

MIT Open Access Articles

Efficiency of fish propulsion

The MIT Faculty has made this article openly available. **Please share** how this access benefits you. Your story matters.

Citation: Maertens, A P; Triantafyllou, M S and Yue, D K P. "Efficiency of Fish Propulsion." *Bioinspiration & Biomimetics* 10, 4 (July 2015): 046013 © 2015 IOP Publishing Ltd

As Published: <http://dx.doi.org/10.1088/1748-3190/10/4/046013>

Publisher: IOP Publishing

Persistent URL: <http://hdl.handle.net/1721.1/110823>

Version: Author's final manuscript: final author's manuscript post peer review, without publisher's formatting or copy editing

Terms of use: Creative Commons Attribution-Noncommercial-Share Alike



Efficiency of Fish Propulsion *

A.P. Maertens, M.S. Triantafyllou & D.K.P. Yue

Center for Ocean Engineering, Department of Mechanical Engineering
Massachusetts Institute of Technology
Cambridge, MA 02139, USA

E-mail: maertens@mit.edu, mistetri@mit.edu, yue@mit.edu

July 20, 2017

Abstract

The system efficiency of a self-propelled flexible body is ill-defined, hence we introduce the concept of *quasi-propulsive efficiency*, defined as the ratio of the power needed to tow a body in rigid-straight condition over the power it requires for self-propulsion, both measured for the same speed. Through examples we show that the quasi-propulsive efficiency is a rational non-dimensional metric of the propulsive fitness of fish and fish-like mechanisms, consistent with the goal to minimize fuel consumption under size and velocity constraints. We perform two-dimensional viscous simulations and apply the concept of quasi-propulsive efficiency to illustrate and discuss the efficiency of two-dimensional undulating foils employing first carangiform and then anguilliform kinematics. We show that low efficiency may be due to adverse body-propulsor hydrodynamic interactions, which cannot be accounted for by an increase in friction drag, as done previously, since at the Reynolds number $Re = 5\,000$ considered in the simulations, pressure is a major contributor to both thrust and drag.

Keywords: fish swimming, self-propelled, swimming efficiency, quasi-propulsive efficiency

1 Introduction

Efficiency is defined as the ratio of useful work over expended energy, measured over a specific time interval. The useful work, for a body moving at constant speed within

*Submitted to Bioinspiration & Biomimetics

a viscous medium, is the work needed to overcome the resisting fluid forces (drag). However, except in very few, limiting cases, this work cannot be measured because the drag of a self-propelled body depends not only on its shape and speed, but also on the type of propulsor used, and, in particular, the body-propulsor hydrodynamic interaction. This is especially true for flexible bodies, where propulsive forces are generated by body deformations that significantly influence the drag forces.

A rational goal of propulsion optimization is set as follows: *For a given shape and size vehicle, find the propulsor that will require the least amount of power to drive the vehicle at a given speed.* In other words, we intend to minimize the “fuel” consumption under certain size and velocity constraints and not the hydrodynamic efficiency of the system. Let us consider the general case of a self-propelled body of mass m moving with acceleration a_c and velocity U_s (both averaged over a period) along the x -direction.

Considering the system {body + propeller} as a whole, the efficiency (referred to as *net propulsive efficiency, η_n*) in its strict definition is the ratio of the power output $\overline{P_{out}}$ over the power input $\overline{P_{in}}$:

$$\eta_n = \frac{\overline{P_{out}}}{\overline{P_{in}}}, \quad (1)$$

where overbars indicate time-averaged values. The power output is given by the rate of change of kinetic energy (averaged over a period) of the body:

$$\overline{P_{out}} = \frac{d}{dt} \left(\frac{1}{2} m U_s^2 \right) = m a_c U_s = \overline{T_n} U_s, \quad (2)$$

with T_n the net thrust produced by the {body + propeller} system, such that:

$$\eta_n = \frac{\overline{T_n} U_s}{\overline{P_{in}}}. \quad (3)$$

This definition of efficiency is traditionally used to measure the performance of an isolated propeller, but is it appropriate for a self-propelled body?

Going back to the intuitive definition of efficiency, viz. the ratio of useful work to total work, different configurations can be compared. A propeller in isolation is meant to produce thrust that will balance the drag on the hull of a ship, so $\overline{T_n} U_s$ is a meaningful measure of useful power output. Similarly, for a fish performing a C-start or an escape maneuver (Domenici & Blake 1997, Liu et al. 2011), its goal is to accelerate, such that η_n is still a reasonable measure of efficiency that quantifies how much work is needed to attain a certain speed in a given amount of time. However, once the cruising speed is reached and the body moves at constant speed, the total average hydrodynamic force on the body must be zero, so using the definition of (3), the net efficiency is 0. As pointed out by Schultz & Webb (2002) among others, “unless

a fish is trying to ‘stir up the water,’ it performs no useful work” when swimming at constant speed:

$$\eta_n = 0 \quad \text{for a self-propelled body in steady state.} \quad (4)$$

This measure of efficiency becomes meaningless when the goal of the system is not to accelerate or produce thrust.

Over a decade ago, Schultz & Webb (2002) discussed at great length how advances in experimental and computational methods have fostered new ways of estimating the drag/thrust of swimming fish. Their conclusion is that “drag and thrust cannot be separated and hence have no meaning”. They suggest measuring performance in terms of swimming speed and power, or variables such as “miles per gallon”, instead. While this is appropriate for a given size body and shape, comparing different geometries and sizes requires dimensionless variables and normalized efficiency-like variables. With each researcher using a different definition of efficiency, it is not always clear what are the assumptions or limitations associated with each definition. The goal of the present paper is to present a brief overview of existing measures of efficiency and discuss when they are appropriate to use. We then present general guidelines for choosing efficiency-like variables and propose a rational measure of efficiency, the quasi-propulsive efficiency, which is a normalized version of the “miles per gallon” metric suggested by Schultz & Webb (2002).

