Optimal Strouhal number for swimming animals

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Abstract

To evaluate the swimming performances of aquatic animals, an important dimensionless quantity is the Strouhal number, St = fA/U, with *f* the tail-beat frequency, *A* the peak-to-peak tail amplitude, and *U* the swimming velocity. Experiments with flapping foils have exhibited maximum propulsive efficiency in the interval 0.25 < St < 0.35 and it has been argued that animals likely evolved to swim in the same narrow interval. Using Lighthill's elongated-body theory to address undulatory propulsion, it is demonstrated here that the optimal Strouhal number increases from 0.15 to 0.8 for animals spanning from the largest cetaceans to the smallest tadpoles. To assess the validity of this model, the swimming kinematics of 53 different species of aquatic animals have been compiled from the literature and it shows that their Strouhal numbers are consistently near the predicted optimum.

Keywords: Swimming, Strouhal number, Constrained optimisation, Potential flow theory

1. Introduction

1.1. Strouhal number

Lord Rayleigh (1915) was the first to define the Strouhal (1878) number, St, to quantify in a proper dimensionless fashion the frequency of vortex shedding behind a bluff body. A decade later, this definition was eventually changed by Bénard (1926) to be the inverse of Rayleigh's suggestion: St = fd/U, where f is the frequency, d is the diameter of the bluff body and U is the flow velocity.

The Strouhal number is intimately linked to the arrangements of vortices in the wake as already pointed out by Rayleigh (1915). Von Kármán (1911) showed that two infinite rows of point vortices are always unstable unless their spacing ratio has a particular value b/a = 0.281 (see Fig. 1*a*). Assuming that the vortices in the wake travel at the velocity $U_w < U$, the vortex shedding frequency is then $f = U_w/a$ and the Strouhal number is linked to the spacing ratio through St = $(b/a)(d/b)(U_w/U)$. The Strouhal number can therefore be predicted based on estimation of the spreading factor b/d and the velocity ratio U_w/U (Roshko, 1954).

A more modern approach to predict the Strouhal number consists in analysing the local stability properties of the wake, a method reviewed by Huerre and Monkewitz (1990). To do so, a base flow is considered which can either be a steady solution of the Navier–Stokes equations around the bluff body or the time-average flow obtained through experiments or numerical simulations. Pier (2002) has shown that, in the near wake of this base flow, a transition from convective to absolute instability occurs. This region acts as a source generating disturbances advected and amplified downstream and tunes the entire wake to its frequency, thus selecting the Strouhal number.

In the context of swimming, the Strouhal number has been introduced in the nineties by Triantafyllou et al. (1991, 1993) with two innovative papers (see also some recent reviews on swimming: Sfakiotakis et al., 1999; Triantafyllou et al., 2000; Lauder and Tytell, 2005). It is defined as

$$St = \frac{fA}{U},$$
(1)

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Figure 1: Schematic view of the (*a*) Bénard-von Kármán (BvK) vortex street behind a circular cylinder and (*b*) reverse Bénard-von Kármán (rBvK) vortex street behind a swimming fish. The lines in the wakes illustrate what can be obtained typically with dye visualisations. The average perturbation flow u(y) in the far wake is a jet toward the cylinder (*c*) and away from the fish (*d*) respectively. Both of these jets are surrounded by a region of counterflow.

where f is the tail-beat frequency, A is the peak-to-peak amplitude at the tail tip and U is the average swimming speed. The argument of Triantafyllou et al. (1993, 1991) relies on the observation that the wake behind a swimming animal resembles the Bénard-von Kármán (BvK) vortex street observed behind bluff bodies except that the sign of vortices are inverted giving a reverse Bénard-von Kármán (rBvK) street (see Fig. 1*b*).

In the BvK street, the average flow exhibits a deficit of velocity compared to the imposed flow U, indicating that longitudinal momentum has been lost and that a drag force is exerted on the bluff body (Fig. 1c). However, swimming animals are self-propelled and therefore no net drag nor thrust is exerted on average when they swim at constant speed: the resulting rBvK wake is therefore momentumless and exhibits on average a jet around the centerline surrounded by a region of counterflow (Fig. 1d).

Applying similar techniques to the ones used to study the stability of bluff body wakes, Triantafyllou et al. (1991, 1993) have shown that wakes associated to net thrust are only convectively unstable (there is no region of absolute instability). Such wakes acts as amplifier in a narrow range of frequencies which was found to correspond to the interval 0.25 < St < 0.35, for a family of two-dimensional wakes obtained by fitting the experimental results of Koochesfahani (1989). They argued that swimming animals likely evolved to exploit this amplification to reduce the swimming costs and hence should be observed to swim in the same narrow interval of Strouhal numbers. In parallel, experiments have been carried out by the same group (Triantafyllou et al., 1993; Anderson et al., 1998; Read et al., 2003; Schouveiler et al., 2005) with rigid airfoils submitted to harmonic flapping, confirming that maximum efficiency could be reached in the same interval.

In their papers, Triantafyllou et al. (1991, 1993) analysed twelve species (dolphins, sharks, some scombroids and other bony fishes) whose swimming kinematics were found in the literature and concluded that most of these swimming animals indeed swim in the interval 0.25 < St < 0.35. More recently, Taylor et al. (2003) have shown that birds, bats and insects in cruising flight flap their wings within a similar narrow range of Strouhal number, 0.2 < St < 0.4. In contrast with this apparent universal range, it has been observed (with no physical explanation) that the Strouhal number decreases as a fish swim faster (Fig. 11.3B in Lauder and Tytell, 2005) or as different species of larger size are considered (Kayan et al., 1978).

