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TOPICAL REVIEW

Fluid-structure interaction of bio-inspired flexible slender structures: a review of selected topics

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Abstract

Flexible slender structures are ubiquitous in biological systems and engineering applications. Fluid-structure interaction (FSI) plays a key role in the dynamics of such structures immersed in fluids. Here, we survey recent studies on highly simplified bio-inspired models (either mathematical or mechanical) that aim to reveal the flow physics associated with FSI. Various models from different sources of biological inspiration are included, namely flexible flapping foil inspired by fish and insects, deformable membrane inspired by jellyfish and cephalopods, beating filaments inspired by flagella and cilia of microorganisms, and flexible wall-mounted filaments inspired by terrestrial and aquatic plants. Suggestions on directions for future research are also provided.

1. Introduction

The interactions of fluid flows with flexible structures are omnipresent in biological systems and biology-inspired designs. In nature, fish and bats propel themselves by bending their fins or wings; jellyfish and squids utilize body contraction and expansion for propulsion; microorganisms locomote in fluids through the beating of cilia or flagella; and stalks and leaves in trees experience reconfiguration when subjected to wind load. Understanding the flow physics of such interactions is important for fundamental research as well as biomimicry engineering.

Since this topic is very broad and impossible to be reviewed within one single paper, the present review selectively covers the literature of fluid mechanics studies that is inspired by macroscopic/microscopic bio-locomotion and plant motion in fluids. For bio-locomotion, three types of propulsion are included; i.e. flapping-based propulsion utilized by fish, jetting- and paddling-based propulsion utilized by jellyfish and cephalopods, and ciliary propulsion utilized by microorganisms. We review theoretical, experimental, and numerical studies on highly simplified

mathematical (or mechanical) models (in terms of geometry, material property, and actuation pattern). The aim of those works is to reveal the flow physics rather than to mimic the intricate structures and functions of complex biological systems. Several types of simplified models and their corresponding sources of biological inspiration are summarized in figure 1.

Further restrictions are applied on the selection of papers for review. We only focus on flexible slender structures. Here the term 'slender' means that the length-scale in one dimension is much smaller than those in other dimensions. Some interchangeable words found in the literature to describe structures of this type include flap, filament, plate, membrane, panel etc. The term 'flexible' means the structures belong to deformable continua. Not reviewed here are studies on rigid flapping foils or rigid flapping foils linked by torsional springs (i.e. structures with torsional flexibility). Other unreviewed systems include non-motile flagella and cilia serving as sensory organelles for sensing chemical and mechanical gradients [2].

We realize that there exist some excellent reviews, the scopes of which partially overlap with that of

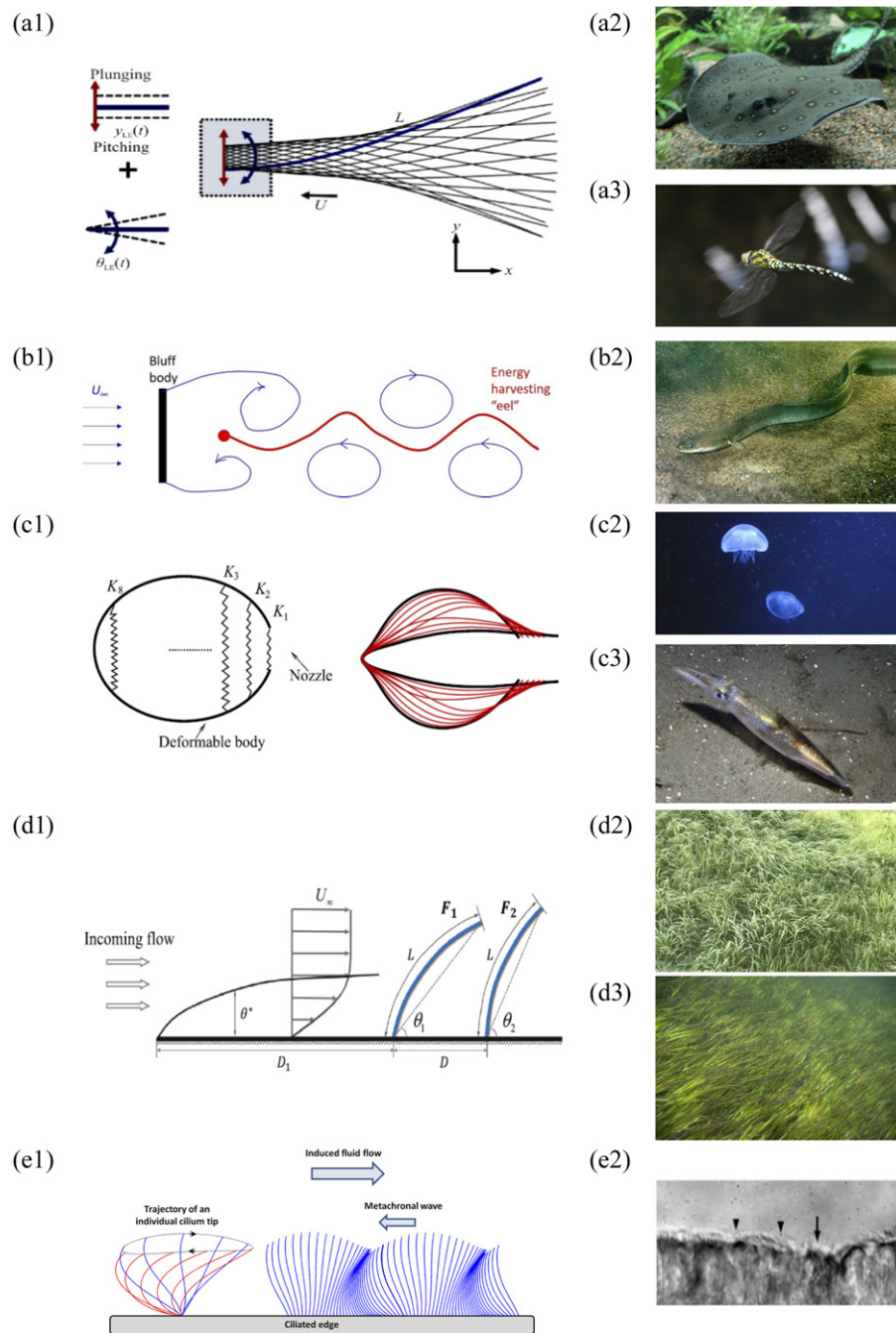


Figure 1. Simplified physics models and corresponding sources of inspiration from biology. (a1) Flexible flapping foil inspired by [fish and insects. Reproduced from [1], with permission from Springer Nature.; (a2) a stingray. [14] CC BY-SA 3.0. This Ocellate river stingray image has been obtained by the author(s) from the Wikimedia website where it was made available under a CC BY-SA 3.0 licence. It is included within this article on that basis. It is attributed to Steven G. Johnson. (a3) a dragonfly. Reproduced from [15]. CC BY 2.0. This Dragonfly in flight image has been obtained by the author(s) from the Wikimedia website where it was made available under a CC BY 2.0 licence. It is included within this article on that basis. It is attributed to Tony Hisgett. (b1) an energy harvester inspired by an eel; (b2) an eel [16]. CC BY-SA 3.0. This *Anguilla anguilla* image has been obtained by the author(s) from the Wikimedia website where it was made available under a CC BY-SA 3.0 licence. It is included within this article on that basis. It is attributed to Gerard Meijssen. (c1) deformable filament inspired by jellyfish and squid. Reprinted from [17], with the permission of AIP Publishing. (c2) a jellyfish. Reproduced from [18]. CC BY 3.0. This *Aurelia aurita* image has been obtained by the author(s) from the Wikimedia website where it was made available under a CC BY 3.0 licence. It is included within this article on that basis. It is attributed to Andreas Augstein. (c3) a squid. [19] (CC BY-SA 3.0. This Opalescent inshore squid image has been obtained by the author(s) from the Wikimedia website where it was made available under a CC BY-SA 3.0 licence. It is included within this article on that basis. It is attributed to Joshua Sera). (d1) wall-mounted flexible filaments inspired by terrestrial and aquatic plants. Reprinted from [20], Copyright © 2019 Elsevier Ltd. All rights reserved. (d2) grass (by Chenglei Wang); (d3) seagrass. Reproduced from [21]. CC BY 2.0. This Seagrass *Halodule uninervis* image has been obtained by the author(s) from the Wikimedia website where it was made available under a CC BY 2.0 licence. It is included within this article on that basis. It is attributed to Paul Asman and Jill Lenoble (e1) schematics of the beating pattern of a flexible filament. Reproduced from [22]. CC BY 4.0. (e2) epithelial cilia exhibiting metachronal waves. Reproduced from [23]. CC BY 4.0.

this paper. For example, reviews on flapping bodies interacting with fluids [3–7], plant–flow interactions [8–10], ciliary propulsion, and flexible fibers in low-Reynolds flows [11–13], just to list a few. Readers are referred to these references for more comprehensive surveys of specific fields.

