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On the diverse roles of fluid dynamic drag in animal swimming and flying

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Questions of energy dissipation or friction appear immediately when addressing the problem of a body moving in a fluid. For the most simple problems, involving a constant steady propulsive force on the body, a straightforward relation can be established balancing this driving force with a skin friction or form drag, depending on the Reynolds number and body geometry. This elementary relation closes the full dynamical problem and sets, for instance, average cruising velocity or energy cost. In the case of finite-sized and time-deformable bodies though, such as flapping flyers or undulatory swimmers, the comprehension of driving/dissipation interactions is not straightforward. The intrinsic unsteadiness of the flapping and deforming animal bodies complicates the usual application of classical fluid dynamic forces balance. One of the complications is because the shape of the body is indeed changing in time, accelerating and decelerating perpetually, but also because the role of drag (more specifically the role of the local drag) has two different facets, contributing at the same time to global dissipation and to driving forces. This causes situations where a strong drag is not necessarily equivalent to inefficient systems. A lot of living systems are precisely using strong sources of drag to optimize their performance. In addition to revisiting classical results under the light of recent research on these questions, we discuss in this review the crucial role of drag from another point of view that concerns the fluid-structure interaction problem of animal locomotion. We consider, in particular, the dynamic subtleties brought by the quadratic drag that resists transverse motions of a flexible body or appendage performing complex kinematics, such as the phase dynamics of a flexible flapping wing, the propagative nature of the bending wave in undulatory swimmers, or the surprising relevance of drag-based resistive thrust in inertial swimmers.

1. Introduction

Fluid dynamic drag as a force that acts opposite to the relative motion of an object with respect to the surrounding fluid is one of the main ingredients of all locomotion problems in nature. Aside from their evident biological relevance, the locomotion strategies found in the flight of birds, bats and insects (e.g. [1,2]) and the swimming of fish and marine mammals (e.g. [3-5]) have long since served as inspiration for the development of artificial systems (e.g. [6-8]). The result of this pluridisciplinary appeal is that literature abounds over an ample spectrum of approaches bounded by biology, physics and engineering. Analysing the case of flying and swimming animals, we will discuss here different facets of the drag problem, beyond the most intuitive one, which is to counter the propulsive effort of an animal that moves from one point to another, consequently setting the average cruising velocity. Owing especially to its engineering relevance, this problem has been widely studied, defining and describing different types of drag, such as skin friction or form drag (e.g. [9-12]). Moreover, a recent study [13] has shown that a scaling law constructed on basic drag considerations links swimming speed to body kinematics for a wide range of scales in macroscopic aquatic locomotion. From a fluid dynamics perspective, there is of course only one hydrodynamic force, which results from integrating the pressure

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Table 1. Cruising Reynolds numbers.

bacterium	$\sim 10^{-5}$
marine invertebrate larvae	~0.1-10
Drosophila	$\sim 10^{2}$
small fish (e.g. guppy)	$\sim 10^{3}$
dragonfly	$\sim 10^4$
tuna	$\sim 10^{5}$
blue whale	$\sim \! 10^{6}$

and viscous forces around the moving object. The physics that links the pressure *p* with the velocity field $\mathbf{u} = (u_x, u_y, u_z)$ is described by the Navier–Stokes equations, which can be written in dimensionless variables as (e.g. [14])

$$\frac{\partial \mathbf{u}}{\partial t} + (\mathbf{u} \cdot \nabla)\mathbf{u} = -\nabla p + \frac{1}{Re}\nabla^2 \mathbf{u} + \mathbf{F}$$
(1.1)

and

$$\nabla \cdot \mathbf{u} = \mathbf{0},\tag{1.2}$$

where $\nabla = (\partial/\partial x, \partial/\partial y, \partial/\partial z)$ is the nabla operator, Re = LU/ν is the Reynolds number, defined in terms of characteristic length L and velocity U scales and of the kinematic viscosity ν_r and F is an external force (usually only gravity for the problems that interest us here). The swimmer, flyer or moving object completes the problem definition by giving the initial and boundary conditions. As such, if an animal starts to move from rest in a quiescent fluid, we can write for the initial condition $\mathbf{u}(t=0) = \mathbf{0}$. Because the fluid extremely close to the animal will follow the motion of the surface of the animal S_{animaly} the boundary condition can be formally written as $\mathbf{u}(\mathbf{x} \in S_{\text{animal}}) = \mathbf{u}_{S_{\text{animal}}}$. Integrating the pressure field obtained from solving the Navier-Stokes equations over the moving boundary can be, in principle, obtained for each particular case, giving the net force, although this remains challenging and is the subject of recent advances when considering velocity field measurements [15-17]. The dynamical balance in equations (1.1) and (1.2) depends on the Reynolds number, which determines the importance of inertial versus viscous forces in the problem. The two limit cases in terms of Re have been widely studied: when $Re \gg 1$, the viscous term is negligible and in practice the Euler equations for an ideal fluid are recovered, the pressure gradient being balanced by fluid inertia. In these high Reynolds number flows, such as the flow around an airfoil, the effects of viscosity are confined to a thin boundary layer that matches over a small length scale the 'outer' inviscid flow and the actual solid boundary, where the no-slip condition applies and the velocity of fluid particles must match the velocity of the boundary. In the other limit, for $Re \ll 1$, it is the viscous term that governs the dynamics. This limit, known as Stokes flow, describes for instance the propulsion of microscopic organisms using cilia or flagella. The Reynolds numbers relevant to animal swimming and flying cover a broad range (table 1), a lot of cases being 'intermediate' with respect to the two limits mentioned above, those that conventional analytical methods are capable of handling [18]. Physical insight relevant to this intermediate range usually requires the correct modelling of the vortex dynamics detaching from the swimmer or flyer, and considerable efforts in this sense have been widely documented in the literature



Figure 1. Schematic diagram of the flow streamlines over an airfoil section showing the boundary layer and its separation on one side defining the width of the near wake. The drag force is in the direction of the uniform flow velocity U far from the streamlined object, lift is perpendicular.

