Bozkurtas, M., Mittal, R., Madden, P. and Lauder, G.** (2010). Computational modelling and analysis of the hydrodynamics of a highly deformable fish pectoral fin. *J. Fluid Mech.* **645**, 345–373. doi:10.1017/S0022112009992941
- Dudley, R.** (2000). *The Biomechanics of Insect Flight: Form Function Evolution*. Princeton University Press.
- Durieux, D. M., Scroggum, G. D., Fender, C., Lewis, D. B., Deban, S. M. and Gemmell, B. J.** (2023). Benthic jellyfish act as suction pumps to facilitate release of interstitial porewater. *Sci. Rep.* **13**, 3770. doi:10.1038/s41598-023-30101-4
- Eldredge, J. D., Wilson, M. and Hector, D.** (2008). An exploration of passive and active flexibility in biolocomotion through analysis of canonical problems. *Advances in Science and Technology* **58**, 212–219. doi:10.4028/www.scientific.net/ast.58.212
- Eldredge, J. D., Toomey, J. and Medina, A.** (2010). On the roles of chord-wise flexibility in a flapping wing with hovering kinematics. *J. Fluid Mech.* **659**, 94–115. doi:10.1017/S0022112010002363
- Ellington, C. P., Van Den Berg, C., Willmott, A. P. and Thomas, A. L.** (1996). Leading-edge vortices in insect flight. *Nature* **384**, 626–630. doi:10.1038/384626a0
- Eloy, C.** (2012). Optimal Strouhal number for swimming animals. *J. Fluid Struct.* **30**, 205–218. doi:10.1016/j.jfluidstruct.2012.02.008
- Espinosa-Garcia, J., Lauga, E. and Zenit, R.** (2013). Fluid elasticity increases the locomotion of flexible swimmers. *Phys. Fluids* **25**, 031701. doi:10.1063/1.4795166
- Floryan, D. and Rowley, C. W.** (2020). Distributed flexibility in inertial swimmers. *J. Fluid Mech.* **888**, A24. doi:10.1017/jfm.2020.49
- Floryan, D., Van Buren, T. and Smits, A. J.** (2019). Large-amplitude oscillations of foils for efficient propulsion. *Phys. Rev. Fluids* **4**, 093102. doi:10.1103/PhysRevFluids.4.093102
- Ford, M. P., Lai, H. K., Samaee, M. and Santhanakrishnan, A.** (2019). Hydrodynamics of metachronal paddling: effects of varying Reynolds number and phase lag. *R. Soc. Open Sci.* **6**, 191387. doi:10.1098/rsos.191387
- Fu, Z. and Liu, H.** (2015). Transient force augmentation due to counter-rotating vortex ring pairs. *J. Fluid Mech.* **785**, 324–348. doi:10.1017/jfm.2015.637
- Gemmell, B. J., Colin, S. P., Costello, J. H. and Dabiri, J. O.** (2015). Suction-based propulsion as a basis for efficient animal swimming. *Nat. Commun.* **6**, 8790. doi:10.1038/ncomms9790
- Gemmell, B. J., Fogerson, S. M., Costello, J. H., Morgan, J. R., Dabiri, J. O. and Colin, S. P.** (2016). How the bending kinematics of swimming lampreys build negative pressure fields for suction thrust. *J. Exp. Biol.* **219**, 3884–3895. doi:10.1242/jeb.144642
- Gries, T., Jöhnk, K., Fields, D. and Strickler, J. R.** (1999). Size and structure of 'footprints' produced by *Daphnia*: impact of animal size and density gradients. *J. Plankton Res.* **21**, 509–523. doi:10.1093/plankt/21.3.509
- Hang, H., Heydari, S., Costello, J. H. and Kanso, E.** (2022). Active tail flexion in concert with passive hydrodynamic forces improves swimming speed and efficiency. *J. Fluid Mech.* **932**, A35. doi:10.1017/jfm.2021.984