The rest of the paper is organized as follows. Section 2 introduces studies related to bio-locomotion on a macroscopic scale, including flexible propulsors inspired by insects, fish, jellyfish, and cephalopods. Section 3 reviews studies related to bio-locomotion on a microscopic scale. Section 4 presents studies on wall-mounted flexible structures inspired by terrestrial and aquatic plants. Section 5 covers studies on flow energy-harvesting using eel-like flexible slender structures. Recommendations for future research directions are provided in section 6.

2. Macroscopic bio-locomotion

The locomotory organs of some animals can be regarded as flexible slender structures. Recent investigations indicate that both active and passive flexibilities in the locomotory organs play an important role in animal propulsion [24]. Motivated by a thorough understanding of how flexibility improves the performance of natural propulsors, much attention has been paid to the flapping dynamics of flexible slender structures. Here, we focus on two types of macroscopic propulsors, namely flapping-based and jetting-based.

2.1. Flexible flapping foils inspired by fish and insects

A flapping foil that undergoes a plunging or pitching motion (or both) with a single-point actuation is a standard model for studying the aerodynamics of flying insects and hydrodynamics of swimming fish.

The interaction between fluids and flapping foils with *active* flexibility can be regarded as a one-way coupling problem in which a known flexure is superimposed with the rigid-body driving motion. There exist a few studies in which the propulsion performance of a flapping foil with *active* flexibility is investigated. For example, Miao and Ho [25] numerically investigated the aerodynamics of a plunging airfoil with a prescribed chordwise deformation. The influence of the flexure amplitude on the propulsion performance has been comprehensively examined.

A more challenging task is to understand the role *passive* flexibility plays in locomotion. Unlike active flexibility, two-way coupling between fluid and structure has to be considered in studies involving passive flexibility.

Some studies were motivated by the aerodynamics of flying animals and thus the emphasis was placed on how flexibility affected the generation of lift [26–31]. Yin and Luo [26] carried out a two-dimensional (2D)

numerical study on a deformable flapping foil in hovering flight. They found that both inertial- and flow-induced deformations can result in lift enhancement, and the latter can also lead to higher power efficiency. Dai *et al* [27] performed three-dimensional (3D) simulations on an elastic rectangular wing undergoing pitching motion in hovering flight. It was shown that the aerodynamic performance can be significantly affected by the amplitude of passive pitching and phase difference between passive and prescribed pitching motions. Shoele and Zhu [28] used a 2D computational model with nonuniform flexibility to represent an insect wing with an embedded skeleton. Their results indicated that wings with a strengthened leading-edge can produce higher lift while maintaining high efficiency. Tian *et al* [29] conducted a 2D simulation to investigate the effect of wing flexibility in forward flight. Their results indicated that wing deformation can enhance thrust without sacrificing lift. Cleaver *et al* [30] showed that spanwise flexibility can also significantly increase the time-averaged lift of plunging wings with high or low aspect ratios. Masoud and Alexeev [31] studied the hovering aerodynamics of flexible plunging wings using 3D numerical simulations. They found that the lift and efficiency of lift production could be greatly enhanced when the wings were driven at the resonant frequency.

The largest proportion of the literature was concerned with the relationship between passive flexibility and swimming performance. Note that the metrics for quantifying swimming performance are different for tethered and self-propelled swimmers. For tethered swimmers, the propulsive force and Froude efficiency are used as two metrics. For self-propelled swimmers, the cruising speed is one metric, while ambiguity still exists in the assessment of efficiency [4]. A commonly used metric for the efficiency of such systems is the cost of transport (COT); i.e. energy consumption per unit mass per unit distance travelled.

In some studies, dimensional analysis was used to unveil the scaling laws for the performance of flexible flapping foils. By using energy-balance arguments, Kang *et al* [32] deduced a relationship that linked the thrust coefficient with effective stiffness (rigidity normalized by fluid pressure) and a dimensionless parameter that characterized the wing-tip deformation. Dewey *et al* [33] derived the scaling laws for thrust and efficiency in flexible pitching panels with different aspect ratios. It was found that experimental data collapsed well only if the characteristic elastic force and the characteristic fluid force were used for the scaling in the flexible regime and the rigid limit regime, respectively. Quinn *et al* [34] then extended the work by Dewey *et al* [33] in several directions; i.e. heaving oscillation, multiple flow speeds, self-propelled condition, and a wider range of flexibility.

In some parametric studies on flexible flapping-foil systems, the influences of stiffness, mass ratio,

planform, phase lag between pitching and heaving actuations, etc, were investigated separately or combinatorially [1, 35–65]. Among these works, a unanimous conclusion is that some degree of flexibility (both chordwise and spanwise) can be beneficial for improving propulsive performance (in terms of thrust, cruising speed, and efficiency). One debatable issue is whether optimal performance can be achieved at structural resonance. (Note that, in discussions on the relation between swimming performance and structural resonance, only chordwise flexibility has been considered.)

Although the maxima in trailing-edge amplitudes were usually found near the natural frequencies, the relation between optimal performance (in terms of thrust, cruising speed, and efficiency) and structural resonance is still muddled [48–65]. The existing disagreements in the literature were often rationalized by different assumptions made in the physical models. In the studies based on inviscid flow models with a small flapping amplitude, optimal performance was usually found to coincide with resonance. On the contrary, in systems with strong nonlinearities (such as viscous flow models with separation and finite flapping amplitude), optimal performance can be achieved at off-resonance points. Zhang *et al* [65] argued that resonance can improve performance only if the fluid force is dominant or at least comparable with the inertia force (i.e. when the mass ratio is not too large). Finally, it should also be reminded that, due to the nonlinear effect in coupled fluid-structure systems, care must be taken in evaluating the natural frequencies [56, 66].

Besides the controversy over structural resonance, some attention has also been paid to the relationship between propulsive performance and wake resonance. The concept of wake resonance was first introduced in Triantafyllou *et al* [67], where linear stability analysis was performed on a time-averaged velocity profile behind a 2D *rigid* pitching foil. They found that the best propulsive efficiency could be achieved if the driving frequency matched the ‘resonant’ frequency of the wake (i.e. the frequency of maximum amplification). The Strouhal number (dimensionless frequency) determined by using this principle was found to lie in the range for natural flyers and swimmers. The wake resonance theory was then re-examined in flexible propulsors [68–70] and the correlation between wake stability properties and swimming performance was also confirmed. However, Arbie *et al* [71] recently argued that this theory was only valid in the wakes of thrust-producing types. For momentumless wake behind self-propelled bodies, however, the applicability of this theory was questionable.

Another research topic that attracted some attention was the influence of flexibility on wake-symmetry properties [72–75]. Marais *et al* [72] first reported that flexibility can inhibit the symmetry breaking of the reverse Kármán vortex street behind

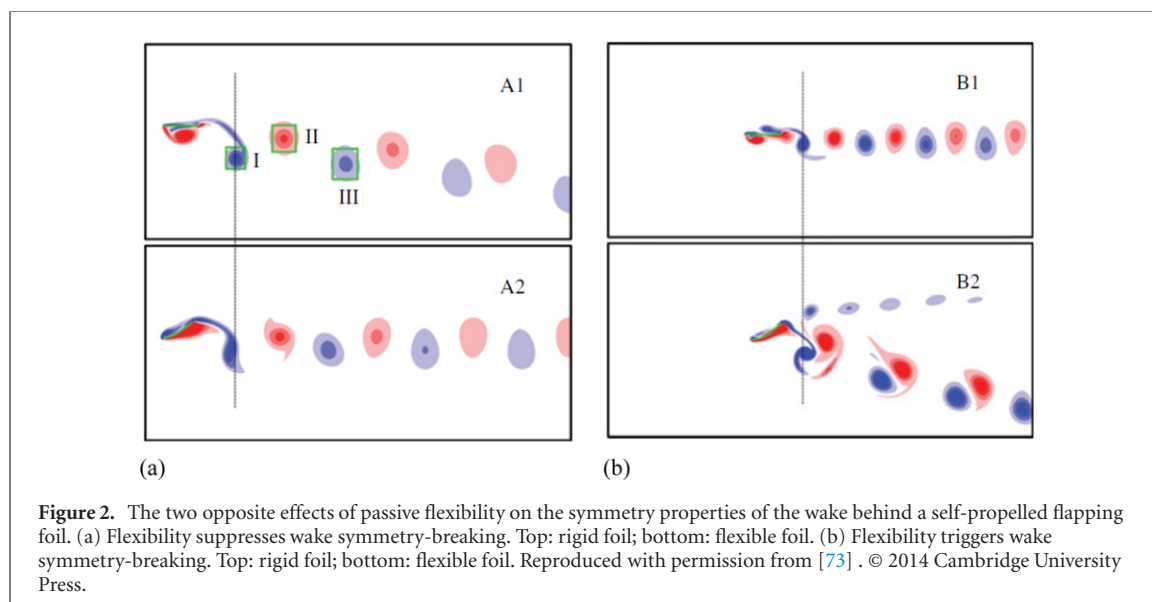
a pitching foil. The suppression of wake deflection by flexibility was later shown by Zhu *et al* [73] in flexible heaving foils under a self-propelled condition. They demonstrated that wake deflection can be enhanced by a higher degree of foil flexibility. The two opposite effects of flexibility on wake symmetry properties are illustrated in figure 2. Shinde and Arakeri [74] showed that the flexibility in pitching foil can also suppress wake deflection and meandering in the limiting case with zero free stream. Kim and Lee [75] found that, for both rigid and flexible heaving foils, the transition between symmetric and asymmetric wake patterns occurred when the sum of leading- and trailing-edge circulations reached a critical value.