(e.g. [19–33]). As we will discuss further, the dynamics of the solid body itself, in particular its elastic properties, also have to be considered. Indeed, in addition to constituting the boundary condition for the fluid problem that will describe the locomotion forces, the deformable body of the animal in question will also respond to the action of the surrounding fluid producing a fully coupled fluid–structure interaction problem.

The separation between skin friction and pressure drag may be exemplified with the traditional picture of aerodynamic flow around an aerofoil (figure 1). There, pressure drag can be obtained from inviscid flow analysis and the skin friction evaluated from boundary-layer solutions (e.g. [11]). In separated flows, pressure drag should be estimated using a more complicated approach due to the degeneration of the shear layer into the wake. A convenient manner of analysing drag in this case is through the definition of the *drag coefficient*,

$$C_{\rm D} = \frac{F_{\rm D}}{(1/2)\rho U^2 S'},\tag{1.3}$$

where the hydrodynamic force F_{D} is rendered dimensionless by comparing it to the dynamic pressure ρU^2 acting on a reference surface S. Different definitions of S are used depending on the problem, so care should be taken when using drag coefficient figures from the literature. For bluff-bodies, S is usually defined by the *frontal area*, i.e. the projected area of the object onto the plane perpendicular to the flow direction, which gives a measure of the characteristic size of the separated region delimiting the zones of rotational and inviscid flows. For streamlined bodies, it is usually the wetted area (the total surface of the body) that is considered, whereas in wing aerodynamics, the reference surface is the wing plan form. Unsteadiness, being an intrinsic feature in flapping and swimming animals of interest here, complicates the straightforward application of the usual formulæ for estimating fluid dynamic forces.

The most subtle part of the drag question in animal locomotion may be that the previous cruising-velocity-limiting role of drag cannot be fully decoupled from the thrust production mechanisms of an undulating body or a flapping appendage. The latter is an obvious statement for low-Reynolds number microorganisms, where viscous drag is the only force available to drive locomotion (e.g. [18]), but not at larger Reynolds numbers, where thrust production mechanisms are usually associated with inertia, in particular to added mass-based effects. Vogel [34] uses a model example to propose that drag-based thrust at high Reynolds numbers (see also [35]) is the best strategy for the initial acceleration manoeuvre of a swimmer, or for a craft starting from rest, whereas lift-based thrust production—as per the one used by swimming penguins [36]—would be advantageous once a cruising speed has been established. In nature, the strategies adopted by swimming animals are, of course, dependent on the circumstance, we refer to the reader to ch. 12 of Vogel [34] for further references to particular examples.

Drag-based mechanisms have also been shown to play an important role in insect flight [37,38]. There again, the problem is far from the traditional picture of aerodynamics that examines lift versus drag coefficients, because of the intrinsic unsteady nature of flapping flight (e.g. [7]); instantaneous velocity around a wing being in that case the vectorial addition of the flapping velocity and cruising velocities. Here, the only difference with swimmers is that flapping flyers must balance drag and their own weight by producing both thrust and lift at the same time. It should be noted that the relative importance of aerodynamic drag to weight increases as the size of an insect decreases, due to the respective surface and volume dependency of both forces. In parallel to the active locomotion strategies, aerodynamic drag may affect the distribution of habitats of insects of different sizes and shapes regarding only their response to the local wind, which will produce drag forces that may exceed rapidly the weight of small insects [39].

Fluid dynamic forces set not only the absolute motion of the swimmer/flyer (acceleration, cruising speed, etc.) but also passive deformations of the flapping/undulating body or appendage (e.g. [40]). Wings, fins or even the whole body of certain animals are indeed compliant structures and, in nature, animals use a combination of muscular action (actively controlling the body deformation) and the passive elastic response of their bodies to produce the observed kinematics. The latter is observed also in the shape reconfiguration of sessile organisms subject to the action of an external flow (e.g. plants in the wind [41] or underwater vegetation [42]). Passive deformations are also of great importance in the mechanisms of locomotion for real animals or artificial swimmers or flyers.

After giving a short overview of recent results concerning drag in deformable bodies, we will discuss the role of local drag forces in the case of a flapping wing or a swimming body. In particular, we will review the role of quadratic drag in the local force balance of slender bodies and discuss its consequences on the locomotion mechanisms and strategies depending on animal shapes and specific gaits. The last part will be dedicated to the extension of these results to understand the passive deformations involved in the conception of artificial swimmers or flapping flyers. We have organized the paper around a few particular examples taken from our own recent research, attempting to illustrate the common thread that connects the different points that we discuss.

We have decided not to include in the present paper the issue of wave drag, thus focusing on flapping flyers and swimmers far from the surface. Wave drag is nonetheless certainly an important point for a large class of problems that concern animals moving at or near the air–water interface. These problems range from small insects dealing with capillary waves [43], to large animals that need to stay close to the free surface to breath and, consequently, are forced to manage the wave drag associated with the perturbation of the interface [44]. The subject of wave drag undoubtedly deserves a dedicated review.