In this work, an optimal Strouhal number will be calculated for swimming animals without explicit reference to the stability or the dynamics of their wakes. First, Lighthill's large-amplitude elongated-body theory will be introduced and discussed. In section 2 the optimal motion of the animal tails will be calculated by solving a constrained minimisation problem. In section 3, the predicted optimal Strouhal number will be compared to the observations on different species of swimming animals found in the literature. Finally, these results will be discussed in section 4.

1.2. Lighthill's elongated-body theory

Consider an aquatic animal of length L performing undulatory propulsion with constant mean velocity U in the x-direction (see Fig. 2). The position of its body at time t is described by the position (x, y) of any point of the



Figure 2: (a) Dimensions considered for the swimming animals and (b) sketch of the problem.

backbone. The plane *Oxy* would be the horizontal plane for fishes and the vertical plane for cetaceans. Defining the curvilinear coordinate *s* as the distance from the tail tip, the functions x(s, t) and y(s, t) fully describe the kinematics of swimming. The velocity of any point on the backbone is the time-derivative of the position, $\mathbf{v} = (\dot{x}, \dot{y})$, which can be decomposed into tangential and normal velocities (see Fig. 2)

$$u = \dot{x}x' + \dot{y}y', \tag{2a}$$

$$w = \dot{y}x' - \dot{x}y', \tag{2b}$$

where the primes and dots denote differentiation with respect to s and t respectively.

Elongated-body theory makes use of the small aspect ratio of the swimming animal. When $h \ll L$, the forces acting on each cross section can be assumed to be the same as those acting on an infinite cylinder with same cross section and moving with the same velocity (u, w), even if Candelier et al. (2011) have shown that, for motions of large amplitude, this is not strictly true. The main idea behind Lighthill's elongated-body theory (Lighthill, 1971) is then to treat perpendicular motions (given by the velocity w) reactively and the tangential motions (given by u) resistively. The elongated-body approximation is therefore valid if the animal is elongated enough such that $h \ll L$, if the cross section varies smoothly along the backbone, and if the Reynolds number, defined as

$$Re = UL/\nu, (3)$$

with v the kinematic viscosity, is asymptotically large (more discussion on the validity of this theoretical framework will be given below).

The origin of the reactive force is the conservation of momentum. It can be understood if one realises that, as the animal swims, a certain volume of water has to be accelerated. This means that a certain force has to be applied to the water and reactively, the opposite force applies to the animal. The reactive force has been calculated by Lighthill (1971) and its remarkable feature is that its time-average depends only on the motion of the tail. Thus the motion of the rest of the body does not need to be known. The same holds true for the kinetic energy given to the fluid per unit time which is the only source of power loss in the elongated-body approximation.

Following Lighthill (1971), the mean thrust $\langle T \rangle$ (which is the reactive force on the animal projected on the *x*-direction) and the power lost in the wake $\langle E \rangle$ are given by

$$\langle T \rangle = \langle m \left[w \left(\dot{y} - \frac{1}{2} w x' \right) \right]_{z=0} \rangle, \tag{4a}$$

$$\langle E \rangle = \langle \frac{1}{2}m \left[w^2 u \right]_{s=0} \rangle, \tag{4b}$$

where the chevrons denote time-average, $m = \rho \pi h^2/4$ is the added mass per unit length at the tail tip (at s = 0) and ρ is the density of water.

In the case of steady swimming, the thrust has to compensate the drag D on average such that $\langle T \rangle = D$. Hence, the role of viscosity being limited to setting the drag, the only relevant parameters are the added mass at the tail tip m, the swimming velocity U and the drag D. Out of these three parameters, a unique dimensionless quantity can be constructed which measures the ratio between the drag D and the typical thrust mU^2 . This new dimensionless number will be called the Lighthill number in the following

$$\mathrm{Li} = \frac{\pi D}{2mU^2} = \frac{S}{h^2}C_d,\tag{5}$$

where S is the total surface of the animal (or wetted surface) and C_d is the drag coefficient such that $D = \frac{1}{2}\rho U^2 S C_d$.

Another way to introduce the Lighthill number would be to make the problem dimensionless by using L and U as characteristic length and velocity respectively. The dimensionless form of the equation $\langle T \rangle = D$ would then be

$$\langle \left[w^* \left(\dot{y}^* - \frac{1}{2} w^* x^{*'} \right) \right]_{s^* = 0} \rangle = \frac{D}{mU^2} = \frac{2}{\pi} \text{Li},$$
 (6)

where $x^* = x/L$, $y^* = y/L$, $s^* = s/L$, $w^* = w/U$, $t^* = tU/L$ are all dimensionless quantities. In (6), it is clear that the only relevant parameter to the present problem is Li which gathers informations on the geometry of the swimming animal (through the ratio S/h^2) and on the Reynolds number (through the drag coefficient C_d). The optimal motion of the tail will thus be a function of Li alone, as it will be shown below. This has to be contrasted with bluff body wakes where the Strouhal number is a function of Re, as it has been shown by Rayleigh (1915).