- Heathcote, S., Wang, Z. and Gursul, I.** (2008). Effect of spanwise flexibility on flapping wing propulsion. *J. Fluid Struct.* **24**, 183–199. doi:10.1016/j.jfluidstruct.2007.08.003
- Hoover, A. P., Cortez, R., Tytell, E. D. and Fauci, L. J.** (2018). Swimming performance, resonance and shape evolution in heaving flexible panels. *J. Fluid Mech.* **847**, 386–416. doi:10.1017/jfm.2018.305
- Hu, W.-R.** (2009). Hydrodynamic study on a pectoral fin rowing model of a fish. *J. Hydrodynam.* **21**, 463–472. doi:10.1016/S1001-6058(08)60172-9
- Hussong, J., Breugem, W.-P. and Westerweel, J.** (2011). A continuum model for flow induced by metachronal coordination between beating cilia. *J. Fluid Mech.* **684**, 137–162. doi:10.1017/jfm.2011.282
- Jing, F. and Kanso, E.** (2012). Effects of body elasticity on stability of underwater locomotion. *J. Fluid Mech.* **690**, 461–473. doi:10.1017/jfm.2011.450
- Kancharala, A. and Philen, M.** (2016). Optimal chordwise stiffness profiles of self-propelled flapping fins. *Bioinspir. Biomim.* **11**, 056016. doi:10.1088/1748-3190/11/5/056016
- Kang, C.-K., Aono, H., Cesnik, C. E. and Shyy, W.** (2011). Effects of flexibility on the aerodynamic performance of flapping wings. *J. Fluid Mech.* **689**, 32–74. doi:10.1017/jfm.2011.428
- Kim, D. and Gharib, M.** (2011). Characteristics of vortex formation and thrust performance in drag-based paddling propulsion. *J. Exp. Biol.* **214**, 2283–2291. doi:10.1242/jeb.050716
- Lauder, G. V.** (2015). Fish locomotion: recent advances and new directions. *Ann. Rev. Mar. Sci.* **7**, 521–545. doi:10.1146/annurev-marine-010814-015614
- Lauder, G., Madden, P., Tangorra, J., Anderson, E. and Baker, T.** (2011). Bioinspiration from fish for smart material design and function. *Smart Mater. Struct.* **20**, 094014. doi:10.1088/0964-1726/20/9/094014

- Lauga, E.** (2011). Life around the scallop theorem. *Soft Mat.* **7**, 3060–3065. doi:10.1039/C0SM00953A
- Le, T. Q., Ko, J. H., Byun, D., Park, S. H. and Park, H. C.** (2010). Effect of chord flexure on aerodynamic performance of a flapping wing. *J. Bionic Eng.* **7**, 87–94. doi:10.1016/S1672-6529(09)60196-7
- Lentink, D., Dickson, W. B., Van Leeuwen, J. L. and Dickinson, M. H.** (2009). Leading-edge vortices elevate lift of autorotating plant seeds. *Science* **324**, 1438–1440. doi:10.1126/science.1174196
- Lighthill, S. J.** (1975). *Mathematical Biofluidynamics*. SIAM.
- Liu, P. and Bose, N.** (1997). Propulsive performance from oscillating propulsors with spanwise flexibility. *Proc. R. Soc. Lond. A: Math. Phys. Eng. Sci.* **453**, 1763–1770. doi:10.1098/rspa.1997.0095
- Lucas, K. N., Johnson, N., Beaulieu, W. T., Cathcart, E., Tirrell, G., Colin, S. P., Gemmell, B. J., Dabiri, J. O. and Costello, J. H.** (2014). Bending rules for animal propulsion. *Nat. Commun.* **5**, 3293doi:10.1038/ncomms4293
- Lucas, K. N., Dabiri, J. O. and Lauder, G. V.** (2017). A pressure-based force and torque prediction technique for the study of fish-like swimming. *PLoS One* **12**, e0189225. doi:10.1371/journal.pone.0189225
- McGhee, G. R.** (1999). *Theoretical Morphology: The Concept and Its Applications*. Columbia University Press.