Figure 2. Skin friction and pressure drag contributions to the total drag coefficient for a family of struts of length *L* and thickness t_h at $Re = 4 \times 10^5$ (data from [45]). The C_D data were obtained by dividing drag-per-unit-length data by $1/2\rho U^2 t_h$. Drag-per-unit-length divided by thickness is thus here equivalent to drag F_D divided by the frontal surface *S* in equation (1.3). (Online version in colour.)

2. Global drag in deformable bodies

A first general question about drag in animal locomotion concerns the way in which the traditional picture of figure 2 showing the contributions of frictional drag and pressure drag to the total drag over a streamlined body—is modified for a body whose shape is changing in time. Part of the difficulty comes from the fact that the same body (or appendage) that is producing the propulsive force by flapping or undulating is also the source of drag [46–48]. Nonetheless, the question of how the swimming kinematics modifies the so-called *dead drag*, i.e. the drag experienced by a rigid model or dead animal towed at its usual cruising speed has remained worthy of attention as we review in this section.

2.1. Skin friction

Skin friction is given by the integral over the body of interest of the local wall shear stress $\tau_0 = \eta (du/dy)_{y=0}$, where *y* is the coordinate away from the body on the local frame of reference and u(y) is the velocity field tangential to the wall along the *x*-direction. Considering a flat plate of length *L*, span *H* and negligible thickness t_h as the most basic model of a streamlined body, the skin friction drag per unit span over the two sides of the plate is given by $D_{sf}/H = 2 \int_0^L \tau_0 dx$. The total skin friction drag can be written in terms of the Reynolds number $Re_L = UL/\nu$, giving (e.g. [49]):

$$D_{\rm sf} = \frac{4}{3} \frac{\rho U^2 L H}{\sqrt{Re_L}} = \frac{4}{3} \rho \sqrt{\nu L} H U^{3/2}, \qquad (2.1)$$

where ν is the kinematic viscosity and U is the mean speed of the plate—the key assumptions for the validity of equation (2.1) are those of boundary-layer theory, i.e. $Re_L \gg 1$ and $\partial/\partial x \ll \partial/\partial y$. Of course, one can define a skin friction drag coefficient by rendering equation (2.1) non-dimensional as $C_{Dskin} = D_{sf}/(\rho U^2 LH)$, where we have used, as mentioned before, the wetted area 2LH as reference surface. This expression has been repeatedly used in the literature concerning undulating slender structures (e.g. [50,51]). However, equation (2.1) relies



Figure 3. (*a*) Trailing stream-wise vortices in the wake of a rectangular wing (from [63]). (*b*,*c*) Stream-wise vortices detached from model undulatory swimmers of two different aspect ratios—(*b*) H/L = 0.3 and (*c*) H/L = 0.7, the foils are shown from behind, i.e. swimming into the plane shown (from [64]). (Online version in colour.)

on a classical steady boundary layer profile, which, as put forward by the Bone–Lighthill hypothesis [52], is considerably modified by the oscillatory motion of a flapping structure. Indeed, it has been measured that swimming fish experience greater friction drag than the same fish stretched straight in a uniform flow [53]. Concerning a full theoretical description, it is only very recently that a skin friction model including the effect of a normal velocity component has rationalized the boundary-layer thinning hypothesis [54,55]. Their expression for the longitudinal drag per unit length reads:

$$D_{\parallel} = C_{3D} \eta U_{\parallel} \sqrt{R e_H \frac{U_{\perp}}{U_{\parallel}}}, \qquad (2.2)$$

where U_{\perp} , U_{\parallel} , Re_H and C_{3D} are, respectively, the wall-normal and longitudinal velocities, the Reynolds number based on the span *H* and the incoming velocity U_{\parallel} and a drag coefficient in the range $1.7 < C_{3D} < 2$. The numerical simulations by Ehrenstein *et al.* [55] reinforce the theoretical prediction of boundary-layer thinning—albeit resulting in a significantly lower enhancement of skin friction than the original values proposed by Lighthill [52]—but the hypothesis is still challenged by recent observations [56].

2.2. Bluff-body drag

Friction drag becomes a minor issue when strong separations occur and pressure drag accounts for most of the total drag. Pressure drag is, in these cases, referred to as bluff-body drag [9] and the reference surface in the definition of the drag coefficient (equation (1.3)) is the cross-section facing the flow (e.g. $S = \pi a^2$ for a sphere of radius *a*). In animal locomotion, one usually expects streamlined shapes to be favoured, but other animal shapes indeed exist and considerations of ecological relevance such as enhanced manoeuvrability have been suggested to be the evolutionary reason for bluff-body type shapes such as the archetypal example of boxfishes (Ostraciidae: Tetrodontiformes) [57], where pressure drag can be expected to be larger than skin friction. Pressure drag is also the main type of drag in transient manoeuvres with impulsive rapid motions and massive separations behind the moving body, such as the rowing-type motions of median and paired fin propulsion in fish swimming, the fast c-starts of body and caudal fin fish swimming [58] or the impulsive accelerations of the strike manoeuvre in aquatic predators [59,60]. For simple models such as flapping foils, bluff-body drag has also been considered using the tip-to-tip amplitude of the trailing edge displacement as the effective width of the frontal area. If the flapping amplitudes are similar to the foil width, the latter has been used as the characteristic length scale for the reference surface [25,30], whereas for slender bodies a reasonable choice is the area swept by the tail tip [61]. Other empirical formulations to model form drag in streamlined bodies have been described by Hoerner [10], based on a reference surface described in terms of a dimensionless streamlining parameter (see also [62]).