Under special circumstances, one could still define a *propulsor efficiency*, η_p , by separating the propulsor thrust T_p from the body drag (one balancing the other on average when $\overline{T}_n = 0$):

$$\eta_p = \frac{\overline{T}_p U_s}{\overline{P}_{in}}. \quad (5)$$

For flexible self-propelled bodies, such as undulating fish, where the distinction between thrust and drag cannot be made, obtaining \overline{T}_p is much more challenging than for a propeller mounted on a rigid body, though Bergmann et al. (2014) still attempted to do it. Since the drag/thrust is a periodic function with zero mean, its amplitude, root-mean-square or mean of the positive part can be used as the normalizing thrust (if the thrust is periodic, all the above are proportional). For instance, Borazjani & Sotiropoulos (2008) use the latter in their investigation of carangiform swimming. The main limitation of this choice is that two gaits with the same swimming power and speed will artificially have different efficiencies if their drag trace is different. Borazjani & Sotiropoulos (2010), also define a non-dimensionalized “miles per gallon” variable. Whereas they call it the mean efficiency, its values ranging from 3 to 3000 show that it is not an efficiency-like measure. Moreover, this paper also illustrates that the choice the measure can condition the conclusions drawn from a study as their Froude efficiency and their mean efficiency do not always have the same order.

It is still possible, in some cases, to estimate the thrust produced by a swimming fish. Indeed, when the Reynolds number is sufficiently high and uncontrolled flow

separation effects are of limited extent, inviscid methods can be used to provide an estimate of the power needed for propulsion, as well as the developing thrust that must equal the resistance. This can be quite accurate if separation effects, other than vorticity shed from body edges and from fin trailing edges, are small, and interaction of the body with shed vorticity is insignificant. For instance, Lighthill (1971), Wu (1971), Drucker & Lauder (1999), Pedley & Hill (1999), Wolfgang et al. (1999), and Zhu et al. (2002) employ inviscid methodologies to estimate the thrust generated and power expended by swimming fish.

Tytell & Lauder (2004) compared elongated body theory (EBT) efficiency from Lighthill (1971) with the efficiency estimated from flow visualization and the significant difference between both estimates illustrates the confusion caused by the lack of a consistent definition. Their conclusion that still holds today, as illustrated by the difference between the EBT efficiency and numerical Froude efficiency in Borazjani & Sotiropoulos (2008) is a good summary of the situation: “Because of the difficulties of estimating efficiencies, it is difficult to compare this value with previously reported values”.

However, the main problem with these definitions of efficiency is that, even in rigid bodies such as ships and submarines, one is not interested in the propulsor efficiency, but the power needed to sustain a certain speed, as stated above. Indeed, it is possible that a very efficient propulsor may cause a large increase in the total drag when attached to the vessel, due to adverse hydrodynamic interference, and hence an increase in the required thrust \overline{T}_p . Then, although the propulsor efficiency is high, the system efficiency is low because the “fuel” needed may be excessive over another propulsor that may be less efficient in isolation but does not increase the resistance. What should be important in terms of the energetics of a certain fish is to employ a swimming mode that minimizes the power needed for propulsion; whether this mode is hydrodynamically “efficient” is secondary.

Since the efficiencies defined above are not appropriate metrics for self-propelled bodies, in section 2 we suggest, instead, the use of η_{QP} , the quasi-propulsive efficiency. We then present in section 3 the model problem of a two-dimensional undulating foil on which we apply the various definitions of efficiency to select an efficient swimming gait in section 4. In sections 5.1 and 5.2, we discuss how the notions of drag and thrust relate to the quasi-propulsive efficiency, and how these notions are commonly used in Naval Architecture. Finally, we present in section 5.3 a measure of performance that is appropriate for more general problems but is not an efficiency-like measure.

2 Quasi-propulsive efficiency

In life sciences, the fitness of a self-propelled system is traditionally measured by the cost of transport (COT), defined as the energy spent per unit distance traveled:

$$\text{COT} = \frac{\overline{P_{tot}}}{U_s}, \quad (6)$$

where $\overline{P_{tot}}$ is the total metabolic power consumed by swimming at speed U_s . While for a given animal, minimizing the COT is equivalent to minimizing the “fuel” consumption, the COT is a dimensional quantity, and there is no natural way to normalize it. For instance, Kern & Koumoutsakos (2006) normalized the COT by $mU_s f/2$, Liu et al. (2012) used $mL f^2$, Eloy (2013) chose $\rho\Omega_b^{2/3}U_s^2$, and Tokić & Yue (2012) normalized it by mgU_s . For the first two normalizations, two gaits with different flapping frequencies f would result in different values of normalized COT even if they have the same cost of transport, which is undesirable. On the other hand, for a given fish, the last normalization is the only one that ensures that two gaits have the same normalized COT if and only if they have the same COT. While this is a preferable property, this normalized COT is not an efficiency-like quantity since it does not have a natural unit scale. Hence, we propose to normalize the COT by the towed resistance R , which, after inversion, provides a fitness measure that we show generalizes the net propulsive efficiency to self-propulsion. Since here we only consider the hydrodynamic efficiency and not the internal losses, the quasi-propulsive efficiency η_{QP} , is employed, defined as:

$$\eta_{QP} = \frac{RU_s}{\overline{P_{in}}}, \quad (7)$$

where $\overline{P_{in}}$ is the power required by the propulsor to drive the vehicle at speed U_s under steady-state conditions ($\overline{T_n} = 0$) and R is the towed resistance at speed U_s . *In the case of a flexible body, the towed resistance must be measured or estimated in a straight configuration, i.e. not allowing any bending of the body.*

Indeed, at constant speed, the role of the propeller (for a ship) or of the swimming motion (for a fish) is to *compensate* for the drag such as to keep the cruising velocity constant. In an ideal fluid, there would be no drag on the body and no work would be needed to sustain velocity U_s : gliding would be enough. However, since water is a viscous fluid, in the absence of a propeller or swimming motion, the body would lose kinetic energy at a rate of:

$$\overline{P_{loss}} = \frac{d}{dt} \left(\frac{1}{2} m U_s^2 \right) = -RU_s < 0, \quad (8)$$

where, again, R is the towed resistance at speed U_s without a propeller (or a swimming motion). The goal of the propeller – or of the swimming motion – is to prevent this

loss of kinetic energy due to the drag on the gliding body. Since the goal in this case is to compensate for the resistance R and prevent the kinetic energy loss $\overline{P_{loss}}$, a reasonable definition of useful power, $\overline{P_{use}}$, is:

$$\overline{P_{use}} = \overline{P_{out}} - \overline{P_{loss}} = (\overline{T_n} + R)U_s, \quad (9)$$

which we use to generalize the quasi-propulsive efficiency η_{QP} to cases where the net thrust is not 0:

$$\eta_{QP} = \frac{\overline{P_{use}}}{\overline{P_{in}}} = \frac{(\overline{T_n} + R)U_s}{\overline{P_{in}}}. \quad (10)$$