More recently, additional complexities were introduced to the standard flapping-foil model, e.g. nonuniform or time-dependent flexibility [76–81], confinement imposed by the ground or sidewall [82, 83], non-sinusoidal or intermittent actuation [84–87], flow-mediated interactions among multiple members [88–93], and hydrophobicity in the body surface [94, 95]. These works provided physical insights into some feasible strategies that can be adopted for improving swimming performance.

2.2. Deformable structures inspired by jellyfish and cephalopods

The swimming of jellyfish and cephalopods is another mode of aquatic locomotion in which periodic body contractions are used for propulsion. Such a locomotion style can be further categorized into two subtypes, namely jetting-based and paddling-based. The former is performed by jellyfish with prolate bell shapes, squids, and octopuses, which swim via expelling a strong jet of fluid. The latter is performed by jellyfish with oblate bell shapes, which swim via a paddling motion on the bell margin. Various mathematical models with different levels of complexity have been proposed to investigate the swimming performance of such locomotion styles. Although the body of a jellyfish or cephalopod may not be regarded as a slender structure, the simplified models usually take the form of a filament or a membrane, which meets the defined criteria of a slender structure. Similar to flapping-foil systems, different metrics are used for quantifying the performances of tethered and self-propelled swimmers.

The simplest physical model is a thin filament (or membrane), the deformation of which is produced solely by *active* flexibility (which mimics the muscle contraction) [96–101]. Peng and Alben [96] numerically investigated the influences of shape and stroke parameters on the performance of an axisymmetric swimmer. It was found that prolate swimmers with high stroke amplitudes were able to swim faster but with a higher energy cost. Contrarily, oblate swimmers with low stroke amplitudes were able to achieve higher efficiency but swam slower. Alben *et al* [97]



investigated the relationship between kinematics and performance of jetting-based swimming by using a combined computational and analytical approach. It was found that high efficiency can be achieved when the bell radius was a nearly linear function of time, or when the intermittent actuation style was adopted. Herschlag and Miller [98] used a 2D jellyfish model and numerically explored the Reynolds number (Re) limit on the swimming performance. It turned out that when $Re < 10$, the cruising velocity decayed rapidly and the work required increased significantly, for both jetting-based and paddling-based locomotion. Bi and Zhu [99] numerically studied the locomotion of an axisymmetric cephalopod-inspired swimmer based on the potential-flow framework. The free-swimming body was driven by repeated deflation–inflation cycles and swam in a bursting-coasting style. It was found that the optimal speed coincided with the critical vortex formation number. They also investigated the thrust generation of an axisymmetric deformable body via pulsed jetting [100]. In this model, both the body deformation and jet speed were prescribed. The vortex ring formation with different jet-speed profiles were compared and three distinctive sources of thrust generation were identified. Luo *et al* [101] extended the work by Bi and Zhu [100] by conducting a 3D simulation and investigated the effect of background flow on vortex formation and thrust generation.

More complex models that take *passive* flexibility into account were also proposed [17, 102–109]. In Park *et al* [102, 103], simulations were conducted on 3D models for oblate and prolate jellyfish, respectively. They examined how the vortex structures were connected with the swimming mechanism and propulsion efficiency. Park and Sung [104] studied the interaction between two tandem self-propelled oblate jellyfish models. It was found that the flow-mediated interactions resulted in stable configurations, increase of cruising speed, and reduction of

cost. Hoover and Miller [105] considered the FSI problem of a 2D model jellyfish bell driven at a frequency ranging from below to above its resonant frequency. It was confirmed that driving the jellyfish near the resonant frequency can result in a significant increase in cruising speed. Hoover *et al* [106] developed a 3D jellyfish model and studied how the swimming performance was affected by the strength of contraction and the flexibility of the bell margin. They demonstrated that flexible margin and sufficiently strong active contraction were the two key factors for fast swimming at low costs. They took it a step further to confirm that the 3D jellyfish model reached the maximum speed when it was driven near the natural frequency [107]. However, if high efficiency (or low COT) was given the priority, the bell should be driven below the natural frequency. Dawoodian and Sau [108] performed 3D simulations to study the swimming and prey capture of a paddling jellyfish. They found that a prolate-type jellyfish was more economical in swimming than an oblate-type jellyfish. Resonant swimming was found to help jellyfish improve energy efficiency over a wide range of applied paddling force. It was also demonstrated that Lagrangian coherent structure analysis can provide a better understanding on predator–prey interactions. Bi and Zhu [17] proposed a 2D squid-inspired inflation–deflation model and investigated its propulsive performance in the tethered mode. By conducting FSI simulations, it was found that the increase in driving frequency can result in higher thrust at the cost of reduced propulsive efficiency. It was also demonstrated that the propulsive performance can be greatly impaired if the wake was disturbed by symmetry-breaking instability. The development of symmetry-breaking instability in the wake behind a squid-inspired swimmer is shown in figure 3. Later, they also focused on the performance of the squid-inspired model in free swimming [17, 110]. It was seen that higher speed can be

achieved by increasing the driving frequency. However, the COT was found to rise as well. Similar to that observed in the tethered mode, in free swimming the symmetry-breaking instability was also found to have an adverse effect on the propulsive performance. In Luo *et al* [109], the effect of the Reynolds number on the performance of this squid-inspired swimmer was explored systematically. It was also found that actuating at the resonant frequency may not lead to better performance (in terms of mean thrust and efficiency).

3. Microscopic bio-locomotion

Flagella and cilia are micro-scale membrane-bounded organelles protruding from cell surfaces, widely existing in protists, plants, and animals and serving as fundamental units of motion [13]. Their length is usually within the range of 10 μm to 100 μm , while their typical beating frequencies vary from 10 Hz to 100 Hz. As such, the Reynolds number is generally much smaller than 1, and viscous force is dominant over inertial force [111]. The length-to-diameter ratio of flagella and cilia ranges from 10 to 100 [112], which can thus be considered as slender bodies.

In general, flagella and cilia share common ultrastructures and compositions, and their internal structure, called the axoneme, is highly conserved across evolution. An axoneme consists of arrays of microtubule doublets and thousands of dynein molecular motors [113]. In most cases, it exhibits either a '9 + 2' pattern composed of nine doublet microtubules and a central pair of single microtubules, or a '9 + 0' pattern where the central pair is absent.

The spatial and temporal regulations of dynein molecular motors yield the motion of the axoneme, which lead to asymmetric planar whip-like (axoneme of '9 + 2' pattern) or oar-like (axoneme of '9 + 0' pattern) beating and fluid pumping. Hence, flagella and cilia can be used for locomotion by unicellular organisms, such as sperm [114] and *Paramecium* [115], or serve to break the left-right symmetry of a developing embryo [116], or transport cerebrospinal fluid in the brain [117] and female reproductive fluid in the oviduct [118], or remove mucus in the respiratory system [119]. Some creatures apply them for generating arrays of vortices for capturing prey [120], or exchanging nutrients and oxygen with the ambient fluid [121]. More functions of flagella and cilia can be found in a recent comprehensive review [122].