2.3. Vortex-induced drag

Skin friction and bluff-body (or pressure) drag can be defined in a two-dimensional framework, e.g. the wake of a cylinder or an airfoil. When considering the three-dimensional reality, pressure drag is modified by an additional mechanism that has its origin in the trailing vortices that appear to ensure the continuity of pressure at the extremities of a finite objet (figure 3*a*). This is a well-known issue in aerodynamics where the downwash velocity associated with these vortices reorients the lift vector giving it a backwards component that adds to the total drag, the so-called *induced drag*

$$D_i = \frac{L^2}{A_0 \rho U^2},$$
 (2.3)

where *L* is the total lift on the wing and A_0 has the dimensions of an area and depends on the circulation distribution around the wing (e.g. [49]). The trade-off between lift and drag is of course one of the basic ingredients behind the richness of wing shapes in nature, in particular for animal gliders (e.g. [1]). The problem gets more complex when analysing the problem of flapping flight, where the beating wings produce both lift and thrust. The intrinsically unsteady mechanisms at play in such a problem have been widely studied and we refer the reader to other reviews [1,2,7,65].

Finite-size effects have also been shown recently to be essential to understand the relationship between thrust and drag in undulatory swimmers [64,66]. A clear example is the system of trailing stream-wise vortices produced at the edges of a self-propelled flexible foil (see fig. 3b-c, from [64]). We will

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Figure 4. Edge vortices along the body of a model fish: (*a*) instantaneous stream-wise vorticity slices and (*b*) pressure field over the cross-section indicated as a dashed line in (*a*) (adapted from [70]). (Online version in colour.)

see in the following that these vortices are intimately linked to the process of resistive force production in inertial swimmers.

3. Local drag in models of animal locomotion

Thrust production for slender undulatory animals or appendages relies on local actions achieved by the muscles or by passive deformations. For low-Reynolds-number flows, the full description of the swimming mechanics depends only on local viscous friction. This case, based on resistive theory, benefits now from a large body of literature (e.g. [67] and references therein). In the case of slender swimmers at intermediate to high Reynolds numbers, the local force balance requires two forces which, as we will see, are used differently depending on the animal. Neglecting the viscous contribution—and in a (x, y, z) frame of reference where the swimming direction is $-\mathbf{e}_x$ and the undulation is described by the x(s, t), y(s, t) coordinates, depending on the curvilinear coordinate s and time t—, these two forces (per unit surface) can be expressed as [68]

$$\mathbf{f}_{\mathrm{ma}} = -\mathcal{M}(h)(\ddot{y} + 2U\dot{y}' + U^2y'')\mathbf{n}$$
(3.1)

and

$$\mathbf{f}_{\rm d} = -\frac{1}{2}\rho C_{\rm d} |\dot{y} + Uy'| (\dot{y} + Uy') \mathbf{n}, \qquad (3.2)$$

where $\mathcal{M}(h)$ represents the local added mass accelerated during swimming—with h(s) being the local span of the cross section of the swimmer—n is the unit vector normal to the fish local surface, and the dot and prime symbols are time and space derivatives, respectively. In addition, ρ is the fluid density and C_d is a drag coefficient weighing the *nonlinear* resistive force. Both forces come from the inertial character of the flow in these Reynolds number regimes, but are of different sources. The first term f_{ma} is the reactive contribution due to the acceleration of the surrounding fluid by the undulating body or appendage, as it was derived using a potential flow assumption by Lighthill's elongated body theory [52,69]. But, the second term f_d represents a resistive force associated with the dynamic stalls at each swimming cycle that result from the large transversal local velocities and the finite geometry of the fish section, as illustrated for instance in figure 4 from a recent simulation of the flow around a model fish (figures from [70]). Although a resistive model to describe the locomotion of long and narrow animals was developed by Taylor in the 1950s [71], ever since Lighthill's works [52,69], the reactive term has been the usual expression used to describe thrust production for high Reynolds number swimmers, marking a clear difference between the basic mechanisms for locomotion



Figure 5. Phase diagrams of drag-driven and added mass-driven propulsion as a function of the aspect ratio and slip ratio for (*a*) anguilliform kinematics and (*b*) carangiform kinematics. The dashed line represents the $\langle T_{ma} \rangle = \langle T_d \rangle$ in the phase space. Experimental data are obtained from: Gray [72], Tytell [73] and Hess [74] for anguilliform swimmers, and Bainbridge [75], Webb [76], Videler [77] and Videler [78] for caranguiform swimmers. (Adapted from [68].) (Online version in colour.)

at low and high Reynolds numbers: the former being resistive and the latter reactive. It is only more recently that models have included both reactive and resistive contributions in the force balance at a cross-section in the elongated-body limit (e.g. [47,62]).

Using anguilliform and carangiform kinematics from the literature, Piñeirua *et al.* [68] showed that both contributions intrinsically depend on the full animal kinematics and geometry. Figure 5—reproduced from [68]—shows the relative weights of resistive and reactive components involved in the thrust production as a function of the gait and aspect ratio for both anguilliform and caranguiform kinematics. $\langle \hat{T}_{ma} \rangle$ is defined as the reactive to total thrust ratio such that $\langle \hat{T}_{ma} \rangle = \langle (\int_{0}^{L} \mathbf{f}_{ma} \cdot \mathbf{e}_{\mathbf{x}} \, ds) / (\int_{0}^{L} \mathbf{f}_{ma} \cdot \mathbf{e}_{\mathbf{x}} \, ds + \int_{0}^{L} \mathbf{f}_{d} \cdot \mathbf{e}_{\mathbf{x}} \, ds) \rangle$ and the gait is characterized through the slip ratio U/v_{φ} , with v_{φ} the phase velocity of the undulatory kinematics. The aspect ratio \hat{h} is defined as max (h(s))/L, with L the total length of the swimmer.