(10) shows that the quasi-propulsive efficiency is the ratio of the useful energy over the expended energy, where the goal of swimming is to overcome the drag and prevent kinetic energy losses. For the case of a self-propelled body moving at constant speed, $\overline{T_n} = 0$, such that the definition of propulsive efficiency proposed in (10) is the same as (7). The power $\overline{P_{in}}$ is either experimentally measured, or evaluated numerically as the time-average of the power needed to actuate the body. Finally, since towed experiments or simulations are often preferred to self-propelled ones for practical reasons, we will show in section 4 that (10) can provide good estimates of the self-propelled quasi-propulsive efficiency under towing conditions.

There are fundamental differences between the propulsive efficiency of (5) and the quasi-propulsive efficiency of (7): First, in the “useful” power of (7), one uses *the towed resistance* of the vehicle measured under steady towing conditions at speed U_s and *without a propulsor* attached; hence, this definition does not suffer from any ambiguity as to what the force should be. Second, in (5) all quantities used refer to the same (self-propulsion) test; in (7) the numerator refers to a towing experiment, while the denominator to a self-propulsion experiment, conducted at the same speed.

It is not difficult to see that, if we maximize the efficiency η_{QP} , we simply minimize the expended power $\overline{P_{in}}$ (since the numerator is independent of the propulsor), in agreement with the original intent. The advantage of η_{QP} is that the towed resistance captures the essential hydrodynamic features of the specific hull or body, and can be used to compare the performance of dissimilar vehicle shapes, and for devising scaling laws. An apparent disadvantage is that the quasi-propulsive efficiency is not strictly an efficiency: it is not necessarily less than one. If the propulsor causes the resistance of the ship to drop substantially – for example by reducing flow separation – then the self-propelled power will possibly be less than the power needed to tow the bare hull, resulting in a value of η_{QP} higher than 100%.

A distinctive advantage of the quasi-propulsive efficiency is its universality. Unlike propulsor efficiencies relying on inviscid thrust models, the quasi-propulsive efficiency is as appropriate for low-Reynolds-number swimming motions as for large-Reynolds-number ones. Becker et al. (2003) define and use a system efficiency which is the same as the quasi-propulsive efficiency definition herein; they study a three-link micro-propulsor, employing flexing of the links to achieve locomotion at very low Reynolds

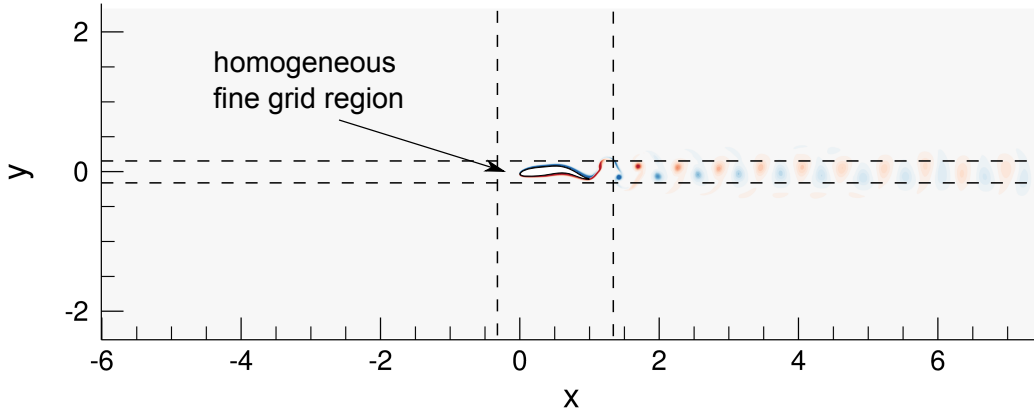


Figure 1: Flow configuration for the BDIM simulations. The Cartesian grid is uniform near the undulating NACA0012 with grid size $dx = dy = 1/320$ and uses a 2% geometric expansion ratio for the spacing in the far-field. Constant velocity $u = U_s$ is used on the inlet, periodic boundary conditions on the upper and lower boundaries, and a zero gradient exit condition with global flux correction. The vorticity field for the carangiform motion with $f = 1.8$ and zero mean drag is shown as an example.

numbers. In the words of the authors, “We define a swimming efficiency as the power necessary to pull the straightened swimmer along its axis at the average speed of the actual swimmer, relative to the average mechanical power generated by the actual swimmer to achieve that speed.” It is important to note that the useful power is defined in terms of the *towed swimmer at rest*. In fact, for very low Reynolds number, it is impossible to distinguish thrust from drag, since viscous forces produce both forces, making the use of the quasi-propulsive efficiency essential. Micro-swimmers have, typically, less than a few percent efficiency.