- Miao, J.-M. and Ho, M.-H.** (2006). Effect of flexure on aerodynamic propulsive efficiency of flapping flexible airfoil. *J. Fluid Struct.* **22**, 401–419. doi:10.1016/j.jfluidstruct.2005.11.004
- Michelin, S. and Llewellyn Smith, S. G.** (2009). Resonance and propulsion performance of a heaving flexible wing. *Phys. Fluids* **21**, 071902. doi:10.1063/1.3177356
- Mistick, E. A., Mountcastle, A. M. and Combes, S. A.** (2016). Wing flexibility improves bumblebee flight stability. *J. Exp. Biol.* **219**, 3384–3390. doi:10.1242/jeb.133157
- Mittal, R.** (2004). Computational modeling in biohydrodynamics: trends, challenges, and recent advances. *IEEE J. Ocean. Eng.* **29**, 595–604. doi:10.1109/JOE.2004.833215
- Mittal, R., Dong, H., Bozkurtas, M., Lauder, G. and Madden, P.** (2006). Locomotion with flexible propulsors: II. Computational modeling of pectoral fin swimming in sunfish. *Bioinspir. Biomim.* **1**, S35–S41. doi:10.1088/1748-3182/1/4/S05
- Moored, K. W., Dewey, P. A., Smits, A. and Haj-Hariri, H.** (2012). Hydrodynamic wake resonance as an underlying principle of efficient unsteady propulsion. *J. Fluid Mech.* **708**, 329–348. doi:10.1017/jfm.2012.313
- Moored, K. W., Dewey, P. A., Boschitsch, B. M., Smits, A. and Haj-Hariri, H.** (2014). Linear instability mechanisms leading to optimally efficient locomotion with flexible propulsors. *Phys. Fluids* **26**, 041905. doi:10.1063/1.4872221
- Mountcastle, A. M. and Combes, S. A.** (2013). Wing flexibility enhances load-lifting capacity in bumblebees. *Proc. R. Soc. B* **280**, 20130531. doi:10.1098/rspb.2013.0531
- Müller, U., Van Den Heuvel, B., Stamhuis, E. and Videler, J.** (1997). Fish foot prints: morphology and energetics of the wake behind a continuously swimming mullet (*Chelon labrosus* Risso). *J. Exp. Biol.* **200**, 2893–2906. doi:10.1242/jeb.200.22.2893
- Nakata, T. and Liu, H.** (2012). Aerodynamic performance of a hovering hawkmoth with flexible wings: a computational approach. *Proc. R. Soc. B* **279**, 722–731. doi:10.1098/rspb.2011.1023
- Pennycuik, C.** (1975). Mechanics of flight. *Avian Biol.* **5**, 1–73.