We see that the consideration of the resistive nonlinear term leads to make the distinction between added mass-driven and drag-driven mechanisms to produce locomotion at high Reynolds numbers. In particular, we note that animals using



Figure 6. Schematic diagram of the fluid and solid dynamics two-way coupling in a fluid – structure interaction problem (adapted from [79]). (Online version in colour.)

an anguilliform gait such as eels, are in fact even in this large Reynolds numbers regime, rather resistive than reactive swimmers (i.e. the physical mechanism to produce thrust is similar to low Reynolds number swimmers). This feature is first due to the slender nature of the body or appendage offering a large resistance in comparison with added-mass-induced reaction, but also because anguilliform animals use fast phase velocity for the propagation of the undulatory waves $(0.4 \le U/v_{\varphi} \le 0.8)$. By contrast, carangiform swimmers, characterized by higher aspect and speed ratios, are gathered in the added-mass-driven propulsion regime. Thus, although in some cases inertia-based locomotion is well described by classical potential flow theories, the problem becomes more complex with slender bodies or appendages. Moreover, the main thrust production mechanism is highly dependent on the kinematics. The above results complete the picture of locomotion mechanisms of inertial regimes animals in general. The existence of the quadratic resistive term may also have consequences on the fluid-structure interaction mechanisms arising for passive deformation of some body parts or in the case of artificial flyers or swimmers, as we discuss in the next section.

4. Local drag in fluid – structure interactions of passive appendages

We will consider in the following a slender body flapping or undulating as a model system to discuss the role of hydrodynamic drag in the fluid-structure interaction problem of animal or bioinspired artificial swimming and flying. We have discussed above different aspects of the fluid problem and shall now explore the motion of the structure, i.e. the swimmer or flyer subjected to aerodynamical loads. While it constitutes the boundary condition for the fluid problem, its own dynamics is, of course, coupled to that of the surrounding fluid, establishing the two-way coupling described schematically in figure 6. The dominant features of the different branches in this full fluid-structure interaction problem picture are ruled by various non-dimensional parameters that weigh the relative importance of the different physical mechanisms at play. Some of these numbers are built solely from the comparison of different dynamical properties of either the fluid (e.g. the Reynolds number) or the solid physics; others are intrinsically built from the comparison between the dynamics of the fluid and the structure.



Figure 7. Beam model for a flapping wing (*a*) or an undulatory swimmer (*b*). In (*a*), the beam represents a section of the wing, shown schematically undergoing a deformation well described by the first mode of a clamped – free beam [82,83]. In (*b*), the deformation of the beam in a higher mode is represented by the undulatory kinematics of the self-propelled swimmer described in [61,84]. The characteristic velocity of the imposed actuation $A\omega$ and the resulting cruising velocity *U* are represented schematically in both cases. Additionally indicated: for the flapping wing, the angle ϕ that characterizes the ratio of these two velocities; and for the undulatory swimmer, the phase velocity of the bending wave v_{φ} . The length *L* of the beam is thus the wing chord in (*a*) or the swimmer body length in (*b*). (Online version in colour.)

For simplicity, we will consider a simple geometry consisting of a slender flexible structure of characteristic length scale L, thickness t_{h} , density $\rho_s = L^{-1}\mu_s$ (μ_s being mass per unit surface) and bending rigidity $B \sim Et_h^3$ (e.g. a beam or a plate) propelling through a fluid at an average cruising speed *U*. A harmonic forcing of angular frequency $\omega = 2\pi f$ and amplitude A is imposed at one of its ends, constituting the input of energy needed to sustain the motion. Such a simple model allows for the introduction of the key parameters that can be used to describe the locomotion problem of a flexible body in a fluid. We have already noted the dynamical regimes defined by the Reynolds number. We have now to also introduce the fluid-solid mass ratio $M^* \sim \rho / \rho_{st}$ the Cauchy number $Cy = \rho U^2 L^3 / B$ [80,81] and the elastoinertial number $\mathcal{N}_{ei} = \mu_s A \omega^2 L^3 / B$ [82] comparing, respectively, the fluid pressure and the solid inertia to the elastic restoring force of the structure.

In the following sections, we will develop these ideas further for several cases, either in air or water (i.e. $M^* \ll 1$ or $M^* \sim 1$). The fluid-structure coupling can be described by



Figure 8. Thrust production of (*a*) heave, (*b*) pitch and (*c*) pitch – heave motions. Comparison between experiments and simulations. Ratio of reactive thrust to total thrust for the simulations in a self-propelled configuration as a function of the non-dimensional flapping frequency and the plate aspect ratio: (*d*) heave (*e*) pitch and (*f*) pitch – heave. The definition of T_{am}^+ here is slightly different from $\langle T_{ma} \rangle$ in figure 5 because it includes only positive contributions of the local force to the integral (see [93] for details; adapted from [93]). (Online version in colour.)

the same Euler–Bernoulli beam (figure 7; e.g [85]), which is written in its general form:

$$\mu_{s} \frac{\partial^{2} \mathbf{X}}{\partial T^{2}} = \frac{\partial}{\partial S} \left(f_{t} \tau - B \frac{\partial^{2} \theta}{\partial S^{2}} \mathbf{n} \right) - \mathbf{f} + \mathbf{W}(t), \qquad (4.1)$$

where μ is the mass per unit length, f_t is an internal tension ensuring the inextensibility condition, $f = f_{am} + f_d$ is the force due to the fluid pressure field as defined in the previous section. n and τ are the unit normal and tangent vectors to the beam. In this model, the internal viscoelastic dissipation in the beam is neglected considering that damping is dominated by the external resistive term due to the lateral fluid quadratic drag f_d . W(t) is the imposed actuation, which for a flapping wing or fin, can be usually modelled by simple harmonic functions.