3 Model problem: two-dimensional undulating foil

In order to illustrate the discussion above, we will show through an example why the quasi-propulsive efficiency is a meaningful way of measuring propulsive efficiency for self-propelled fishes or vehicles. In this example, the vehicle is represented by a self-propelled two-dimensional undulating NACA0012 foil of length L swimming at average velocity U_s , chosen such that the Reynolds number is $Re = U_s L / \nu = 5000$ (unless specified otherwise), where ν is the fluid dynamic viscosity. All lengths are normalized by L , velocities by U_s and times (resp. frequencies) by L/U_s (resp. U_s/L). The deformation and swimming speed of the foil are prescribed, while its heave and pitch motion are caused by the hydrodynamic forces. These forces are estimated through two-dimensional viscous simulations on a Cartesian grid using the boundary

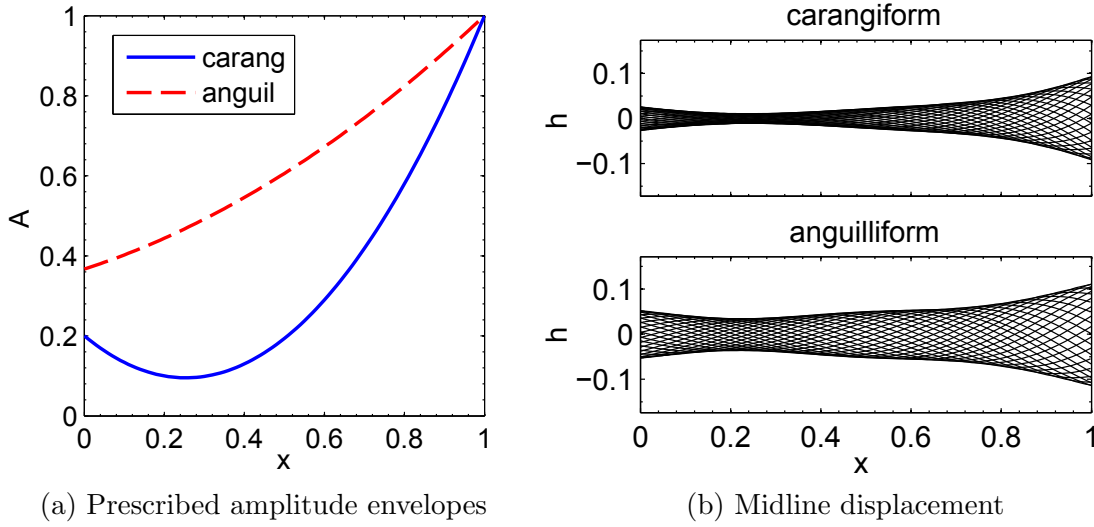


Figure 2: Carangiform and anguilliform motion for $f = 1.8$ and $\alpha = 0.1$.

data immersion method (BDIM) described in Weymouth & Yue (2011) and Maertens & Weymouth (2014) on a domain represented in Figure 1.

The leading edge of the foil is located at $x = 0$ and its trailing edge at $x = 1$. The lateral displacement $h(x, t)$ of a point located at x along the foil is given at time t by:

$$\begin{aligned} h(x, t) &= h_0(x, t) + B(x, t) \\ &= \alpha A(x) \sin(2\pi(x/\lambda - ft)) + B(x, t) \end{aligned} \quad (11)$$

where

$$A(x) = 1 + (x - 1)c_1 + (x^2 - 1)c_2 \quad (12)$$

is the envelop of the prescribed traveling wave of wavelength λ and frequency f , and

$$B(x, t) = (a_r + b_r x) \sin(2\pi(ft + \phi_r)) \quad (13)$$

is the recoil term due to the hydrodynamic forces on the foil. α is the amplitude of the deformation h_0 at the trailing edge. It is either kept constant ($\alpha = 0.1$) or adjusted through a feedback control loop to ensure that the average drag on the foil is 0.

Two envelopes, represented in figure 2a, will be compared. The first one, widely used to represent carangiform gaits (Videler & Hess 1984), is characterized by:

$$\text{carangiform : } \quad c_1 = -0.825, \quad c_2 = 1.625. \quad (14)$$

The second one, representative of an anguilliform swimmer (Tytell 2004), has parameters:

$$\text{anguilliform : } \quad c_1 = 0.323, \quad c_2 = 0.310. \quad (15)$$

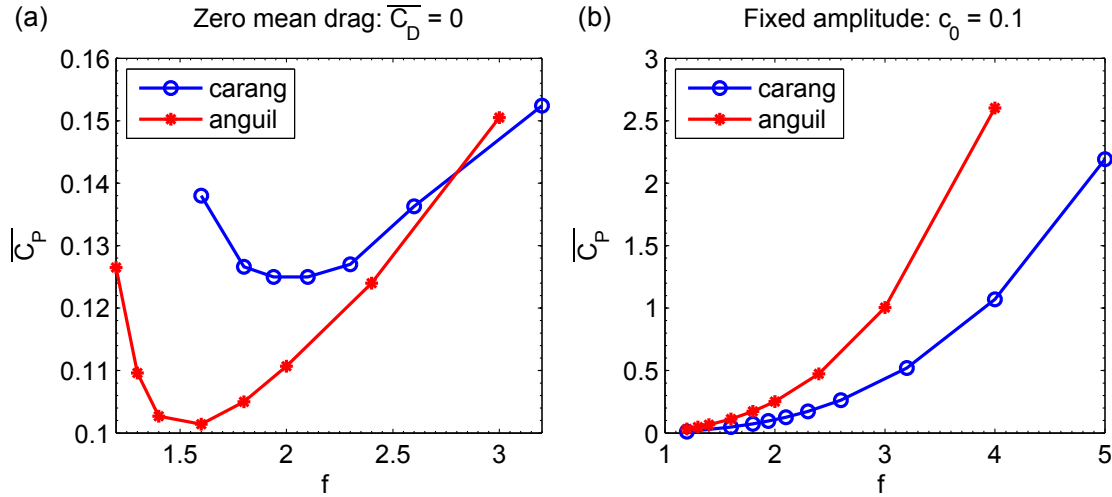


Figure 3: Time-averaged power coefficient as a function of undulating frequency for (a) the zero drag and (b) the fixed amplitude configurations.

$\lambda = 1$ is used for all cases, while f is varied in order to identify the *most efficient* undulating frequency for both gaits. Figure 2b illustrates the deformation and motion (with recoil) of the body by representing the total displacement $h(x)$ of the mid-line at several times t for $f = 1.8$.