2. Optimisation

2.1. Constrained optimisation problem

Consider now that the incident angle (i.e. the angle between the tail and the swimming direction) is given in the vicinity of the tail tip by the harmonic function

$$\theta(s,t) = \theta_0 \cos\left(\omega t\right), \quad \text{for } s \ll 1. \tag{7}$$

Here the curvature θ' has been assumed to be zero at s = 0 as it should be the case if one assumes that the tail is elastic and that the internal torque at the tail tip is zero. Taking the cosine and sine of θ yields x' and y', which appear as infinite sums of even and odd harmonics respectively (formulas 9.1.44–45 in Abramowitz and Stegun, 1965)

$$[x']_{s=0} = \cos \theta = J_0(\theta_0) - 2J_2(\theta_0)\cos(2\omega t) + \cdots,$$
(8a)

$$[y']_{s=0} = \sin \theta = 2J_1(\theta_0) \cos(\omega t) + \cdots,$$
(8b)

where $J_{v}(x)$ is the Bessel function of the first kind. The higher harmonics will be neglected in the following owing to the fact that they have a negligible influence on the final result.

To calculate the tangential and normal velocities given by (2a,b), the functions \dot{x} and \dot{y} need to be known at the tail. Keeping the same harmonics as in (8a,b), the general form of these functions is

$$[\dot{x}]_{s=0} = U + \alpha U \cos(2\omega t + \phi), \qquad (9a)$$

$$[\dot{y}]_{s=0} = \pi \operatorname{St} U \cos(\omega t + \psi), \tag{9b}$$

where ϕ and ψ are unknown phases, α is a dimensionless amplitude and St is the Strouhal number given by (1).

Inserting (2a,b), (8a,b) and (9a,b) into (4a,b) and calculating the time-averages allows to express the mean thrust $\langle T \rangle$ and the mean power loss $\langle E \rangle$ as a function of the five dimensionless variables: θ_0 , St, α , ϕ and ψ . The constrained optimisation problem then consists in finding

$$\min \langle E \rangle \quad \text{such that} \quad \begin{cases} \langle T \rangle = D, \\ 0 \le (\operatorname{St}, \alpha) < \infty, \\ 0 \le \theta_0 \le \pi/2, \\ 0 \le (\phi, \psi) < 2\pi. \end{cases}$$
(10)

This problem has been solved for 100 different values of the Lighthill number in the interval 0.01 < Li < 1 using the function fmincon in MATLAB (The MathWorks, Inc., Natick, MA, USA). The results are a predicted optimal Strouhal number St(Li) and optimal angle θ_0 (Li) which are both monotonically increasing functions of Li (see Figs. 4–5 below). This optimisation also shows that, for any value of the Lighthill number, the optimal set of dimensionless variables is always such that $\alpha = \psi = 0$. The functions \dot{x} and \dot{y} can thus be written in a simpler form for the optimal cases

$$[\dot{x}]_{s=0} = U, (11a)$$

$$[\dot{y}]_{s=0} = V[y']_{s=0}, \qquad (11b)$$



Figure 3: Froude efficiency as a function of the Lighthill number for the optimal case (solid line) and for the acceptable range (dashed line).

where V appears as a wave speed at the tail tip and is given by identifying (11b) with (8b) and (9b) when $\psi = 0$

$$V = \frac{\pi \mathrm{St}}{2J_1(\theta_0)} U. \tag{12}$$

The wave speed V is always greater than the swimming speed U and the ratio U/V is customarily called the slip ratio.

The fact that \dot{y} and y' are in phase in the optimal case (i.e. $\psi = 0$) could have been anticipated since the same holds true in the linear limit, as shown by Lighthill (1970). The relations (11a,b) mean that a simpler version of the optimisation can be performed with only two variables, θ_0 and St (or St and U/V alternatively), leading to the same results. Note also that since \dot{x} does not depend on time, the path followed by the tail tip in the frame of reference attached to the animal is a straight line in the y-direction. In other words, the figure of eight observed in some experiments (Gray, 1933; Webber et al., 2001) which exists only if $\alpha \neq 0$ is not optimal within the present elongated-body framework.

To estimate the range on which the Strouhal number can change without affecting appreciably the swimming performances, the Froude efficiency η is introduced

$$\eta = \frac{DU}{DU + \langle E \rangle},\tag{13}$$

which expresses the ratio between the average useful power $\langle TU \rangle = DU$ and the total power spent for swimming. For a given Lighthill number, the constrained optimisation yields a maximum efficiency $\eta_{max}(Li)$. In the following, any Strouhal number leading to an efficiency greater than $\eta_{max} - 0.1$ will be considered as acceptable (Fig. 3).

2.2. Limit of validity

Elongated-body theory is inviscid in nature. As a results, all the viscous effects (i.e. the resistive forces) are gathered into a single drag force D, which is usually not modeled. In fact, it is still a controversial issue today to know whether this drag force is enhanced or reduced by the swimming motion (Barrett et al., 1999; Anderson et al., 2001). It has even been argued that the very idea of separating thrust and drag is impossible because they balance each other on average during steady swimming (Schultz and Webb, 2002; Fish and Lauder, 2006; Shirgaonkar et al., 2009). However, this argument can be disputed: skin friction drag, which is the main source of drag for streamlined bodies, can always be defined, if not measured. Lighthill (1971), quoting discussions with Bone, proposed what is sometimes called the 'Bone–Lighthill boundary-layer thinning hypothesis': they suggested that the boundary layer may be 'compressed' or 'thinned' by the body motion, resulting in larger velocity gradients and thus enhanced skin friction. Although this effect was evidenced by Anderson et al. (2001) by measuring boundary layer velocity profiles

on swimming fish, the Bone–Lighthill hypothesis remains to be tested and quantified. Therefore, to compare the present optimisation calculation (for which a model for D is not needed) with measurements on aquatic animals, the drag force D will have to be estimated with an empirical formulation, as explained below.