4.1. Thrust production of an elastic flapping plate

Our first example of fluid-structure interaction involving a passive structure concerns the thrust production of a slender rectangular flexible flapping plate in water, a basic model of a swimmer that has been the subject of several recent studies [51,64,86-93]. The usual problem here is to determine how the local actuation imposed at one of the extremities of the plate gives rise to thrust production and consequently to locomotion. The mechanical response of the plate is characterized by resonance modes, which are intimately related to the amplitude of the deformations and hence to the swimming performance. Figure 8a-c shows experimental thrust measurements compared to a numerical solution of equation (4.1) for three different forcing conditions of the elastic plate: a pure heaving motion, a pure rotating motion and a combination of heaving and pitching [93]. In the example, the swimming velocity is set to zero to focus on the production of propulsive force that can be accurately measured experimentally. The modal response of the plate is clearly observed for the three actuations, and we can see that the match between computational results and the experimental data is satisfactory. This validates the simplified fluid/structure model, in particular in the choice of the fluid forcing terms. The interesting feature of the modelling approach is precisely that it enables comparison of the weight of the different fluid terms, reactive and resistive: figure 8d-f shows the ratio of reactive thrust to total thrust $\langle T_{ma} \rangle$ for the three different actuations, this time for self-propelled situations where the swimming velocity is set by the equilibrium between thrust and drag. In the same manner as shown previously in figure 5, these results confirm the strong role of nonlinear local drag and the importance of the kinematics in the case of bioinspired artificial locomotion.

Depending on the forcing imposed at one of the plate extremities and of the geometry of the swimmer, the sources of propulsion can be fundamentally different. We see, for example, that a pure heaving propulsion for low-aspectratio plates is essentially drag-based, which contrasts with the almost fully added-mass-driven propulsion of the pure pitching case. In the combined pitch–heave case, thrust production is based primarily on either drag or added mass depending on the aspect ratio: larger aspect ratios dominated by the reactive term, while lower aspect ratios are dominated by the resistive term. These conclusions significantly modify the usual distinction made between resistive and reactive locomotion in terms of viscous versus inertial potential flow-based propulsion (or low *Re* versus high *Re* approach).

4.2. Propagating fish-like kinematics of a passive slender elastic body

Another interesting feature of the presence of quadratic damping in the fluid/structure problem of an actuated elastic plate moving in a flow is the modification of the modal response to local excitation. Figure 9*a* shows visualizations of an experiment by Ramananarivo *et al.* [94] on a vibrating elastic plate in both air (left) and water (right). In air, the quadratic drag is negligible because of the very low fluid density and it is seen that the dynamical response of the plate is a classical standing wave predicted



Figure 9. (*a*,*b*) Vibration experiments described in [94] performed on a Mylar plate flapped with a shaker in air (*a*) and in water (*b*). In air, a standard standingwave solution is observed, that is characteristic of systems influenced by the boundary conditions. In water, with a stronger damping, the plate now exhibits a travelling solution. (*c*-*h*) Dynamics of the elastic undulatory swimmer described in [61]. (*c*) Definition of the coordinates and geometry of the beam model. (*d*-*f*) Simulated motion of the beam when implementing equation (4.2) gradually: (*d*) with only the two first terms describing a classic elastic beam (*e*) adding the 'flag' terms in brackets, (*f*) adding the quadratic fluid term. (*g*) Successive computed shapes superimposed to pictures of a 4.5 cm long swimmer forced at *f* = 19 Hz. (*h*) Experimental envelope to be compared with the computed envelope in (*f*). Scale bar in (*a*,*b*) is 1 cm. (Adapted from [61,94].) (Online version in colour.)

by weak damping vibration theory. The same experiment performed in water, though, showed very different behaviour, exhibiting pure propagating waves as observed in unbounded media. It was shown that the difference between both kinematics was due to the magnitude of the drag term leading, in the case of water, to continuously strong kinematic losses during the propagation of the waves. The irreversible loss of kinetic energy transferred from the swimmer's body to the fluid (represented in the beam model by the quadratic dissipation term) is the dynamical ingredient that enables a propagative bending wave to be established. This feature, here described in a simple vibrating plate experiment, has also been observed and studied for self-propelled artificial swimmers. As a model, we still consider a passive elastic body where the actuation is localized at one extremity as defined by equation (4.1). Practical examples of such systems have been investigated recently experimentally [51,88,90,92,95-97] and numerically [66,86,89,98]. Equation (4.1) can be written in the weak amplitude approximation, except for the dissipation term, which holds due to the high transversal velocities involved along the body. The resulting beam equation now reads:

linear beam with added mass

$$\overbrace{(1+\tilde{m})\ddot{y}+y'''}^{\text{'flag' terms}} + \widetilde{\tilde{m}[2\tilde{U}\dot{y}'+\tilde{U}^2y'']}$$
quadratic dissipation