As mentioned above, the viscous simulations provide an estimate of the swimming power P_{in} and thrust T_n :

$$P_{in} = \oint_{\partial B} \mathbf{v} \cdot \mathbf{f}^h ds \quad \text{and} \quad T_n = \oint_{\partial B} -f_x^h ds, \quad (16)$$

where \mathbf{f}^h are the hydrodynamic forces on the foil (with x -component f_x^h), \mathbf{v} the local velocity of the undulating foil (as given by (11)) and ∂B the surface of the foil. From these values, we define the dimensionless power coefficient C_P and thrust coefficient C_T :

$$C_P = \frac{P_{in}}{\frac{1}{2}\rho U^3 L} \quad \text{and} \quad C_T = \frac{T_n}{\frac{1}{2}\rho U^2 L} \quad (17)$$

where ρ is the fluid density. We similarly define the drag coefficient $C_D = -C_T$, as well as the friction (C_{Df}) and pressure (C_{Dp}) drag coefficients such that $C_D = C_{Df} + C_{Dp}$.

Figure 3a shows that the self-propelled undulating NACA0012 foil travels with the least energy when using the anguilliform gait with frequency $f = 1.6$, in which case $\overline{C_P} = 0.10$. If the carangiform gait was chosen, the most *efficient* frequency would be $f = 2$ with a power coefficient of $\overline{C_P} = 0.13$. Though dimensionless, the power coefficient is not an intuitive measure of efficiency and does not allow easy comparison between various geometries.

4 Application to gait selection: anguilliform vs carangiform gaits

From the prescribed undulation $h_0(x, t)$ and the recoil $B(x, t)$ calculated by the viscous BDIM simulation, Wu’s potential flow theory (Wu 1961, Wu 1971) can estimate the input power and propulsor thrust $T_{Wu} \approx T_p$. Using the input power $\overline{P_{in}}$ and the net thrust $\overline{T_n}$ estimated from the BDIM simulation, as well as thrust and power estimates from Wu’s theory, we will now compare the efficiency of the various gaits using the three measures defined above.

Note that, unlike Borazjani & Sotiropoulos (2010) and Tytell et al. (2010), we use the same speed for all kinematics while the amplitude is varied to achieve the desired speed. Indeed, comparing the “miles per gallon” performance between kinematics is mostly meaningful when the swimming speed is the same. The undulating frequency is also systematically varied such that the optimal frequency can be identified for each kinematics.

4.1 Net propulsive efficiency

As discussed in the introduction, the net efficiency $\eta_n = \overline{T_n U_s} / \overline{P_{in}}$ is zero when the mean drag on the foil is 0, which is the case for the self-propelled cases (0 drag) in Figure 4. In these cases, it is therefore impossible to compare the performance of the two gaits or of the various frequencies using η_n . As soon as the mean drag is non zero in the towed simulations ($a_0 = 0.1$), it becomes clear that the anguilliform undulation is more efficient at accelerating than the carangiform but, with values ranging from -0.6 to 0.3 , these undulating foils seem to be very poor propellers.

It is interesting to note that, at low frequency, the net efficiency is negative due to a net drag on the undulating foil. What is the meaning of this negative efficiency? If we were considering a propeller, a net drag on the propeller would be counter productive

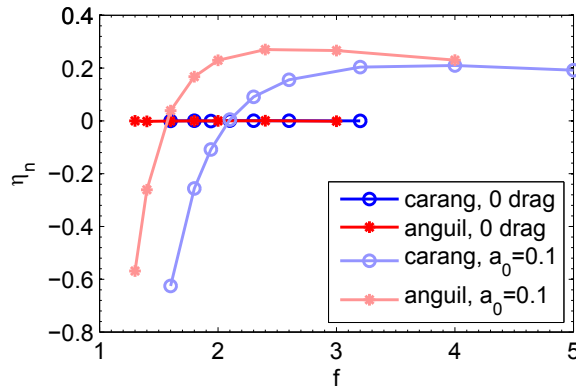


Figure 4: Net propulsive efficiency.

and the ship might “perform” better without the propeller, so one accepts the notion of a negative efficiency. However, in the case of a self-propelled undulating foil, an undulation is counter productive only if it increases the drag, not merely because it is not able to completely overcome it. Since, in the present case, the drag on the towed undulating foil is less than on the towed rigid foil, one would intuitively expect the efficiency to be positive. The quasi-propulsive efficiency solves this paradox by offering a measure of efficiency that is compatible with our intuition.

If we turn to the case where the goal is to accelerate the foil, a net thrust is needed. According to the net propulsive efficiency, the optimal undulating frequency is around $f = 2.5$ ($\eta_n = 0.27$) for the anguilliform motion and $f = 3.5$ ($\eta_n = 0.21$) for the carangiform motion. These frequencies minimize the work required to attain a given acceleration. However, once the cruising speed has been reached and the goal is to minimize the power spent swimming in steady state, there is no guarantee that these frequencies are optimal. Indeed, these *optimal* frequencies are different from those selected from the power coefficient in figure 3.

4.2 Potential flow propulsor efficiency

In order to calculate the hydrodynamic efficiency of the undulating foil in the stationary regime, the thrust produced by the swimming motion needs to be estimated independently of the drag on the foil. This thrust can, for example, be estimated by one of the numerous inviscid methods. Here we use Wu’s (1961) two-dimensional theory which has an analytical expression for thrust and power. The dependency of $\eta_{Wu} = \overline{T_{Wu}}U_s / \overline{P_{Wu}}$ on the undulating frequency f , shown in Figure 5, is qualitatively consistent with figure 3.

Similarly to what had been observed from the viscous power estimates, Wu’s method suggests that, in general, the anguilliform motion is more efficient than the carangiform one. The maximum efficiency for the anguilliform gait is $\eta_{Wu} = 0.69$ at

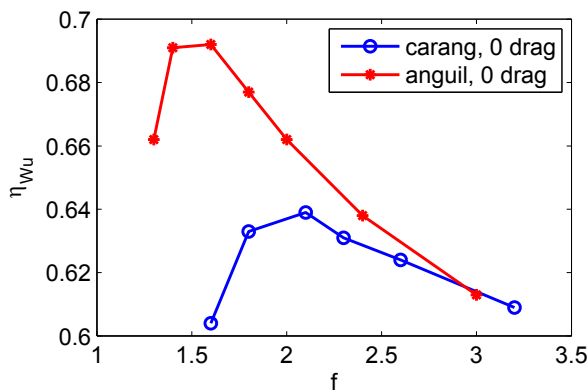


Figure 5: Propulsor efficiency estimated from Wu’s potential flow theory.