Another key hypothesis of elongated-body theory is that the resistive forces corresponding to perpendicular motions can be neglected. Assuming that this force acts on the whole length L and that its drag coefficient is of order one (as it is the case for a cylinder), its x-projection scales as

$$F_{\text{resistive}} \sim \rho h w^2 L y',$$
 (14)

and has to be negligible in comparison with the reactive force which scales as

$$F_{\text{reactive}} \sim mw\dot{y}.$$
 (15)

This is true if $(Lw)/(hV) \ll 1$ and since $w \sim U(1 - U/V)$ St, this corresponds to

$$\frac{U}{V}\left(1-\frac{U}{V}\right)St \ll \frac{h}{L}.$$
(16)

This condition will be fulfilled for most animals with a fairly wide tail. However, elongated fishes such as eels and lampreys, for which h/L < 0.1, will not in general meet this criterion. For these animals, a model taking into account the resistive normal force would be necessary. This may seem counterintuitive, but it means that Lighthill's elongated-body theory (Lighthill, 1971) is not valid when the body is too elongated.

The last assumption behind elongated-body theory is that the animal cross section varies on a typical length scale larger than h. This is not true for scombrids, dolphins and sharks that share a large aspect-ratio tail. For these animals, a two-dimensional approach would be more suited to study the propulsive performance of the tail. However, the existing two-dimensional models (Lighthill, 1970; Wu, 1971) are linear and do not allow the same sort of optimisation calculation as the one presented here.

It can be difficult to assess the validity of Lighthill's elongated-body theory because there has not been any fair comparison with numerical results so far. The recent paper by Candelier et al. (2011) is one notable exception in which they ran numerical simulations for an eel-like swimmer with aspect ratio h/L = 0.1, slip ratio U/V = 0.4, Reynolds number Re = 6×10^5 , and for two different Strouhal numbers St = 0.2 and 0.8. In the first case (St = 0.2), the validity condition (16) is fairly satisfied (the left-hand side being equal to 0.048) and the thrust is well approximated by Lighthill's elongated-body theory. In the second case (St = 0.8), the condition (16) is not satisfied and viscous forces play a significant role in the thrust. Note that, in these simulations, the swimmers are not self-propelled and more numerical results are clearly needed to assess the validity of Lighthill's elongated-body theory, in particular for larger aspect ratio ($h/L \approx 0.2$).

3. Comparison with aquatic animals

To assess the validity and the interest of the present theoretical results, the swimming kinematics of various species of aquatic animals have been compiled. Comparing these experiments and the model relies on the implicit assumption that aquatic animals swim optimally or, equivalently, that that their Froude efficiencies are maximised. This assumption is far from being obvious and one could argue that some species have evolved in ecological niches where economical steady swimming is not crucial. One could also remark that Froude efficiency is only a part of the full picture: the complete energy cost should take into account the efficiency of muscles (which depends critically on frequency and amplitude) and the losses due to the viscoelasticity of soft tissues or damping at the intervertebral joints (Cheng et al., 1998; Long, 1992; Long et al., 2002; McMillen and Holmes, 2006).

3.1. Preliminary remarks on experimental studies

The comparison with aquatic animals has to cope with several limitations of the experimental methods, some of which are listed below.

1. The measurements should be made when the animal is swimming steadily. Any small positive or negative acceleration can alter the results because the mean thrust is no longer equal to the drag in that case (Videler and Hess, 1984).

- 2. The drag on swimming animals has been recognised to be difficult to measure adequately (Anderson et al., 2001; Fish and Rohr, 1999; Wu, 2011). It usually depends on the swimming velocity (Videler, 1981) and can be greatly increased when the animal is close to the water surface (Videler, 1993).
- 3. In most experimental works cited here, the Strouhal number have not been calculated directly by the authors. It results that St had to be calculated using the average tail amplitude $\langle A \rangle$, the average frequency $\langle f \rangle$ and the average swimming velocity $\langle U \rangle$. When the quantities vary over large intervals, it can result in non negligible errors since the mean of a product is usually not equal to the product of the means. The same holds true for the Lighthill number.
- 4. Most kinematics studies have been performed in water channels (also called flumes or tunnels) where the animals swim against the current imposed by the experimentalist. The presence of walls close to the animal and the turbulence rate can affect the swimming mode as it has been shown by Webb (1993). This effect can be particularly large when the experiments are performed in respirometers where the volume of the test section has to be small enough to allow correct measurements of the variation of oxygen concentration.
- 5. The wave speed V usually depends on the curvilinear coordinate and it can be shown to either accelerate toward to tail tip (Gillis, 1997) or decelerate (Videler and Hess, 1984). This wave speed can also be calculated through the apparent wavelength λ of the animal deflection as $V = \lambda f$, but this method usually gives a result different from the direct measurement (Webb et al., 1984). These differences come from the fact that the wave speed is non local in nature: contrarily to the Strouhal number and the maximum angle it does not only depend on measurements made at the tail tip.

The limitations of the experimental studies listed above make the comparison with the present analysis difficult. In particular, the Lighthill number can only be estimated in most cases (if not because of the lack of geometrical measurements, because of the drag coefficient). The other important point is that the optimality of swimming can never be guaranteed.

3.2. Methods

Despite the limitations listed above, most of the data available in the literature on swimming kinematics of aquatic animals have been compiled. From these sources, the Lighthill and the Strouhal numbers have been determined together with the maximum angle at the tail tip and the slip ratio U/V when possible. The following methods have been used to extract the experimental data.