$$+ \widetilde{\tilde{\alpha}|\dot{y}+\tilde{U}y'|(\dot{y}+\tilde{U}y')} = 0, \qquad (4.2)$$

which is written in dimensionless variables, $\tilde{U} = UL\sqrt{\mu_s/B}$ is the reduced velocity, $\tilde{m} = M/\mu_s$ the mass ratio and $\tilde{\alpha} = \frac{1}{2}\rho dC_d L/\mu_s$ the non-dimensionalized damping coefficient. Note that $\tilde{\alpha}$ depends on *L*, which reflects the increasing effect of damping when the filament is longer [61]. We can note in particular: (i) the effect of added mass term, (ii) a potential flow model for the surrounding fluid that brings two extra terms that depend on the swimming velocity (labelled 'flag' terms in the equation as they are responsible for the flapping flag instability when an outer flow of sufficient velocity is imposed, e.g. [99]) and (iii) the quadratic dissipation term opposing lateral motions. The latter turns out to be by large, the most important effect of the fluid for the beam model in the slender swimmers of [61], always one to two orders of magnitude larger than the added mass and flag terms.¹

Equation 4.2 is solved numerically using the parameters of the experiment [61]. The output of this model successfully recovered the elastic wave kinematics measured experimentally-figure 9g. The model can be simulated, by parts, increasing gradually the number of terms in order to pinpoint their respective physical contribution to the elastic response of the filament. The model with only the first two terms is shown in figure 9b, adding the convective terms (or 'flag' terms) in figure 9c and adding the quadratic damping in figure 9*d*. As can be seen, the first gives the standard standing wave solution expected for a linear non-damped system. The presence of the second term barely changes the global elastic response of the filament. However, the addition of the quadratic dissipation drastically affects the resulting solution, changing to a fish-like propagating wave. This is an important point that can be non-intuitive: the direct consequence of dissipation due to the lateral quadratic drag on the elastic response of a body that is actuated locally is thus to enable the production of a propagating wave kinematics; such kinematics will increase the locomotion efficiency with respect to what would be achieved with standing wave kinematics, as was already shown by Lighthill in his 1960 paper [69].

4.3. Phase dynamics in flexible flapping wings

As a last example of the role of fluid dissipation in the description of a flexible structure, we consider the case of flapping flyers or insect-inspired flexible flapping wings. Of course, 'insect-inspired' is a rather broad label, considering the wide variety of insect wing morphologies and kinematics, and one can reasonably expect different force balances in, say, tiny



Figure 10. (*a*) Photograph of a flapping wing from Ramananarivo *et al.* [83] showing successive states of the bending wing during one stroke cycle. As can be seen, the deformation is mainly performed on the first mode. In this case, the phase lag is quite large, leading to a strong increase of flight performance. Scale bar is 1 cm. (b-c) Evolution of the non-dimensional amplitude (*b*) and phase (*c*) of the trailing edge wing response as a function of the reduced driving frequency for two flapping amplitudes A = 0.8L and A = 0.5L (filled symbols correspond to measurements in air, open symbols in vacuum). Those results are compared to nonlinear predictions from equation (4.3) with (grey line) and without (black line) nonlinear air drag. The vertical grey band in (*b*) and (*c*) marks the optimum of performance quantified by a dimensionless thrust power (see [83] for details; adapted from [83]). (Online version in colour.)

insects performing clap-fling [100,101] or larger insects in cruising flight [102] or taking-off [103]. Wing compliance has been identified as one of the key points that determine the performance of flapping wings [82,83,104–106]. More precisely, it has been observed that during a stroke cycle, the trailing edge response of the wing was characterized by a strong lag with respect to the imposed motion of the leading edge. The presence of this phase lag is a vital ingredient in terms of performance, as it ensures the best instantaneous aerodynamic shape for thrust production. This feature is exemplified in figure 10*a*: large phase lags will provide the largest bending of the wing at maximum flapping speed, leading to a more favourable repartition of aerodynamic forces.

The amplitudes of deformation of a compliant wing flapping in air can also be derived from equation (4.1) with a model that includes only solid inertia and elasticity Ramananarivo *et al.* [83], as depicted schematically in figure 7. In that framework, equation (4.1) may be rewritten including nonlinear terms due to inertia and curvature. For high-amplitude and frequency-flapping strokes (i.e. involving strong transversal velocities), the quadratic term is also needed in the equations describing the dynamics. Here, a new dimensionless variable w(x, t) = (h(x, t) - W(t))/L is introduced to describe the system in the reference frame of the leading edge, the beam equation reads:

linear beam curvature nonlinearity

$$\widetilde{w'''} + \widetilde{w} = \underbrace{-(w'w'^2 + w'''w'^2)'}_{\text{inertial nonlinearity}} \\
\underbrace{-\frac{1}{2} \left[w' \int_{1}^{x} \frac{\partial^2}{\partial t^2} \left[\int_{0}^{x} w'^2 \, dx \right] dx \right]'}_{\text{linear damping quadratic damping}} \\
\underbrace{-\xi \widetilde{w}}_{-\xi n | \widetilde{w} | \widetilde{w}} \underbrace{-\xi_{n | | \widetilde{w} | \widetilde{w}}}_{-\xi_{n | | \widetilde{w} | \widetilde{w}}} \underbrace{-\frac{A}{L} \widetilde{w}}_{(4.3)}$$

Keeping only the first mode of an expansion of the displacement as $w(x,t) = \sum_{1}^{\infty} X_p(t) \Phi_p(x)$ (where Φ_p are the non-dimensional *linear* modes for clamped-free beams) and using a classical multiple scales method [83], the amplitude *a* and phase γ of the oscillation of the trailing edge can be obtained (figure 10*a*,*b*).