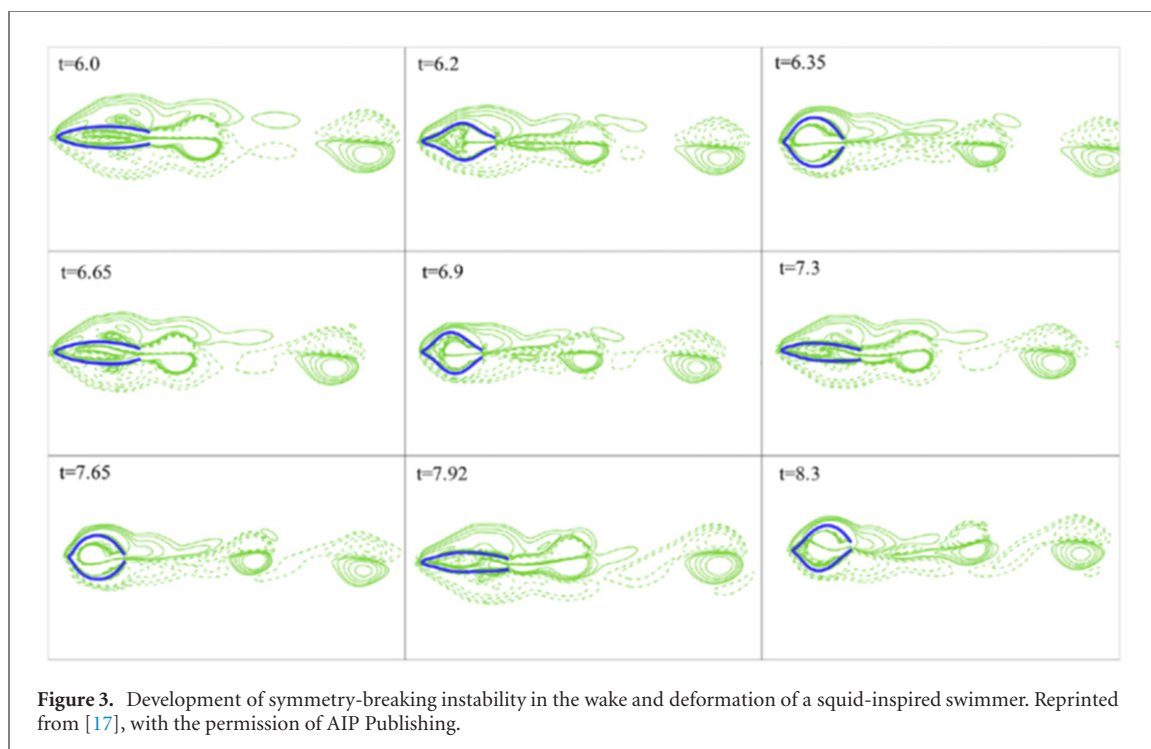
Although sharing the same ultrastructure, and their names are often interchangeable, flagella and cilia are different [13, 123]. In practice, organelles are called flagella when they are sparsely distributed on unicellular organisms, such as sperm and the green alga *Chlamydomonas reinhardtii*, and they usually produce bending waves along their axis. By contrast, cilia refer to those that are grouped compactly and

extensively in animal organs, such as the ciliated epithelial cells in human lungs, or densely anchored on the surface of protozoans, such as *Opalina*. Under this condition, they usually undergo breaststroke-like asymmetric beating motion with alternative power stroke (fast stroke with elongated shape) and recovery stroke (slow stroke with cilia bent and close to the cellular surface).

3.1. Theoretical and numerical modelling

Theoretical modelling and numerical simulation have been extensively applied to reveal the hydrodynamic performance, interactions, and coordination of flagella and cilia. As the flow is usually in the creeping flow regime, flagella and cilia have to break spatial-temporal symmetry to escape the scallop theorem [124] by adopting wave-like or breaststroke-like asymmetric beating motions. Even though the structural components of flagella and cilia have been identified, the mechanisms of how such components coordinate to produce asymmetric beating motions remain elusive. For effective explorations, theoretical models that are able to reproduce asymmetric motions are indispensable, the development of which is one focus of recent studies.

Some previous works developed minimal or reduced models that neglect biological complexity; i.e. the kinetics of molecular motors and the internal mechanics of the axoneme. In these works, flagella and cilia are modelled as oscillators [125–128], or chains of spherical colloidal particles [112] or elastic filaments [129–131], where geometric switch schemes are adopted for actuation. Another type of model was developed by optimizing pumping efficiency of a single flagellum [130, 132] or cilia array [133], although their beating patterns could not be hydrodynamically optimal in nature [134]. By considering the effects of kinetics and dynamics of flagellar and ciliary internal structures, more realistic models have been proposed. For instance, as the internal axial stresses are sufficiently large to trigger the instability via Hopf bifurcation, it was assumed that beating flagella and cilia are driven by dynamic instability [135–137]. When the spatial and temporal regulations of dynein molecular motors are modeled based on some control schemes, such as sliding control [138], curvature control [139], and geometric clutch [113], more realistic beating patterns can be attained. It was found that the curvature control-based model is able to produce the breaststroke-like beating patterns of *Chlamydomonas* [140], while the geometric clutch-based one can generate both flagellar and ciliary waveforms [113]. By combining the sliding control and curvature control schemes, Chakrabarti and Saintillan [123] developed a model that can exhibit various beating patterns presented in nature.



3.2. Coordination and collective behavior of flagella and cilia

Flagella and cilia can exhibit rich dynamic behaviors when they coordinate with their neighbors. In particular, a few to hundreds of sperm can gather through mechanical coupling and display various collective patterns, such as massal motility, sperm trains, and sperm bundles. The collective locomotion can yield hydrodynamic benefits [114]. For example, when two sperm get sufficiently close, their flagella can flap in phase and their beating frequency and swimming velocity can be enhanced [141]. Sperm can also exhibit collective behaviors on larger scales, including sperm vortices [142] and sperm turbulence [143]. The main factors determining the aforementioned collective behaviors have not been elucidated completely. It was found that the coordination could depend on cellular morphology [144] and concentration [142], while the adhesion may be dispensable [145]. More details about collective dynamics of sperm can be found in recent comprehensive reviews [114, 145].

As for other organisms, such as *Chlamydomonas*, each individual often has one pair of flagella that can beat in-phase and anti-phase for controlling and adjusting their swimming speed and orientation. For some other unicellular organisms, such as *Pyramimonas*, each one has multiple pairs of flagella, which usually act in group and exhibit more complex synchronization. However, the underlying mechanisms have not been fully understood, while the existing ones are sometimes controversial. Some studies found that the synchronization can arise purely from hydrodynamic interactions [125, 146], which may also cause stochastic transition from one synchronized

mode to the another [131]. Nevertheless, Quaranta *et al* [147] suggested that the synchronization is caused by cell internal fibers that mechanically connect the flagella, whereas the hydrodynamic interaction plays a marginal role. A later study found that both these two factors, i.e. hydrodynamic interaction and mechanical connection, are essential, and their competition determines the flagellar coordination [148]. Different from the above works, Geyer *et al* [149] found that ‘cell-body rocking’ is crucial rather than direct hydrodynamic interaction.

Ciliary spatial coordination is another fantastic but more complex phenomenon. Cilia do not beat randomly, but often coordinate with their neighbors, giving rise to various metachronal waves (MCWs), including transverse (laeoplectic or diaplectic) and longitudinal (symplectic or antiplectic) waves, which are wave-like patterns with phase differences exhibited among neighboring cilia [150, 151], as shown in figure 1(e2). The functions of MCWs have been extensively explored in previous studies. It was found that MCWs can enhance flow transport velocity and efficiency [139] as well as fluid mixing [112], on which an antiplectic wave usually outperforms a symplectic one no matter whether cilia are immersed in one- or two-component flow [112, 152, 153]. Through an optimal-efficiency-based beating model, Osterman and Vilfan [133] found that laeoplectic waves could be more efficient if cilia beat clockwise. Based on a numerical model where artificial cilia were magnetically actuated, Khaderi and Onck [154] demonstrated that laeoplectic waves inside a microchannel can create secondary flows that could be adopted for fluid mixing.

Although their functions have been extensively investigated, the mechanisms of the emergence of MCWs remain largely unknown. Thus far, it has been found that hydrodynamic interaction can yield MCWs [129, 139, 156–161], as shown in figure 4. For instance, Gueron *et al* [156] and Elgeti and Gompper [139] showed that, initially, in-phase beating cilia can form MCWs after a few beating cycles via hydrodynamic interaction. However, how these interactions cause MCWs is still understudied. Some recent explorations proved that inhomogeneities can lead to wave emergence. For instance, using a minimal model, Nasouri and Elfring [162] demonstrated that the emergence of wavelike behavior of a cilia array around a sphere can arise from the difference in beating rate between one cilium and its neighbors. With a similar model, Ghorbani and Najafi [127] found that the trajectory of the cilium mass center that moves on an elliptic orbit is crucial for the emergence of symplectic or antiplectic waves, when cilia are attached to a closed-body model. Through a more realistic 2D model, Chakrabarti *et al* [163] confirmed that one-dimensional (1D) MCWs can emerge robustly when spatial inhomogeneity is involved. Furthermore, some other factors, such as ciliary density [153], ciliary flexibility [129, 164], and biochemical noise [165], can also influence the emergence of MCWs.

Besides MCWs, other types of ciliary coordination have also been observed, usually at larger scales. For instance, on coral epithelium, beating cilia can generate arrays of counterrotating vortices of a size that is around hundreds of cilium length, so as to enhance nutrient and oxygen mixing with nearby fluid [121]. In a cilia–mucus system reconstructed *in vitro*, cilia can collaboratively beat together to produce large mucus swirls, the diameters of which can be up to thousands of cilium length [166]. Although the mechanisms of these long-range ciliary coordinations remain largely unexplored, it has been demonstrated that hydrodynamic coupling could play an essential role. For example, in a cilia–mucus system, it was found that such coupling could affect the 2D organization of planar cell polarity proteins, which thus dictates the coordination of the ciliary beat direction [166].