When it was possible, the value chosen for the swimming velocity was 75% of the critical velocity U_{crit} . The critical velocity, as introduced by Brett (1964), measures the maximum sustained speed for a given time (between 2 and 30 minutes depending on the authors and on the species). The reason to choose this particular value of the velocity is that it allows a large enough swimming speed (for lower speed, the swimming mode may not be optimal) without being too close to the critical value where data is usually lacking. Note that, in most studies, U_{crit} has not been measured, and that this somewhat arbitrary choice of 75% of the critical velocity does not qualitatively influence the results.

To evaluate the tail span of a given species, the following rules have been used. When available, the data found in the source papers have been used. Otherwise, pictures have been collected on Internet and used to estimate the ratio of tail span to body length. For species with no marked tail (such as eels, leeches, or crocodiles), the maximum value of the animal span in its posterior half have been taken in place of the tail span. To estimate the wetted surface of each species, rough estimates have been used because this data was rarely given in the source papers.

As discussed above, measuring the drag on swimming fishes, and even defining it, is a difficult task and the data found in the literature are not always consistent. An estimate is however needed if one wants to use Lighthill's elongated-body theory. A simple way to estimate the drag coefficient, which compares reasonably well with some of the available data (Lighthill, 1971; Videler, 1981; Webb et al., 1984; Fish and Rohr, 1999; Anderson et al., 2001), is to take the double of the drag coefficient for a flat plate in laminar flow for small Reynolds number, and the turbulent drag coefficient of a flat plate for larger Reynolds number. The drag coefficient is then

$$C_d(\text{Re}) = \max\left(2 \times 1.328 \,\text{Re}^{-1/2}, 0.072 \,\text{Re}^{-1/5}\right).$$
 (17)

The above relationship is usually an underestimate of the drag coefficient, particularly for animals with relatively poor streamlining. The relation (17) has been used to calculate the drag coefficient for all animals except some mammals

Species	I(cm)	S/h^2	Re	Li	St	U/V	A. (deg)
Species		5/1	Ke		51	0/1	00 (ucg)
Mammals							
Beluga ^a	364	7.3	8.0×10^{6}	0.145	0.35	0.48	31
Bottlenose dolphin ^{<i>a</i>}	258	7.9	1.2×10^{7}	0.063	0.26	0.52	25
False killer whale ^a	379	7.8	2.1×10^{7}	0.044	0.26	0.57	28
Florida manatee ^b	334	7.5	4.4×10^{6}	0.025	0.31	0.66	
Harp seal ^c	153	7.7	1.6×10^{6}	0.123	0.27	0.45	22
Killer whale ^{<i>a</i>}	473	7.3	2.6×10^{7}	0.015	0.28	0.56	29
Ringed seal ^c	106	8.7	1.3×10^{6}	0.105	0.30	0.44	24
White-sided dolphin ^a	221	6.5	1.3×10^7	0.018	0.24		
Sharks							
Blacktip reef shark ^d	97	7.6	8.3×10^{5}	0.036	0.25	0.66	
Bonnethead shark ^d	93	5.5	8.0×10^{5}	0.026	0.27	0.74	
Nurse shark ^d	220	17.8	1.8×10^{6}	0.072	0.41		
Scalloped hammerhead ^{e*}	59	4.9	3.8×10^5	0.027	0.37		
Scombrids							
Atlantic mackerel ^f	32	6.7	5.8×10^{5}	0.034	0.25	0.73	
Chub mackerel ^g	21	10.5	1.6×10^{5}	0.070	0.25		
Chub mackerel ^{<i>h</i>*}	21	10.5	1.8×10^{5}	0.067	0.26	0.63	
Giant bluefin tuna ^{<i>i</i>}	250	4.8	5.7×10^{6}	0.015	0.24		
Kawakawa tuna ^h *	21	5.0	1.8×10^{5}	0.032	0.21	0.60	
Pacific bonito ^{<i>j</i>}	47	6.2	4.5×10^{5}	0.033	0.23		
Skipjack tuna ^k	57	5.8	2.2×10^{6}	0.022	0.27		
Yellowfin tuna ^{l}	53	5.5	6.1×10^{5}	0.028	0.29	0.48	

Table 1: Swimming kinematics for 53 different species of mammals, fish, amphibians and reptiles (continued in Tables 2,3). The different columns are: the animal length, L; the surface ratio, S/h^2 ; the Reynolds number, Re; the Lighthill number, Li; the Strouhal number, St, the slip ratio, U/V; and the maximum incident angle at the tail tip, θ_0 . The superscript '*' marks the juvenile animals and the superscripts < and > indicate the minimum and maximum values of the continuous dataset on the raibow trout (Webb et al., 1984). Sources: *a*: Fish (1998); Fish and Rohr (1999); Rohr and Fish (2004), *b*: Kojeszewski and Fish (2007), *c*: Fish et al. (1988), *d*: Webb and Keyes (1982), *e*: Lowe (1996), *f*: Videler and Hess (1984), *g*: Dickson et al. (2002), *h*: Donley and Dickson (2000), *i*: Wardle et al. (1989), *j*: Dowis et al. (2003), *k*: Yuen (1966), *l*: Dewar and Graham (1994).

(beluga, bottlenose dolphin, false killer whale, harp seals, killer whale and ringed seals) for which the authors provided a drag coefficient corrected for surface effects (Fish, 1998; Fish et al., 1988). For the different morphotypes of goldfish studied by Blake et al. (2009), the drag coefficient has also been calculated from the data fit given by the authors because these morphotypes have been selected artificially for aesthetic reasons, and as a result have a relatively large drag.