The main observations are the following: (i) the amplitude of the response increases rapidly with frequency, which is readily explained by the inertial forcing to the system (last term in equation (4.1)), until it saturates because of the geometric limitation imposed by the finite chord length of the wing. Measurements in air and vacuum are approximately the same, proving that solid inertia is the main bending factor [82,107]. (ii) No clear resonance is observed around $\bar{\omega}_{\rm f} = 1$ at these large-amplitude oscillations-only a barely visible peak is observable when testing a lower flapping amplitude as shown in the insert in figure 10b. A slight but rather broad peak can nonetheless be observed in the nearness of $\omega_0/3$ in the amplitude curve, which can be explained as a superharmonic resonance consequence of the cubic nonlinearities in equation (4.1) [83]. (iii) Concerning the phase γ , the results in figure 10c recover the trend of what has been reported previously in the literature [108–111]: $|\gamma|$ increases monotonically with the forcing frequency $\bar{\omega}_{\rm f}$. A remarkable point is that, contrary to what we have noted for the amplitude *a*, there is a large difference in the evolution of the phase γ between the case in vacuum and that in air at atmospheric pressure. It is clearly observed that γ decreases more slowly in the low-density environment. From the beam model point of view, this shows that the quadratic damping term due to aerodynamic drag is responsible for the rapid phase lag observed when increasing the flapping frequency. Now, considering together the performance peak in the aerodynamic power —marked as a grey band in figure 10a,b—and the corresponding increasing phase lag, supports the idea of a more favourable repartition of the aerodynamic forces by the bent wing shown in figure 10a. Indeed, as γ increases the wing experiences larger bending at the maximal flapping velocity where the beneficial effect of bending the wing is most useful.

5. Conclusion

After recalling briefly the basic concepts of hydrodynamic drag, we have discussed the specificities that arise when applying them to the problems of animal locomotion in the inertial regime. Firstly, we have considered a global point of view, where the different types of drag that oppose the propulsive effort of an animal have been identified. Although this is an old question, we have seen that recent analyses have clarified a few delicate points, such as the changes in skin friction due to the deformations of an undulating body or the important role of stream-wise vortices. Secondly, we have discussed the role of drag from a *local* point of view: on the one hand, we have used the case of slender undulatory swimmers to describe the crucial role of drag in the force production balance along the body of an animal with a prescribed kinematics; on the other hand, we have discussed the fluid-structure interaction problem that arises when considering a passive body or appendage with localized actuation.

Summarizing, we have seen above that lateral drag is essential in the force balance that governs the deformation dynamics of elongated undulatory swimmers. Although resistive force production has been computed since the pioneering work of Taylor [71] for the case of slender undulating animals, when discussing inertial swimmers, the estimation of thrust is usually described using Lighthill's elongated-body theory [69], which considers reactive forces. Some models have included both reactive and resistive contributions in the force balance at a cross-section in the elongated-body limit [47,62], but it is only recently that a quantitative assessment of the relative role of the resistive/ reactive forces as a function of kinematics and morphology of a model swimmer has been performed [68]. This resistive force can be as large as, or even larger than, the reactive force usually computed using Lighthill's elongated body theory, and is needed to obtain a correct description of the fluid-structure interaction problem of undulatory swimming [93]. Physically, the quadratic drag that resists the lateral motion of a cross-section of an elongated swimmer comes from the strong separations at the edges of the undulating body (figure 4). How this lateral drag force can produce unexpected thrust has been pointed out recently in the case of fish larvae that exploit edge vortices along their dorsal and ventral fins folds to propel themselves [70]. Hydrodynamic thrust generation and power consumption in future bioinspired undulatory swimmers will thus be the outcome of a strongly coupled fluid-structure interaction problem where local dissipation is a key issue. Moreover, the mechanisms that we have described will also be at play when considering actively enforced body kinematics, such as the case of robotic piezoelectric fins [112]; and other passive systems like bioinspired underwater canopies [113] that can be modelled as assemblies of reconfigurable elastic beams [114].

In the last part of the paper, we have considered the case of elastic insect-inspired wings. We have pointed out that through a phase lag mechanism, local dissipation is behind the performance of flapping flyers with flexible wings. Again, a mechanism that can be pivotal for the design of efficient insect-inspired micro-air-vehicles. Open questions remain in this matter, concerning in particular the way in which the dissipation by local drag that we have discussed here enters problems with more complex kinematics. Problems with full three-dimensional deformation and torsional actuation are obvious leads to be explored, and the challenges are especially significant where elastic phenomena are linked to fluid dynamical transient regimes such as, for example, the onset of hydrodynamic instabilities.

We can give consideration to the biological implications of the physical mechanisms that we have reviewed here: natural selection may not just act to increase locomotion efficiency via drag-reducing morphologies, but also rely on more subtle potentially beneficial aspects of local drag. Certainly, as we have shown, local drag is at the base of several fundamental aspects of biolocomotion, such as the alternative thrust production mechanisms for a large range of inertial swimmers, or the establishment of the undulatory kinematics in swimmers and the phase dynamics in flapping wings through passive elastic responses.

Data accessibility. All the source data presented in this review have been previously published.

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¹In the range of parameters of the experiment: $\tilde{m} \approx 1$, $\tilde{U} \approx [0.2-4]$

and $\tilde{\alpha} \approx [50-150]$. Equation (4.2) is solved numerically using the

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Endnote

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