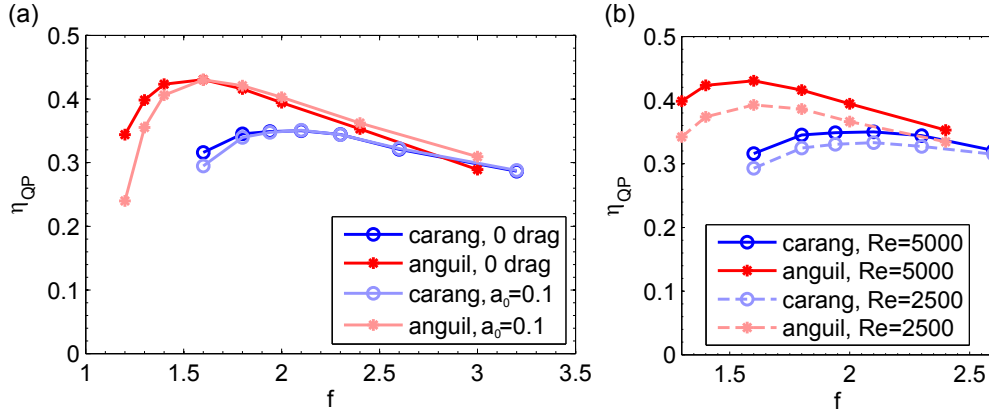


Figure 6: Quasi-propulsive efficiency. (a): Comparison of towed estimates with self-propelled values ($Re = 5000$). (b): Comparison of efficiency for $Re = 2500$ and $Re = 5000$ (self-propelled).

$f = 1.6$ whereas the carangiform gait is most efficient at $f = 2$ with $\eta_{Wu} = 0.64$. However, this approach might overestimate the efficiency by rewarding high thrust, which is also synonym of enhanced drag. Whereas, here, the most efficient gait and frequency according to Wu's theory correspond to the gait and frequency with least power, there is no guarantee that this will be true in general.

4.3 Quasi-propulsive efficiency

Finally, $\eta_{QP} = (R + \overline{T}_n)U_s/\overline{P}_{in}$, with values comprised between 0.2 and 0.5, provides an intuitive and meaningful measure of the efficiency for the two undulating gaits at the various frequencies. Figure 6 shows that the anguilliform gait, requiring less power, is an energetically better choice for a cruising undulating foil, and the best frequency is $f = 1.6$ with an efficiency of 43%. For the carangiform undulation, the maximum efficiency drops to 35% for the frequency $f = 2$. Since the goal here is primarily to illustrate the differences between various definitions of efficiency, two-dimensional simulations have been used. However, the results seem consistent with the three-dimensional results from Borazjani & Sotiropoulos (2010) and Tytell et al. (2010) showing that, at Reynolds number $Re = 4000$, an anguilliform swimming motion is more efficient.

Since self-propelled experiments and simulations are often more challenging than towed ones, it is of high practical interest to be able to estimate the quasi-propulsive efficiency from towed experiments. Figure 6a shows that the estimates obtained by keeping the amplitude a_0 constant instead of ensuring 0 mean drag are very close to the self-propelled values (except at the very low frequencies).

Within the same hydrodynamic regime, the values of η_{QP} for different Reynolds numbers are also of comparable amplitude, on a natural unit scale. For instance,

figure 6b compares the efficiency of the same self-propelled undulating motion for two different Reynolds numbers: $Re = 2500$ and $Re = 5000$. Even though the power coefficient increases by 50% from $Re = 5000$ to $Re = 2500$, the difference in efficiency between the two Reynolds numbers is no more than 7% and their trends are very similar. This result therefore corroborates what the intuition would expect: within a given hydrodynamic regime, the efficiency only weakly depends on the Reynolds number. This also illustrates that, even though both $\overline{C_P}$ and $1/\eta_{QP}$ are normalized versions of the swimming power, $\overline{C_P}$ is not very convenient to use due to its strong dependence on Reynolds number.

Finally, we would like to remark that, as the thrust produced by the undulating foil increases, η_{QP} converges to η_n . Indeed, if $\overline{T_n} \gg R$, then $\eta_{QP} \approx \overline{T_n} U_s / \overline{P_{in}}$. Since this is typically the case for a propeller, the drag on the hull being much larger than that of the propeller, η_{QP} can be seen as a generalization of the traditional propeller efficiency to the low thrust regime.

5 Discussion

5.1 Efficiency and the notion of drag/thrust on a self-propelled body

Schultz & Webb (2002) already discussed the difficulty of establishing a system propulsive efficiency for self-propelled bodies. They applied the concept of propulsor efficiency to define the system efficiency; since the net force is zero (as it must be in every self-propelled body in steady state), the system efficiency defined in this manner is zero as well; this is not a helpful result, because any system, however wasteful its propulsor may be, will be deemed equally (in)efficient as any other.

The difficulty of establishing a propulsive efficiency stems from the impossibility to separate drag and thrust since they balance on average and pressure (resp. viscosity) is the primary source of both at large (resp. low) Reynolds number. Inviscid approaches propose thrust estimates, but these are not always applicable and remain controversial due to the blurry definition of thrust for a self-propelled body. For instance, it is sometimes argued that Lighthill's (1971) model overestimates the thrust (Hess & Videler 1984, Anderson et al. 2001, Shirgaonkar et al. 2009). The quasi-propulsive efficiency moves away from the ill-defined notion of drag on a self-propelled body, using the well defined drag on a towed body instead. It results in an intuitive measure of efficiency that can be used to minimize the "fuel" consumption rather than the hydrodynamic efficiency.