4. Plant motions in air or water

Besides ciliary propulsion in microorganisms, plant–flow interaction is another source of biological inspiration for FSI in wall-mounted flexible structures. Such studies are not only crucial for agricultural and forestry production, but also have important consequences in coastal erosion control and renewable energy harvesting.

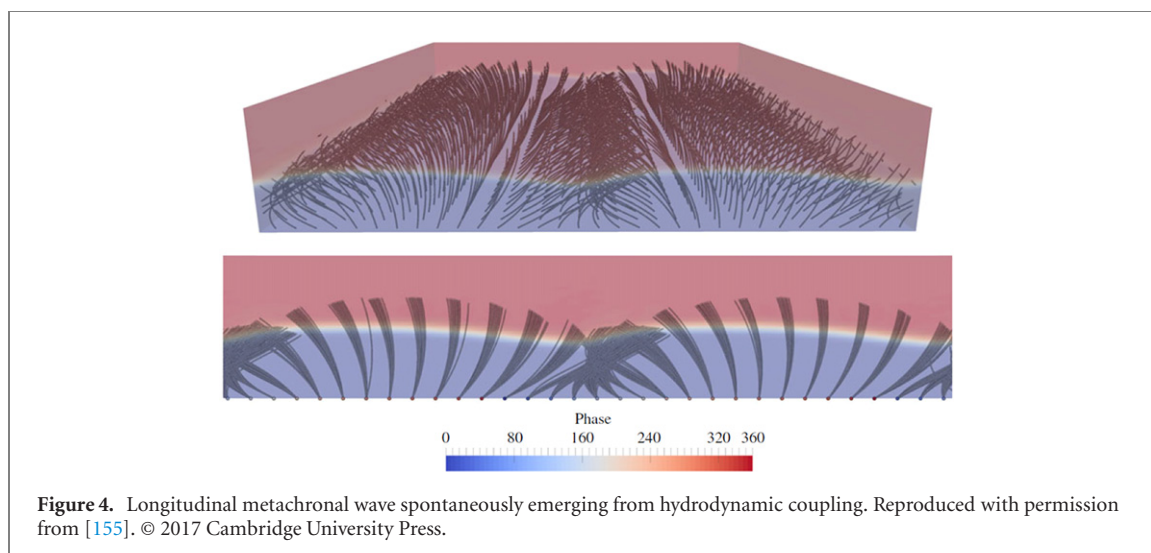
Unlike the studies dealing with locomotion, the flexible structures involved in this section are completely passive. When subjected to fluid flow, two

types of reconfiguration can be found in flexible structures, namely static and dynamic [167–175]. Static reconfiguration refers to the situation where the structures become more streamlined in shape, and therefore, the drag forces exerted on them can be reduced. Dynamic reconfiguration refers to a situation where the structures oscillate in various ways. It should be stressed that, in comparison with FSI studies in open space, those with wall confinement may involve two additional complexities. First, the existence of a boundary layer completely alters the flow structures, which in turn affects the response of the structures indirectly. Second, the presence of wall confinement also directly hinders the movement of the structures. This may occur either through hard collision or through soft collision due to the lubrication barrier force exerted on the structures.

Henriquez and Barrero-Gil [176] investigated the static reconfiguration of a flexible plate subjected to a sheared incoming flow. Leclercq and De Langre [177] later extended this study to include the effect of structural nonuniformity. In these two works, the fluid loads on the structures were calculated using a theoretical model in which the nonuniform velocity profiles were taken into consideration.

In a series of works, Jin and coauthors experimentally investigated the interaction of wall-mounted thin plates with uniform flows at low or high turbulent levels [178–181]. Jin *et al* [178] demonstrated that the frequency of the structures under streamwise motions can be decoupled from that of the wake fluctuations. Jin *et al* [179] studied the influence of the tip shape on the structure dynamics and near-wake turbulence. Jin *et al* [180] also investigated the coupled dynamics of two flexible plates in tandem arrangement. They found that the upstream plate always oscillated at its natural frequency, while the motion of the downstream one was significantly influenced by the vortex shedding. Jin *et al* [181] focused on the dynamics of wall-mounted flexible plates under inclined flows. Three distinct modes of tip oscillation were identified with different combinations of Cauchy number and flow inclination angle.

Recently, some numerical simulations were conducted to study the FSI of wall-mounted flexible structures under a variety of configurations. In Zhang *et al* [20], the interactions of single and two-tandem filaments with a fully-developed laminar boundary layer were studied. The influences of bending rigidity, mass ratio, Reynolds number, and gap distance on the structure dynamics and wake pattern were systematically explored. At extremely low rigidity, the lodging state (which can be regarded as one special case of static reconfiguration) was exhibited. Under certain conditions, the cavity-oscillation state (which can be regarded as one special case of dynamic reconfiguration) has been discovered in the double-filament systems. The dynamic behaviors of single and dual wall-mounted flexible filaments subjected



to fluid load, together with their corresponding flow field, are shown in figure 5. In a similar study by Wang *et al* [182], the interactions of wall-mounted filaments with an oncoming Poiseuille flow were investigated. This work was then extended by Chen *et al* [183] through 3D FSI simulations on a single and two tandem wall-mounted flexible plates.

A few more recent studies were concerned with an array of a large number of flexible structures [182, 184–187]. In Wang *et al* [182], the dynamics of the system with 50 wall-mounted filaments was explored. The transition from the static deflection mode to the flapping mode was observed when the gap distance exceeded a critical value. In Revell *et al* [184], the interactions of Poiseuille and Womersley flows with an infinite series of flexible 2D filaments were investigated by imposing a periodic boundary condition. It was shown that the structure responses were significantly affected by the Reynolds number. Favier *et al* [185] simulated the two-way coupled dynamics of an array of ten filaments in a Womersley flow. They observed the waving behavior at the tips of the filaments and the formation of vortices in the gaps between the two adjacent filaments. O'Connor and Revell [186] investigated the interaction between a row of 128 filaments and a 2D open-channel flow under a steady-flow condition. Their results indicated that four distinct states can be identified, i.e. static, regular waving, irregular waving, and flapping. The regular waving was found to occur when the frequency of the mixing layer instability and the natural frequency of the array were close to each other. Tschisgale *et al* [187] performed large eddy simulations on a model-submerged aquatic canopy that was made up of 800 highly flexible blades in regular arrangement. They focused on the interplay between coherent flow structures and the motion of the blades. Figure 6 shows the instantaneous coherent vortex structures represented by pressure iso-surfaces. The results of this study provided an improved understanding of the wave-like motion of the canopy in a streamwise

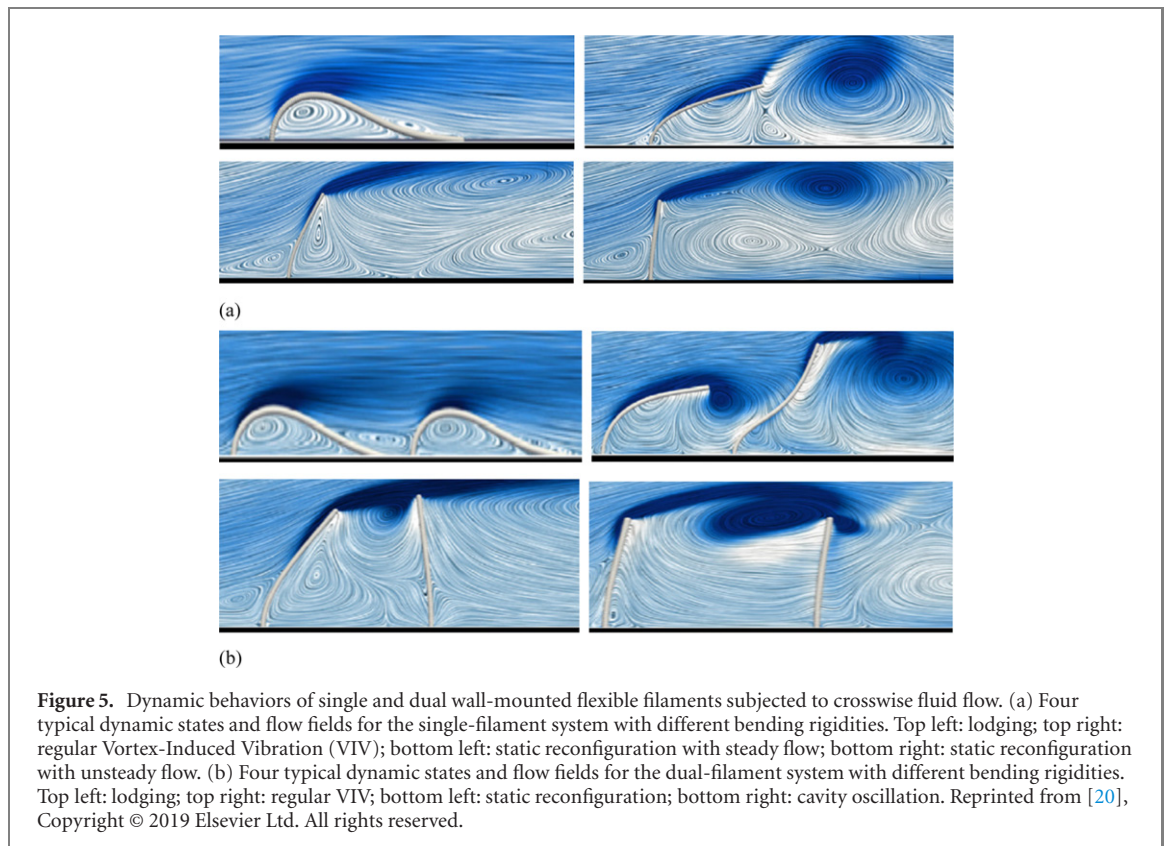
direction (also known as the honami or monami phenomenon).