- Quinn, D. B., Lauder, G. V. and Smits, A. J.** (2014). Scaling the propulsive performance of heaving flexible panels. *J. Fluid Mech.* **738**, 250–267. doi:10.1017/jfm.2013.597
- Quinn, D. B., Lauder, G. V. and Smits, A. J.** (2015). Maximizing the efficiency of a flexible propulsor using experimental optimization. *J. Fluid Mech.* **767**, 430–448. doi:10.1017/jfm.2015.35
- Ramanarivo, S., Godoy-Diana, R. and Thiria, B.** (2011). Rather than resonance, flapping wing flyers may, on aerodynamics to improve performance. *Proc. Natl. Acad. Sci. USA* **108**, 5964–5969. doi:10.1073/pnas.1017910108
- Raup, D. M. and Michelson, A.** (1965). Theoretical morphology of the coiled shell. *Science* **147**, 1294–1295. doi:10.1126/science.147.3663.1294
- Read, D. A., Hover, F. and Triantafyllou, M.** (2003). Forces on oscillating foils for propulsion and maneuvering. *J. Fluid Struct.* **17**, 163–183. doi:10.1016/S0889-9746(02)00115-9
- Ristroph, L., Bergou, A. J., Guckenheimer, J., Wang, Z. J. and Cohen, I.** (2011). Paddling mode of forward flight in insects. *Phys. Rev. Lett.* **106**, 178103. doi:10.1103/PhysRevLett.106.178103
- Rohr, J. J. and Fish, F. E.** (2004). Strouhal numbers and optimization of swimming by odontocete cetaceans. *J. Exp. Biol.* **207**, 1633–1642. doi:10.1242/jeb.00948
- Samson, J. E., Miller, L. A., Ray, D., Holzman, R., Shavit, U. and Khatri, S.** (2019). A novel mechanism of mixing by pulsing corals. *J. Exp. Biol.* **222**, jeb192518. doi:10.1242/jeb.192518
- Sane, S. P.** (2003). The aerodynamics of insect flight. *J. Exp. Biol.* **206**, 4191–4208. doi:10.1242/jeb.00663
- Schouveiler, L., Hover, F. and Triantafyllou, M.** (2005). Performance of flapping foil propulsion. *J. Fluid Struct.* **20**, 949–959. doi:10.1016/j.jfluidstruct.2005.05.009
- Shelley, M. J. and Zhang, J.** (2011). Flapping and bending bodies interacting with fluid flows. *Annu. Rev. Fluid Mech.* **43**, 449–465. doi:10.1146/annurev-fluid-121108-145456
- Shyy, W. and Liu, H.** (2007). Flapping wings and aerodynamic lift: the role of leading-edge vortices. *AIAA J.* **45**, 2817–2819. doi:10.2514/1.33205
- Smits, A. J.** (2019). Undulatory and oscillatory swimming. *J. Fluid Mech.* **874**, P1. doi:10.1017/jfm.2019.284
- Spedding, G., Rayner, J. and Pennycuik, C.** (1984). Momentum and energy in the wake of a pigeon (*Columba livia*) in slow flight. *J. Exp. Biol.* **111**, 81–102. doi:10.1242/jeb.111.1.81
- Suryadi, A. and Obi, S.** (2011). The estimation of pressure on the surface of a flapping rigid plate by stereo PIV. *Exp. Fluids* **51**, 1403–1416. doi:10.1007/s00348-011-1150-y
- Tangorra, J. L., Lauder, G. V., Hunter, I. W., Mittal, R., Madden, P. G. and Bozkurtas, M.** (2010). The effect of fin ray flexural rigidity on the propulsive forces generated by a biorobotic fish pectoral fin. *J. Exp. Biol.* **213**, 4043–4054. doi:10.1242/jeb.048017
- Taylor, G. K., Nudds, R. L. and Thomas, A. L.** (2003). Flying and swimming animals cruise at a Strouhal number tuned for high power efficiency. *Nature* **425**, 707. doi:10.1038/nature02000
- Thiria, B. and Godoy-Diana, R.** (2010). How wing compliance drives the efficiency of self-propelled flapping flyers. *Phys. Rev. E* **82**, 015303. doi:10.1103/PhysRevE.82.015303
- Tobing, S., Young, J. and Lai, J.** (2017). Effects of wing flexibility on bumblebee propulsion. *J. Fluid Struct.* **68**, 141–157. doi:10.1016/j.jfluidstruct.2016.10.005