Although the notion of thrust is ill-defined, attributing high (respectively low) quasi-propulsive efficiencies to a drag reduction (respectively enhancement) is a possible way of interpreting the performance of a propulsion system. Indeed, if one considers a {body+propeller} system, a low quasi-propulsive efficiency is either the result of an inefficient propulsor, or adverse hydrodynamic interactions between the

gait	f	St	η_{QP}	η_{Wu}	C_{Df}/C_{Df_0}	η_{Wu}/η_{QP}
carangiform	1.8	0.41	0.40	0.63	1.45	1.60
	2.1	0.38	0.40	0.64	1.41	1.58
	2.6	0.36	0.39	0.62	1.39	1.59
anguilliform	1.3	0.42	0.42	0.66	1.49	1.58
	1.6	0.35	0.46	0.69	1.38	1.50
	2.4	0.32	0.41	0.64	1.34	1.57

Table 1: Efficiency and drag amplification for various gaits at Reynolds number $Re = 5000$. At this Reynolds number, the friction drag accounts for 65% of the towed drag.

propeller and the body (or a combination of both factors). Adverse hydrodynamic interactions between the body and the propulsor can be interpreted as an increase in drag due to the propulsor:

$$\eta_{QP} = \frac{RU_s}{P_{in}} = \eta_p \frac{R}{\overline{T}_p} \quad (18)$$

where $\overline{T}_p/R = \eta_p/\eta_{QP}$ is the drag amplification. This drag increase due to body undulations, which has often been reported in the literature, is at the core of a century long controversy opposing the drag reduction proponents (Gero 1952, Fish & Hui 1991, Fish & Lauder 2006) in the wake of Gray and his famous *paradox* (Gray 1936), to the drag enhancement advocates (Lighthill 1971, Webb 1975, Goldspink 1977, Videler 1981). While the latter have long conjectured that body undulations must significantly increase the skin friction along the body due to what is often referred to as the *Bone-Lighthill boundary-layer thinning hypothesis* (Lighthill 1971), such an increase has never been confirmed. Instead, experimental visualization of the boundary layer of dead towed and live self-propelled fishes showed that the skin friction on a fish, undulating or not, was just higher than the drag on a flat plate (Anderson et al. 2001). Similarly, theoretical analysis from Ehrenstein & Eloy (2013) suggested an increase in the skin friction drag on the order of 1.2, well below the Bone-Lighthill hypothesis values of 3 to 5 (Lighthill 1971). Our viscous simulations of undulating self-propelled foils in which power, friction and pressure forces are simultaneously estimated can help shed a new light on this controversy. Using Wu's potential flow theory to estimate the propulsor efficiency, the drag amplification due to the undulating motion can be estimated as the ratio between the propulsor efficiency and the quasi-propulsive efficiency. Table 1 shows that, for the examples considered in this study, the drag amplification is between 50% and 60%. This drag increase is traditionally attributed to an increase in the friction drag, and the amplification of the friction drag is indeed of the same order. However, while the friction drag

increases with increasing undulation frequency, the total drag amplification does not follow these trends. This observation seems in contradiction with the results from Borazjani & Sotiropoulos (2008) and Borazjani & Sotiropoulos (2009). This apparent contradiction illustrates once more how much conclusions can be affected by the definition of drag or efficiency, as well as the assumptions made. Since the skin friction mostly contributes to drag, their conclusions regarding skin friction are similar to ours. Separating pressure drag from pressure thrust is much less straightforward. Since they define form drag as the positive part of the longitudinal pressure force and keep the undulation amplitude constant, there is no reason why their drag should follow the same trend as ours.

In general, increases in friction drag alone cannot account for low swimming efficiencies. It seems from table 1 that, for the examples used here, the optimal gait is the one with the most efficient propulsor and least total drag amplification, rather than the one with least friction drag amplification. However, minimizing the friction drag can help reduce the fuel consumption. For instance, experiments on a robotic tuna by Barrett et al. (1999) suggested that, especially at high Reynolds number, it is possible for the undulating motion to interact beneficially with the drag on the body and obtain quasi-propulsive efficiencies larger than 1. Barrett et al. (1999) directly measured the power needed to drive the tuna-like motion of a robotic mechanism under self-propulsion conditions. Inviscid theory provided values for the self-propulsion power very close to the experimentally measured values (Barrett et al. 1999, Kagemoto et al. 2000, Smith & Wright 2004). The quasi-propulsive efficiency, estimated as proposed herein, provided values up to 150%, well in excess of 100%, which simply means that the resistance of the actively swimming body was less than the drag under straight-towing conditions. The measurements were at the transitional Reynolds number of around $Re = 800\,000$ where re-laminarization of the boundary layer and separation suppression is possible. Indeed, simulations (Shen et al. 2003) and experiments (Techet et al. 2003) on an actively flapping two-dimensional sheet demonstrated clear turbulence reduction, in addition to flow separation suppression, which was noted earlier by Taneda (1977). This can explain the drop in drag under self-propulsion conditions and hence the high quasi-propulsive efficiency values; indeed Barrett et al. (1999) found the equivalent drag coefficient of the actively swimming mechanism to be closer to laminar boundary layer values, whereas the drag coefficient of the straight-towed mechanism was close to turbulent boundary layer values.

5.2 Quasi-propulsive efficiency in Naval Architecture

In Naval Architecture, the use of the quasi-propulsive efficiency is standard (Comstock 1967) – and straight-forward to use because the body is rigid. Usually, to estimate the required power P_{in} , one uses the propeller characteristics as measured in *open water*, i.e. with the propeller tested in isolation, without a hull in front. The interaction between hull and propeller is accounted for through factors derived either empirically

or through additional experimental tests.

The resistance of the ship under self-propelled conditions, R_{sp} , will in general be larger than the towed resistance, because the stern stagnation pressure (which is beneficial, reducing the drag) is reduced due to the presence of the propeller which accelerates the flow. R_{sp} is related to the towed resistance R through the “thrust deduction factor” t , which depends on the hull characteristics, the propeller characteristics and, primarily, the hull-propeller interaction:

$$R_{sp} = \frac{R}{1 - t}. \quad (19)$$

The factor t is usually positive, reflecting the expectation that the self-propelled resistance is larger than the towed resistance; there may however be some cases where the reverse occurs, for hulls which are bluff, i.e. not well streamlined, because of a reduction in the separation effects. Another, but physically incorrect way to view relation (19) is that the propeller thrust T , which must be equal to R_{sp} in order to achieve self-propulsion, is *reduced* when the propulsor is placed behind the vehicle, hence the name thrust deduction.