From the literature, 89 different swimming kinematics have been identified. After analysis, 23 of these data have been discarded, either because better data were available for the same or a similar species, because the quality of the data was doubtful (when it was based on a single experiment, for instance) or because the validity of elongated-body theory as defined by equation (16) was not ensured (this is mainly why there is no snake and no larva in the data set). The remaining 66 data represents 53 different species which have been divided in 7 different groups (Tables 1–3): 8 different species of mammals, 4 of sharks, 8 of scombrids (a family which includes tunas, bonitos and mackerels), 11 of fishes from the order of Perciformes and Salmoniformes (excluding the family of scombrids), 19 of fishes from other families (including Cypriniformes, Gadiformes and Mugiliformes), 10 of 'elongated' fishes (including eels, needlefish of the family of Belonidae, and other fishes with surface ratio S/h^2 greater than 17) and 6 species categorised as 'others' gathering one reptile (crocodile), two frog tadpoles, two amphibians (axolotl and siren) and one annelid (leech).

Species	$L(\mathrm{cm})$	S/h^2	Re	Li	St	U/V	θ_0 (deg)
Perci/salmoni-formes							
Atlantic salmon ^a	66	6.7	3.7×10^{5}	0.037	0.26	0.63	
Bluefish ^b	42	5.3	5.0×10^{5}	0.028	0.33		
Lake trout ^b	21	5.4	2.0×10^{5}	0.034	0.33		
Largemouth bass ^c	24.5	6.4	1.2×10^{5}	0.050	0.23	0.68	44
Pacific jack mackerel ^d	27	5.7	5.0×10^{5}	0.030	0.31		
Rainbow trout ^{e*<}	5.5	8.8	1.6×10^4	0.184	0.38	0.57	
Rainbow trout ^{e>}	56	9.0	2.5×10^{5}	0.054	0.25	0.71	
Rainbow trout ^f	20.1	8.2	1.1×10^{5}	0.067	0.26	0.75	47
Sockeye salmon ^g	20.4	10.4	8.0×10^{4}	0.097	0.31	0.60	
Yellowbelly rockcod ^{h*}	7.6	22.2	2.3×10^{4}	0.385	0.38		
Yellowbelly rockcod ^h	29	10.5	2.2×10^5	0.065	0.30		
Other fishes							
Atlantic cod ⁱ	25	16.4	1.2×10^{5}	0.124	0.30	0.62	
Atlantic cod ^j	63	10.6	3.1×10^{5}	0.061	0.28		
Atlantic cod^k	49	10.6	3.7×10^{5}	0.059	0.25	0.75	
Atlantic silverside ^l	7.5	10.9	1.7×10^{4}	0.224	0.27		
Common bream ^m	19	3.4	8.5×10^{4}	0.031	0.29	0.76	
Common dace ⁿ	17.5	4.9	3.5×10^{5}	0.027	0.29		
Goldfish (Eggfish) ^o	5.3	10.6	7.1×10^{3}	0.538	0.54	0.41	
Goldfish (Fantail) ^o	5.7	10.4	7.7×10^{3}	0.512	0.47	0.53	
Goldfish (Common) ^o	5.1	4.7	2.1×10^4	0.093	0.40	0.80	
Goldfish (Comet) ^o	5.7	3.9	2.3×10^4	0.067	0.44	0.58	
Goldfish ⁿ	18.8	4.3	1.5×10^{5}	0.030	0.30		
Lake sturgeon ^p	15.7	12.8	4.1×10^{4}	0.168	0.48	0.65	46
Mullet ^b	27	9.6	3.0×10^{5}	0.056	0.33		
Saithe ^q	36.4	7.0	3.9×10^{5}	0.038	0.23	0.76	
Thinlip grey mullet ^a	36	7.7	3.8×10^{5}	0.042	0.23	0.76	
Thicklip grey mullet ^{r*}	12.6	6.4	2.3×10^{4}	0.113	0.34	0.70	31
Tiger musky ^f	18.3	9.4	9.6×10^4	0.081	0.25	0.60	50
West African lungfish ^s	55	14.6	7.0×10^3	0.463	1.02		
West African lungfish ^s	55	14.6	6.0×10^4	0.158	0.75		

Table 2: Same as Table 1. Sources: *a*: Videler (1993), *b*: Kayan et al. (1978), *c*: Jayne and Lauder (1995), *d*: Hunter and Zweifel (1971), *e*: Webb et al. (1984), *f*: Webb (1988), *g*: Webb (1973), *h*: Archer and Johnston (1989), *i*: Webb (2002), *j*: Webber et al. (2001), *k*: Videler (1993); Videler and Wardle (1978), *l*: Parrish and Kroen (1988), *m*: Bainbridge (1963), *n*: Bainbridge (1958), *o*: Blake et al. (2009), *p*: Webb (1986), *q*: Hess and Videler (1984), *r*: Müller et al. (2002), *s*: Horner and Jayne (2008).