- Toomey, J. and Eldredge, J. D.** (2008). Numerical and experimental study of the fluid dynamics of a flapping wing with low order flexibility. *Phys. Fluids* **20**, 073603. doi:10.1063/1.2956372
- Trager, G., Hwang, J.-S. and Strickler, J.** (1990). Barnacle suspension-feeding in variable flow. *Mar. Biol.* **105**, 117–127. doi:10.1007/BF01344277
- Triantafyllou, G. S., Triantafyllou, M. S. and Grosenbaugh, M. A.** (1993). Optimal thrust development in oscillating foils with application to fish propulsion. *J. Fluid Struct.* **7**, 205–224. doi:10.1006/jfls.1993.1012
- Triantafyllou, M. S., Techet, A. H. and Hover, F. S.** (2004). Review of experimental work in biomimetic foils. *IEEE J. Ocean. Eng.* **29**, 585–594. doi:10.1109/JOE.2004.833216
- Tytell, E. D., Leftwich, M. C., Hsu, C.-Y., Griffith, B. E., Cohen, A. H., Smits, A. J., Hamlet, C. and Fauci, L. J.** (2016). Role of body stiffness in undulatory swimming: insights from robotic and computational models. *Phys. Rev. Fluids* **1**, 073202. doi:10.1103/PhysRevFluids.1.073202
- Tytell, E. D., Carr, J. A., Danos, N., Wagenbach, C., Sullivan, C. M., Kiemel, T., Cowan, N. J. and Ankarali, M. M.** (2018). Body stiffness and damping depend sensitively on the timing of muscle activation in lampreys. *Integr. Comp. Biol.* **58**, 860–873. doi:10.1093/icb/icy042
- Vanella, M., Fitzgerald, T., Preidikman, S., Balaras, E. and Balachandran, B.** (2009). Influence of flexibility on the aerodynamic performance of a hovering wing. *J. Exp. Biol.* **212**, 95–105. doi:10.1242/jeb.016428
- Videler, J.** (1993). *Fish Swimming*. New York: Chapman & Hall.
- Videler, J., Stamhuis, E. and Povel, G.** (2004). Leading-edge vortex lifts swifts. *Science* **306**, 1960–1962. doi:10.1126/science.1104682
- Villanueva, A., Smith, C. and Priya, S.** (2011). A biomimetic robotic jellyfish (Robojelly) actuated by shape memory alloy composite actuators. *Bioinspir. Biomim.* **6**, 036004. doi:10.1088/1748-3182/6/3/036004
- Vincent, L., Zheng, M., Costello, J. H. and Kanso, E.** (2020). Enhanced flight performance in non-uniformly flexible wings. *J. R. Soc. Interface* **17**, 20200352. doi:10.1098/rsif.2020.0352
- Warrick, D. R., Tobalske, B. W. and Powers, D. R.** (2005). Aerodynamics of the hovering hummingbird. *Nature* **435**, 1094–1097. doi:10.1038/nature03647
- White, F. M. and Majdalani, J.** (2006). *Viscous Fluid Flow*. New York: McGraw-Hill.
- Willert, C. E. and Gharib, M.** (1991). Digital particle image velocimetry. *Exp. Fluids* **10**, 181–193. doi:10.1007/BF00190388
- Wilson, M. M. and Eldredge, J. D.** (2011). Performance improvement through passive mechanics in jellyfish-inspired swimming. *Int. J. Non-Linear Mech.* **46**, 557–567. doi:10.1016/j.ijnonlinmec.2010.12.005
- Young, J., Walker, S. M., Bompfrey, R. J., Taylor, G. K. and Thomas, A. L.** (2009). Details of insect wing design and deformation enhance aerodynamic function and flight efficiency. *Science* **325**, 1549–1552. doi:10.1126/science.1175928
- Zhang, J.** (2017). Footprints of a flapping wing. *J. Fluid Mech.* **818**, 1–4. doi:10.1017/jfm.2017.173
- Zhong, Q., Zhu, J., Fish, F., Kerr, S., Downs, A., Bart-Smith, H. and Quinn, D.** (2021). Tunable stiffness enables fast and efficient swimming in fish-like robots. *Sci. Robot.* **6**, eabe4088. doi:10.1126/scirobotics.abe4088
- Zhu, J., White, C., Wainwright, D. K., Di Santo, V., Lauder, G. V. and Bart-Smith, H.** (2019). Tuna robotics: a high-frequency experimental platform exploring the performance space of swimming fishes. *Sci. Robot.* **4**, eaax4615. doi:10.1126/scirobotics.aax4615