Some studies aiming to provide biomimicry solutions to engineering problems were also found in the literature. Inspired by the calming effect of aquatic plants, Nové-Josserand *et al* [188] experimentally explored the effects of flexibility and spatial arrangement on the wave energy damping capability of an array of partially submerged flexible filaments in a water tank. Nové-Josserand *et al* [189] developed a simplified 1D model for the experiments presented in [188] and predicted the optimal configuration regarding energy absorption. Park [190] proposed to use a wall-mounted flexible filament as a vortex generator in a Poiseuille channel flow to improve the convective heat flux. The influences of inclination angle and bending rigidity of the filament on thermal performance were examined. Chen *et al* [191] extended the work of Park [190] by using six to 12 wall-mounted filaments uniformly distributed on two channel walls. They conducted a parametric exploration to identify the effects of staggered and tandem gap distances, bending rigidity, and channel height on overall thermal performance.

5. Energy harvesting

The interaction of a flexible slender structure with surrounding fluid flow can be utilized to extract energy from ambient flow such as winds, river currents, and ocean tides, which are vital sources of renewable energy. One of the major advantages of extracting flow energy from the flow-induced motion of flexible slender structures is that, compared to conventional wind/tidal turbine technology, it can be made very small and portable, so that it is very suitable for charging small-sized, low-power, portable, and remote devices such as unattended sensors or robots.

Flexible slender structures can interact with ambient flow in many ways. Here, we restrict ourselves to the configuration where the slender structure



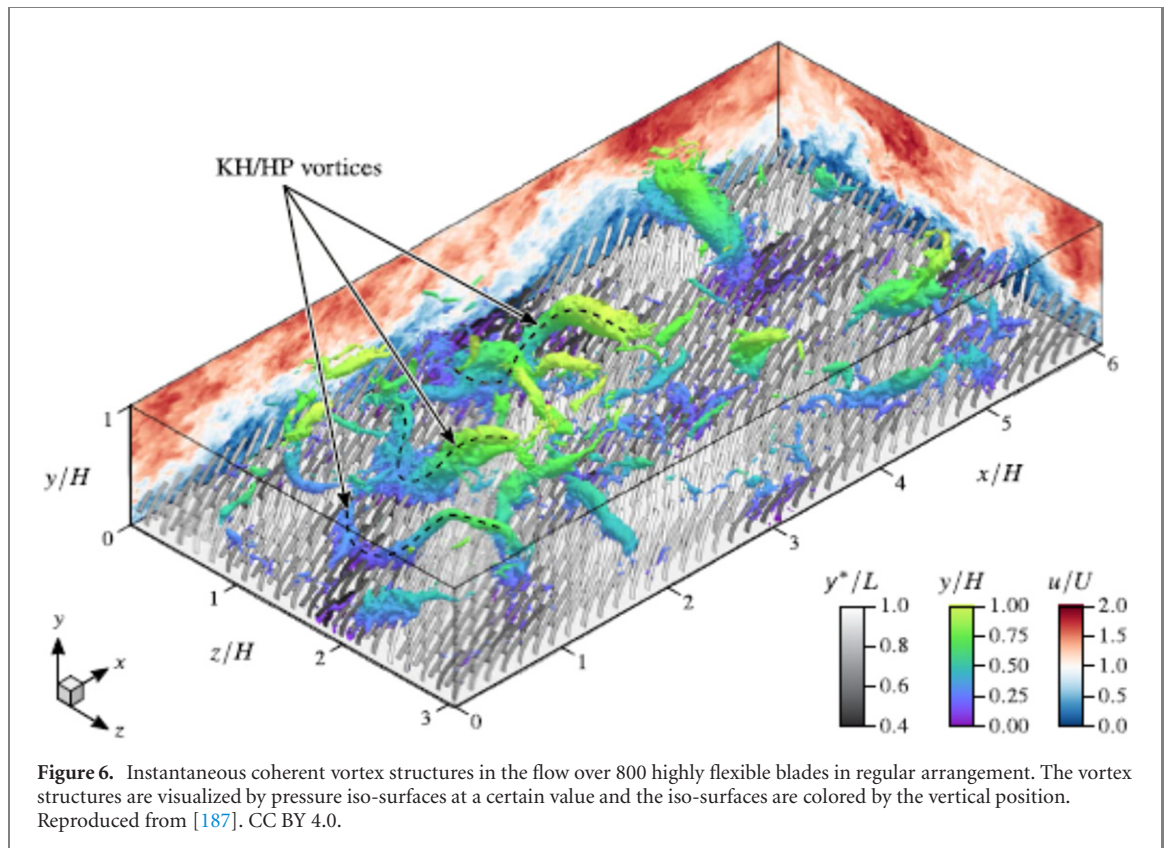
is placed in line with the flow. With this configuration, the structure can vibrate under two different types of flow-induced forcing [192]: one is extraneously induced excitation (EIE) where the structure is excited and sustained through external, time-varying flow pressure gradients such as a trail of traveling vortices behind a bluff body; the other is movement-induced excitation (MIE) where the structure is self-excited and self-sustaining through aero-/hydro-elastic instability.

A seminal work in the EIE type was the *energy-harvesting eel* proposed by Allen and Smits [193]. They placed a piezoelectric membrane in the wake of a flat plate that was placed perpendicularly to the flow, and used the formed Kármán vortex street to induce undulating motion of the membrane, as sketched in figure 1(b1), analogous to the motion of a swimming eel. A number of different membranes, including polyvinylidene fluoride (PVDF), were tested in a water channel at Reynolds numbers ranging from 5×10^3 to 4×10^4 . Their experimental data showed that, as Re increases, the membrane behaviors tend to be optimal, where the eel-undulation frequency matches the natural vortex shedding frequency, i.e. $f_{eel}/f_{nat} \approx 1$. Under this optimal condition, the eel distortion is in synchronization with the convecting vortical structures alternatively shed from the bluff body, and the undulation amplitude is of the order of the bluff body width.

This energy-harvesting eel concept was then realized by Taylor *et al* [194] through introducing a switched resonant-power conversion circuit to a

24.1 cm long, 7.6 cm wide, and $150 \mu\text{m}$ thick, undulating eel that was made of PVDF layers with multiple electrode pairs. This model was tested in water flows at different speeds, and was able to produce about 2 V output voltage at 0.5 m s^{-1} . The same optimal or ideal coupling between the eel undulation and the vortex shedding was confirmed for power extraction. But obvious distortion in both dynamics and power output along the eel length was observed. Pobering and Schwesinger [195] also built a similar but much smaller prototype using a piezoelectric bimorph cantilever 14 mm long, 11.8 mm wide, and 0.35 mm thick, which was clamped in an upstream bluff body 10.35 mm high. Instead of undulating, the cantilever fluttered in its first bending mode, and only produced an output voltage of 0.8 V and electrical power of around 0.1 mW in a 45 m s^{-1} wind, corresponding to a very low power conversion efficiency. Obviously, the cantilever worked under conditions that are still far from optimal, evidenced by deflection amplitudes of only about tens of micrometers.

Akaydin *et al* [196] adopted a slightly different configuration for energy harvesting, in which a piezoelectric beam (30 mm long, 16 mm wide, and 0.2 mm thick) was placed with its free end pointing upstream towards a cylinder of diameter 30 mm. When the freestream velocity was tuned such that the vortex shedding frequency matched the resonance frequency of the piezoelectric beam (at $Re \approx 1.5 \times 10^4$), the beam vibrated violently in its first bending mode. By moving the piezoelectric beam around, the maximum



electrical power (at μW level) was obtained when the beam was located with its free end two diameters away from the cylinder and along its centerline.