Species	$L(\mathrm{cm})$	S/h^2	Re	Li	St	U/V	θ_0 (deg)
Elongated							
Atlantic needlefish ^{<i>a</i>}	23	21.7	1.2×10^{5}	0.167	0.34	0.69	
American eel^b	21	25.8	6.0×10^{4}	0.280	0.31	0.73	
American eel ^c	36	25.8	1.3×10^{5}	0.192	0.37	0.79	
European eel^d	22	27.9	4.0×10^{4}	0.369	0.48	0.60	
European eel^e	73	27.9	2.5×10^{5}	0.167	0.52		
Garfish ^f	44	18.0	4.0×10^{5}	0.098	0.34		
Great sand-eel ^g	30	19.2	1.2×10^{5}	0.148	0.31	0.67	
Hagfish ^h	31	33.2	6.4×10^{4}	0.347	0.56	0.49	
Lesser sand-eel ^g	9.0	16.4	2.2×10^{4}	0.296	0.41	0.64	
Longnose gar ⁱ	57	21.9	3.3×10^5	0.125	0.59	0.67	
Others							
Axolotl ^j	17.7	19.2	4.4×10^{4}	0.242	0.57	0.59	
Bullfrog tadpole ^{k*}	4.7	11.0	2.3×10^{4}	0.193	0.79	0.58	
Green frog tadpole ^{k*}	5.0	10.6	2.1×10^{4}	0.195	0.60	0.60	
Lesser siren ^l	34	31.3	1.7×10^{5}	0.202	0.54	0.61	
Medicinal leech ^m	10.0	19.5	1.8×10^{4}	0.384	0.63	0.70	
Saltwater crocodile ⁿ	93	62.5	4.2×10^{5}	0.339	0.78		

Table 3: Same as Table 1. Sources: *a*: Liao (2002), *b*: Tytell and Lauder (2004), *c*: Gillis (1998), *d*: D'Août and Aerts (1999), *e*: Ellerby et al. (2001), *f*: Kayan et al. (1978), *g*: Videler (1993), *h*: Long et al. (2002), *i*: Long et al. (1996), *j*: D'Août and Aerts (1997), *k*: Wassersug and Hoff (1985), *l*: Gillis (1997), *m*: Jordan (1998), *n*: Seebacher et al. (2003).



Figure 4: Strouhal number of 53 different species of aquatic animals as a function of the Lighthill number. These animals are divided in different categories corresponding to the different symbols displayed in the legend. The solid line is the predicted optimal Strouhal number and the dashed line correspond to the interval for which efficiency is larger than $\eta_{max} - 0.1$. The horizontal dotted lines correspond to the interval 0.25 < St < 0.35 suggested by Triantafyllou et al. (1993). The solid line between two triangles corresponds to the continuous results of Webb et al. (1984) on the rainbow trout.



Figure 5: (a) Maximum angle at the tail tip θ_0 and (b) slip ratio U/V as a function of the Lighthill number (same legend as in Fig. 4).

3.3. Results

The Strouhal number, the maximum angle at the tail tip and the slip ratio predicted by the present theoretical model are compared to the observations on the different species in Figs. 4–5. In these figures, the thick line correspond to the optimal case with Froude efficiency η_{max} , and the dashed lines correspond to the 'acceptable' interval for which the Froude efficiency is $\eta > \eta_{\text{max}} - 0.1$, as defined above (Fig. 3).

As seen in Fig. 4, the present analysis predicts that the optimal Strouhal number increases with the Lighthill number from 0.15 for the largest cetaceans to 0.8 for the smallest animals considered (or, more precisely, for animals with the largest Lighthill number). This optimal Strouhal number curve can be approximated by a power law: St \approx 0.75 Li^{1/3}. Although the experimental observations are fairly scattered, this general trend is clearly observable for all the aquatic animals, more than 85% of the data points having a Strouhal number within the acceptable range.

Among these data, the results of Webb et al. (1984) on the rainbow trout stand out. They studied animals with total length ranging from L = 5.5 cm to 56 cm and deduced from hundreds of measurements how the different geometric and kinematic quantities varies with the length and the swimming speed of the trouts. This allows, for a single species, to see how the Strouhal number varies with the Lighthill number (the thin solid line in Fig. 4). Remarkably, this line is parallel (on the log-log scale of Fig. 4) to the the theoretical prediction.

Because equation (17) probably tends to underestimate the drag coefficient, the actual Lighthill number may be larger than the estimates used in Figs. 4–5. For animals with relatively poor streamlining, this increase may be as large as a factor 2 or 3. It means that error bars on Li are rather large and that some data points may have to be shifted to larger values of Li. As for the Strouhal number, the typical range of variation between different animals or between different measurements on the same animal is generally of the order of $\pm 25\%$ which would give a conservative estimate of the error bars on St. It can be argued however that the optimal swimming cases probably correspond to the smallest observed St and thus some data points of Fig. 4 may have to be shifted to smaller values of St.

The comparison between the predicted maximum angle at the tail tip and the experimental observations (Fig. 5*a*) is less conclusive, mostly because of the lack of data and because the acceptable range is fairly large. However, the observations for mammals ($\theta_0 \approx 25 \text{ deg}$) and fishes ($\theta_0 \approx 45 \text{ deg}$) fall within the predicted range.

The predicted slip ratio U/V has also been compared with observations on animals (Fig. 5b). In each group, the slip ratio is decreasing with the Lighthill number, as predicted, but the mammals and the scombrids are clearly below the prediction, while elongated fishes are clearly above. This discrepancy will be discussed below. Another feature of the slip ratio is that the optimal case corresponds to a maximum: for a given Lighthill number, when efficiency is lower than the optimal, so is U/V.

Note that, again, the slip ratio deduced from the results of Webb et al. (1984) on the rainbow trout (the thin solid line in Fig. 5*b*) agrees remarkably well with the present prediction.



Figure 6: Strouhal number as a function of the Reynolds number (same legend as in Fig. 4).