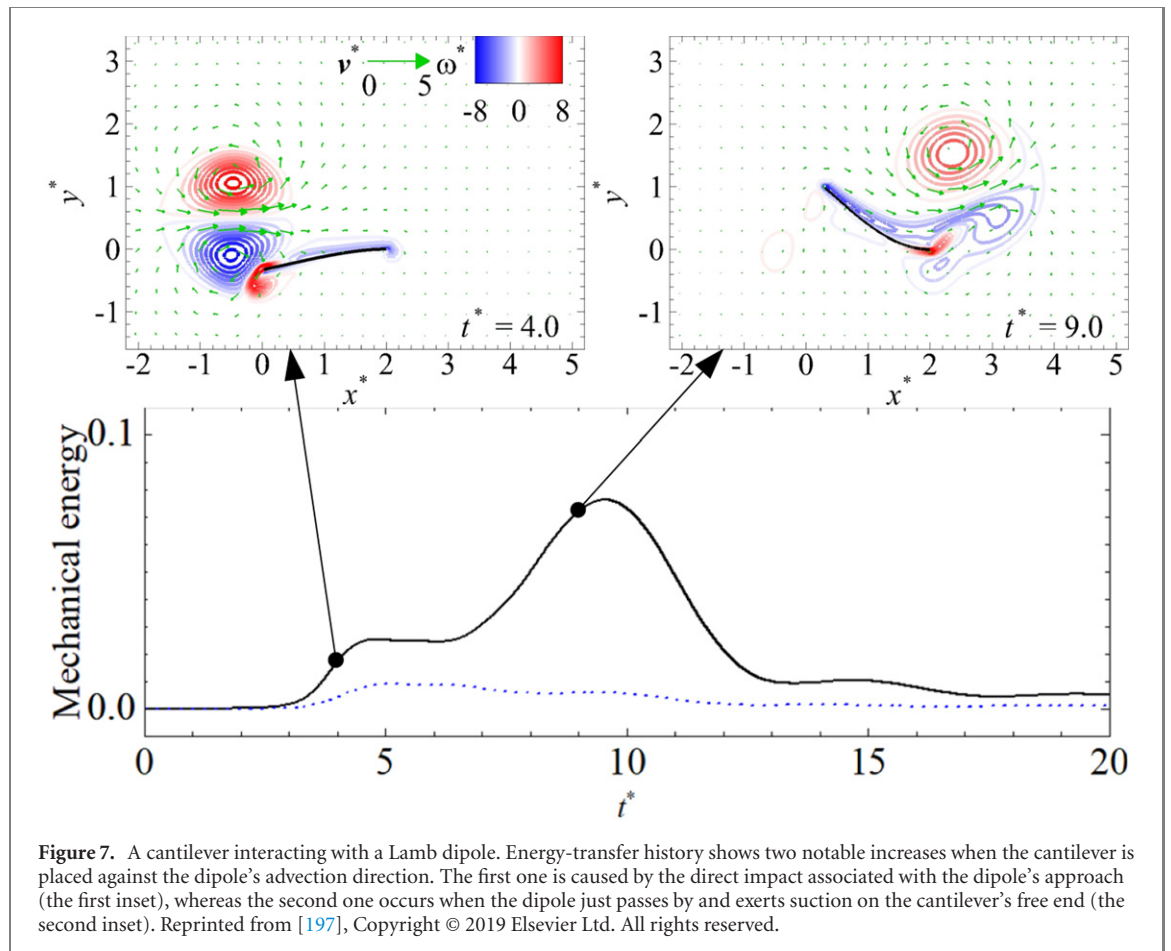
Instead of from a train of vortices, Wang and Tang [197] studied the energy transfer from a single vortex structure, i.e. a Lamb dipole, to a flexible cantilever. The cantilever had a fixed mass ratio of 1.0 and was placed either along or against the dipole's advection direction. Their simulation results revealed that, when the lateral distance was around the dipole radius, placing the cantilever against the dipole's advection direction was more favorable for energy transfer. With this setting, the cantilever generally experienced two notable increases in its mechanical energy (figure 7). The first one was caused by the direct impact associated with the dipole's approach, whereas the second one occurred when the dipole just passed by and exerted suction on the cantilever's free end. Each increase led to a peak, and the second peak was much larger (which symbolizes the maximum transferred energy). At $\text{Re} = 200$, when the lateral distance was about a half of the dipole radius, the cantilever's length was about one dipole radius, and its bending stiffness was moderate, the energy harvesting efficiency could be as high as 10.6%. It was further revealed that this energy-transfer process does not change too much over a wide range of Reynolds number.

In some EIE-type energy-harvester designs, an appendage was adopted to enhance the FSI and force the connected power-generating cantilever to vibrate with large amplitudes. This type of

appendage includes a compliant or revolvable flap in the stalk-leaf architecture [198–200, 201] and a bluff body experiencing flow-induced vibration [202–205]. Most of these designs adopted piezoelectric materials to generate electricity, which has been comprehensively reviewed by Safaei *et al* [206].

More studies were conducted on MIE-type energy harvesters. Beyond a certain flow speed, usually known as the critical velocity, negative damping of an elastic structure occurs, which causes divergence of structural deformations (or the classical aeroelastic phenomenon called flutter). Argentina and Mahadevan [207] developed scaling laws for 2D compliant beams in a viscous flow, which showed the relationship between the critical flutter speed U_c , flutter frequency ω , and other system parameters as $U_c \sim \left(\frac{Eh^3}{\rho_f L^3}\right)^{\frac{1}{2}}$ and $\omega \sim \left(\frac{\rho_f U^2}{\rho_s h L}\right)^{\frac{1}{2}}$, where U is the freestream velocity. ρ_f and ρ_s are the fluid and beam densities, respectively. h , L , and E are the beam thickness, length, and elastic modulus, respectively. These scaling laws were then verified by Deivasigamani *et al* [208] in 3D, rectangular beams in their wind-tunnel experiments. They indicated that the stiffness of the beam must be low enough or the length of the beam must be long enough so that a realistic critical flutter speed can be obtained.

It has been demonstrated that the MIE flutter is a combination of mode shapes, usually the first and second modes of vibration [209]. This is true if the



structure-to-fluid mass ratio $m^* = \rho_s h / \rho_f L$ is relatively large. For sufficiently small mass ratios, however, the beam flutter motions were governed mainly by fluid-added mass and viscous effects, rather than adhering to predicted modal displacements [210].

Three distinct regimes of MIE structure dynamics have been identified, depending on the beam length, stiffness, and flow speed [211]: (1) fixed-point stability, where subsequent to an initial disturbance the system experiences positive damping and the beam returns to a stretched-straight position; (2) limit-cycle oscillations (LCOs), where MIE flutter eventuates and the beam tip displacements closely resemble a sinusoidal function; and (3) chaotic flapping, where the flutter is characterized by random snap-through events, large increases in drag, and a broad band frequency response. It was also pointed out that maximum bending strain energy was contained in the LCO regime, while energy outputs decreased significantly when the beam transitioned to chaotic flutter [212, 213].

The mechanical energy transferred from the flow to the MIE structure can be further converted into electrical energy through various types of power take-off mechanisms, such as electromechanical induction, piezoelectricity, and triboelectricity. Fei and Li [214] developed the first electromagnetic MIE-type harvester. This harvester was composed of a long

clamped-clamped polymer film (hence called *wind-belt*) 1.2 m long, 25 mm wide, and 0.2 mm thick, and an electromagnetic converter located just a few dozen centimeters from one of the membrane's ends. An adjustment system was added to modify the length of the film, which enabled it to change the tension of the film and the oscillation frequency. The large surface of this structure enabled it to generate 1.3 mW at a low wind speed of 3.1 m s^{-1} . In a follow-up study, they further improved the system to generate about 7 mW of electrical power at about 3 m s^{-1} wind speed [215].

Using piezoelectric materials, the bending strain energy in fluttering membranes can be converted into electricity, typically in the order of mW. Examples include the aforementioned PVDF-based energy-harvesting eel developed by Taylor *et al* [194] and the piezoelectric bimorph cantilever developed by Pobering and Schwesinger [195], both being the EIE-type flutter and operating in flowing water. Taylor *et al* [194] further proposed the use of electrostrictive polymers as an alternative to conventional PVDF for the eel due to its much larger piezoelectric conversion efficiency. Other flutter-style piezoelectric energy harvesters operating in air flows were also developed and have been well reviewed by Safaei *et al* [206]. Among them, an airfoil-based hybrid harvester design

was proposed by Dias *et al* [216, 217], which utilized both piezoelectric transduction and electromagnetic induction for power generation.

Electricity can also be generated using the coupling of triboelectrification and electrostatic induction through frequent contact and separation between a fluttering conducting (or dielectric) foil and nearby dielectric (or conducting) plates. By utilizing the wind-induced resonance vibration of a fluorinated ethylene propylene film with a surface of nanowire structures between two aluminum plates, Yang *et al* [218] demonstrated that a triboelectric nanogenerator (TENG) with a 22 cm long and 2.5 cm wide foil and a 1.25 cm foil-plate gap, which can deliver an output voltage up to 100 V, an output current of 1.6 μA , and a corresponding output power of 0.16 mW under an external electric load of 100 M Ω , is enough to directly light up tens of commercial light-emitting diodes.

In another similar study, Bae *et al* [219] found three distinct contact modes between the fluttering foil and the nearby plate, i.e. single-contact mode, double-contact mode, and chaotic-contact mode, which are determined by the dimensionless wind speed and the mass ratio of the foil. In this flutter-driven TENG, the flexible foil was made of Au-coated conductive textile, and the rigid counter plate was made of a dielectric polytetrafluoroethylene (PTFE) film, leaving a 1 cm separation between them. When the foil was short with dimensions of 7.5 cm length and 5 cm width, it worked in the single-contact mode, in which it heavily collided and left the counter plate periodically using its trailing edge, similar to a flail with a free-swinging stick or a double pendulum. When the foil was long with dimensions of 12 cm length and 3 cm width, it worked in the double-contact mode, where the first contact occurred at the foil's mid-section and propagated with the travelling wave towards the trailing edge, and the second contact then arose at the trailing edge with a much smaller contact strength, after which the foil moved away from the counter plate. The chaotic-contact mode occurred when the wind speed was above a critical speed that is a function of the mass ratio. In this mode, the foil's fluttering motion lost its regularity and became random and chaotic, causing very irregular contacts. Their experiments showed that the contacting frequency and the charge collection rate generally increased with the wind speed, but the single-contact mode worked much better than the double-contact model. With the short foil, the TENG could deliver a maximum voltage of 250 V and current of 70 mA at a wind speed of 22 m s⁻¹. If adopting a dual-plate design, the TENG could deliver an output voltage of up to 200 V and a current of 60 mA with a high frequency of 158 Hz at wind speed of 15 m s⁻¹, giving an average power density of approximately 0.86 mW.

In general, conventional wind turbines are not placed in tandem due to adverse wake effects, which

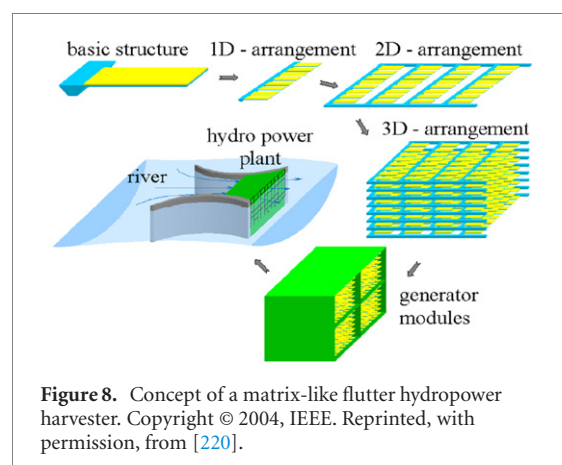


Figure 8. Concept of a matrix-like flutter hydropower harvester. Copyright © 2004, IEEE. Reprinted, with permission, from [220].

cause problems in trailing turbines (loss of power, turbulence-induced vibration, gearbox resonance, etc). However, flutter harvesters under certain conditions appear to perform beneficially when placed in tandem. The ability to potentially extract more power from a trailing harvester in the wake of another harvester is attractive. However, the benefit decays after three or four harvester-lengths downstream [200]. This phenomenon could allow for more space-efficient designs compared with existing wind-farm layouts, such as the matrix-like flutter harvester design (figure 8) proposed by Pobering and Schwesinger [220]. This is especially useful in highly urban environments, where space is usually considered a constraint.

In addition to experimental investigations, theoretical and computational models were also developed to predict the energy-harvesting performance of fluttering plates/beams. Tang *et al* [221] modeled the interactions between a cantilevered flexible plate and its surrounding axial flow using a panel method, i.e. the unsteady lumped vortex model [222]. With this model, they managed to give a breakdown of the total energy transfer between the fluid flow and the plate in different plate sections and in different bending modes. It was found that energy is pumped from the fluid flow into the plate at some locations, while it is transferred from the plate to the fluid flow at other locations. Interestingly, no matter what the structure-to-fluid mass ratio is, energy is transferred from the plate to the fluid flow at the most downstream section of the plate, corresponding to positive thrust generation. It was also found that, at large mass ratios, the energy transfer occurs largely in the first two bending modes, consistent with the findings reported by Zhang *et al* [209]. Moreover, the energy is always transferred from the fluid flow to the plate in the second bending mode. With these understandings obtained, a *flutter-mill* concept was further proposed theoretically that was supposed to operate at large mass ratios and generate electricity using electromagnetic induction. By simply assuming a 10% mechanical-to-electrical

energy-conversion efficiency without considering the induced electromagnetic force acting on the plate, they compared the flutter-mill with a real horizontal-axis wind turbine and concluded that this theoretical concept can achieve an output capacity comparable to the wind turbine and that can operate in the same range of wind speeds.

With a fully coupled fluid-structure-electrical interaction model, Michelin and colleagues [213, 223, 224] studied the linear stability and dynamics of a fluttering flexible plate that is connected to a dissipative electrical circuit through piezoelectric layers. They found that the number and position of piezoelectric elements play a critical role in energy-harvesting performance. The continuous limit was then applied in their model by assuming the piezoelectric material is small compared to the typical wavelength of the plate's deformation. The modeling results suggested that the flow-to-electrical energy conversion is more efficient when the structure-to-fluid mass ratio is small, which can be achieved when the plate's length is long or when the fluid inertia is large compared to the structure's, e.g. in water flows. With small mass ratios, it was found that the optimal location for piezoelectric energy harvesting along the plate is on the downstream half, consistent with the findings reported in Singh *et al* [225]. The results also emphasized the importance of the output circuit in the energy transfers: a careful tuning of the circuit characteristic time-scale to that of the fluid-structure oscillations can significantly enhance the conversion efficiency from the structure to the electric system. Furthermore, linear stability analyses revealed that the piezoelectric coupling generally stabilized the plate's fluttering modes, and the maximum energy-conversion efficiency can be scaled as the square of the piezoelectric coupling coefficient.

6. Outlook

The investigations based on experimental, analytical, and numerical approaches have significantly improved our understanding of the coupling between bio-inspired flexible slender structures and ambient fluid flows. This has also expedited the development of new bio-inspired strategies for solving complex problems in various engineering disciplines. Several directions are recommended here for future research endeavors.

Most of the numerical studies focus on 2D problems (planar or cylindrical) and 3D simulations are relatively scarce. From the point of view of real application and basic research, the 3D effect is an indispensable aspect that should be addressed. Three-dimensional simulations usually necessitate large-scale parallel computation. This remains challenging in the sense that some technical difficulties need

to be overcome to achieve highly efficient parallel computing.

Whether the best performance in flapping foil and jellyfish-like swimming can be achieved at structure resonance is an unsolved issue, although some clarifications have been made in several recent papers. A more in-depth exploration in this research topic is still needed. The relation between performance and wake resonance is also an open question. The validity of the 'wake resonance argument' in all types of wakes (including drag-producing, thrust-producing, and neutral) is questionable.

The symmetry-breaking of wakes is another hot research topic in flapping foil and jellyfish-like propulsions. Here the term 'symmetry' has slightly different meanings in the two systems. In the case of flapping-foil propulsion, it refers to spatial-temporal symmetry, while in the case of jellyfish (or cephalopods) propulsion, it refers to spatial reflection symmetry. For both systems, what triggers the symmetry-breaking instability is largely unknown. In most studies, the stability boundary was determined by physical or numerical experiments. Global stability analysis is a promising method for revealing the physical mechanism behind the symmetry-breaking of the wakes produced by rigid [226] and flexible [227, 228] flapping bodies.

Even though numerous models have been proposed for flagella and cilia, a commonly accepted one, which can reproduce realistic 3D beating patterns, is still lacking mainly due to biological complexity. This imposes great challenges on consistently exploring the flagellar or ciliary hydrodynamic performance and the underlying mechanisms of their short- and long-range coordination. Furthermore, in most existing studies, the fluid is assumed to be Newtonian. However, a more complex fluid environment can be involved in the coordination. For instance, in mucociliary transport, fluid composed of a low-viscosity periciliary layer and a high-viscosity mucus layer usually exhibits non-Newtonian behaviors, such as shear-thinning and viscoelastic behaviors. The mechanism of ciliary coordination in such a complex flow is still poorly understood.

In large arrays of wall-mounted flexible structures, the role that passive flexibility plays in the formation of waving motion (i.e. honami or monami) has not yet been well understood. With the advent of more powerful computers, it is now possible to perform simulations that resolve the flows around each individual element (even in the turbulent flow regime). The modal decompositions, such as proper orthogonal decomposition and dynamic mode decomposition that treat the flow and structure together [229], are well-suited tools for revealing the physical mechanism of this mysterious phenomenon.

As for energy harvesting, it should be pointed out that, although promising, so far all the developed flutter-type energy harvesters can only generate a

small amount of electricity at the mW or even μ W level. To achieve a power output at a 1 W level, as proposed in the energy-harvesting eel project [194], more efforts are required on efficiency enhancement, prototype scale-up, and array arrangement.

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Data availability statement

No new data were created or analysed in this study.

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