4. Discussion

In this paper, Lighthill's elongated-body theory has been used to predict the optimal Strouhal number for swimming animals. Using the elongated-body assumptions, it appeared that the optimal Strouhal number depends on a single dimensionless quantity, which has been called the Lighthill number, and which can be regarded as the ratio of the animal drag to its typical achievable thrust. Together with the optimal Strouhal number, were predicted the maximum incident angle at the tail tip and the slip ratio, which also depend uniquely on the Lighthill number. These theoretical predictions for optimal motion of the tail tip have been then compared with the swimming kinematics of 53 different species of swimming animals. It appeared that the general trends predicted by the present model are recovered in the zoological data, indicating that animals generally swim near the predicted optimum (Figs. 4–5).

Additionally, the present model elucidates three previous unexplained observations: first, the Strouhal number, St, was shown to be a decreasing function of the animal velocity (Fig. 11.3B in Lauder and Tytell, 2005); then, St was observed to decrease as an animal grows (Webb et al., 1984) and finally, St has been measured to decrease with increasing Reynolds number as different species are considered (Kayan et al., 1978).

In Fig. 6, the Strouhal number has been plotted as a function of the Reynolds number for the same species. A general trend can be identified, showing that St is generally decreasing with Re. This is compatible with the present model, although the aspect ratio of the animal is not taken into account when considering the dependence on Re only. Moreover, there is no physical argument that could explain this dependence on the Reynolds number. Based on analogies with bluff bodies wakes, one could even expect the opposite trend (i.e. St increasing with Re).

The validity of the elongated-body theory is limited by two geometric quantities. First, the variations of the crosssection should occur on typical scales of the order of the animal length. This is clearly not the case for animals with high aspect-ratio tails (also called lunate tails) like cetaceans, scombrids and sharks. For sharks, additional difficulty is caused by the asymmetry of the tail and one could ask whether the Strouhal number should be based on the motion of the largest lobe, the smallest lobe, or some average of the two. Second, the elongated-body theory is not adapted to anguilliform animals like eels for which the tail depth is difficult to define. For these very elongated animals, an additional effect come into play as resistive forces cannot be neglected anymore, as pointed out above. These limitations probably explain why the slip ratio for the cetaceans and the scombrids is approximately 0.2 smaller than predicted while the elongated fishes seem to have a slip ratio larger than predicted.

As noted above, the key feature of Lighthill's elongated-body theory is that the two quantities needed to perform the optimisation, namely the average propulsive thrust and the average power loss in the wake, only depend on local quantities evaluated at the tail tip. This property has been essential in developing the present model, but a natural question would be now to ask whether the predicted optimal tail motions are compatible with the complete kinematics of a swimming animal. In particular, it would be important to evaluate the role of recoil (Webb, 1992), the effect of passive elasticity of the tail and the role of the internal mechanics in general (see Cheng et al., 1998; Long, 1992;



Figure 7: Schematic three-dimensional views of the (a) BvK and (b) rBvK vortex streets, corresponding to the two-dimensional views of Fig. 1.

Long et al., 2002; McMillen and Holmes, 2006, for instance).

Let us now examine the relation between the Strouhal number and the characteristics of the wake. First, it may be important to remind that Lighthill's elongated-body theory includes a wake behind the swimmer (see Fig. 7 in Candelier et al., 2011, for instance). This wake is composed of an infinitely thin sheet of vorticity left by the passage of the trailing edge in the water. Applying Kelvin's circulation theorem, this wake is found to be composed of flatten vortex rings and contains the kinetic energy given by the animal to the fluid. But, in Lighthill's elongated-body theory, the dynamical evolution of this wake is not described because it has no influence on the dynamics of the swimmer.

One plausible scenario for the wake is that the vorticity sheet predicted by Lighthill's elongated-body theory will eventually roll-up to form a chain of vortex rings as sketched in Fig. 7b. The wake would then resemble the experimental observations of different groups (Blickhan et al., 1992; Lauder and Tytell, 2005; Müller et al., 1997; Nauen and Lauder, 2002; Videler, 1993). Another possible scenario is that, due to their self-induced velocities, these concatenated vortex rings will separate in two rows of vortex rings as observed for eels both experimentally (Lauder and Tytell, 2005; Müller et al., 2001; Tytell and Lauder, 2004) and numerically (Borazjani and Sotiropoulos, 2008; Kern and Koumoutsakos, 2006). In both cases, each vortex rings is expected to have a vertical extension approximately equal to the tail span and a horizontal extension approximately equal to U/2f. This means that the aspect ratio of the vortex rings varies from near circular to elongated in the swimming direction (for elongated fishes). As a rule, there is a major difference between the inherently three-dimensional wake behind a swimming animal and the two-dimensional wake observed behind an infinite cylinder (as drawn in Fig. 7).

Now coming back to the results of Triantafyllou et al. (1991, 1993) on the stability and efficiency of wakes, it appears that both their theoretical model and their experiments (Anderson et al., 1998; Read et al., 2003; Schouveiler et al., 2005; Triantafyllou et al., 1993) are based on two-dimensional flows. If this limit case can be suited to animals with large aspect-ratio tails, some specific work seems needed to apply it to other animals.

For animals with large aspect-ratio tails though, one striking fact is that the present model (where the wake has no influence) and the theoretical predictions of Triantafyllou et al. (1991, 1993) (based on the wake characteristics) converge to give a similar interval for the Strouhal number: roughly 0.2 < St < 0.4. One possibility is that these animals have evolved to optimise both the formation of a coherent wake and the elongated-body efficiency. This would explain why the geometrical characteristics of these animals, in particular the ratio of tail span to body length, vary so little among the species.

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