Finally, since the propeller operates inside the wake of the vehicle, the oncoming velocity is reduced compared to the free stream velocity U ; an averaged incoming velocity is used, U_A :

$$U_A = U(1 - w), \quad (20)$$

where w , the “wake fraction”, is derived empirically or with separate experiments. Hence, the useful power of the propeller must be equal to $R_{sp}U_A$ in order to drive the vehicle in self-propulsion. If the propeller efficiency has been measured to be equal to η_p under “open water conditions”, i.e. separately from the vessel, then the input power must be equal to the useful power divided by the propeller efficiency:

$$Q_{in} = \frac{R_{sp}U_A}{\eta_p} = \frac{RU(1 - w)}{\eta_p(1 - t)}. \quad (21)$$

Substituting in (7) one finds:

$$\eta_{QP} = \eta_p \frac{1 - t}{1 - w}. \quad (22)$$

Finally, a factor is required to account for Reynolds number effects on the propeller torque, caused by testing in model scale and in uniform flow, the so-called “relative propulsive efficiency”; but this factor is not essential and we will not pursue it in the present discussion.

As seen in (22), the quasi-propulsive efficiency is the product of the propeller efficiency η_p and the so-called hull efficiency, η_H , defined as:

$$\eta_H = \frac{1 - t}{1 - w}, \quad (23)$$

which accounts for the hydrodynamic interference between the hull and the propeller. Then, (22) turns into:

$$\eta_{QP} = \eta_p \eta_H. \quad (24)$$

It is usual, for example to have $\eta_{QP} > \eta_p$; and is even possible, albeit rare, that $\eta_{QP} > 1$ if the factors t and w reflect a large, favorable overall hydrodynamic interference. (24), then, explicitly relates the system efficiency (η_{QP}) to the efficiency of the propulsor (η_p), correcting for possible hydrodynamic interference (η_H).

5.3 Measure of performance for optimizing velocity and body shape

We have shown through examples that the quasi-propulsive efficiency η_{QP} is a rational measure of the efficiency for a self-propelled body in steady motion. There is no theoretical guarantee that η_{QP} will be smaller than 1, and it can indeed be greater than 1 for very efficient fish (Barrett et al. 1999) and ships. However, it gives an intuitively meaningful number that allows the comparison of various geometries and propulsion systems. It can, for instance, be used to compare the efficiency of man-made systems and biological ones. It can not, however, be used to compare or optimize the performance of hull or body shapes (Kagemoto 2013, van Rees et al. 2013), or swimming velocities (Liu et al. 2012).

A more general goal than that of Section 2 can be expressed as: *Find the body size, shape, propulsor and velocity that will require the least amount of energy per unit mass to drive the vehicle from point A to point B in a fluid of kinematic viscosity ν and density ρ with gravitational acceleration g .*

In other words, the goal is to minimize the energy per unit mass and unit length traveled mass in a given fluid. For this problem, the natural units are:

$$\text{mass} : \rho \frac{\nu^2}{g}, \quad \text{length} : \left(\frac{\nu^2}{g} \right)^{1/3}, \quad \text{time} : \nu \left(\frac{\nu}{g^2} \right)^{1/3}. \quad (25)$$

If the average swimming power is $\overline{P_{in}}$ and the average velocity is U_s , the average energy \overline{E} spent per unit mass and length (using the length unit defined above) is:

$$\overline{E}_m = \frac{\overline{P_{in}}}{mU_s} \left(\frac{\nu^2}{g} \right)^{1/3}. \quad (26)$$

The corresponding dimensionless coefficient, which we will call energy coefficient $\overline{C_E}$, is:

$$\overline{C_E} = \frac{\overline{P_{in}}}{mgU_s}. \quad (27)$$

This energy coefficient is convenient for comparing various geometries and propulsion strategies, but $\overline{C_E}$ is decreasing with Reynolds number, therefore any optimization would conclude that a swimming speed of zero is optimal since it does not require energy. Indeed, the coefficient $\overline{C_E}$ takes into account the hydrodynamic power spent to travel from A to B , but nothing ensures that the travel will be accomplished in a finite time, which is why the total metabolic power $\overline{P_{tot}}$ needs to be used instead of $\overline{P_{in}}$. The metabolic power, which includes a cost $\overline{P_m}$ proportional to time, can be expressed as Liu et al. (2012):

$$\overline{P_{tot}} = \frac{\overline{P_w}}{\beta} + P_m, \quad (28)$$

where β is the muscle power efficiency, P_m is the standard metabolic rate independent of swimming speed and P_w is the hydrodynamic power (similar to the definition of P_{in} in Eq. 16).

We now define the performance index:

$$C_\eta = \frac{mgU_s}{\overline{P_{tot}}} = \frac{mg}{\text{COT}}, \quad (29)$$

that can be used to solve the very general problem of optimizing the body shape, swimming speed and propulsion system. C_η is exactly the performance index used in Tokić & Yue (2012). Even though the performance index could also be used to solve the optimization problem presented in Section 2, its order of magnitude varies a lot with Reynolds number; the quasi-propulsive efficiency, with a natural scale going from 0 to 1, is much more intuitive and easy to work with.

6 Conclusion

The optimal propulsor for a self-propelled system is the one that minimizes fuel consumption for a given body size and speed. The hydrodynamic efficiency is not a good measure of optimality, because the numerator (the useful energy) is not easily defined in fish, since drag is difficult to measure and, far more importantly, its value depends on the propulsion mode employed.

There does not exist a universal measure of swimming performance but, for a given problem, it is possible to define rational fitness indicators. If, for a given body and speed, one wants to find the “best” propulsion system, the quasi-propulsive efficiency, η_{QP} , is a meaningful efficiency-like measure defined as the ratio of the energy needed to tow the fish straight at a given speed divided by the power to self-propel itself at the same speed. Traditionally used in Naval Architecture, η_{QP} is also the inverse of a normalized Cost of Transport, COT, built upon the intuition that a propulsor is meant to overcome the drag that the body would be experiencing in the absence of propulsion.

As Fish (2005) demonstrates in his outline of the controversial *Gray's paradox*, estimates of the propulsive parameters must be made very carefully, especially because the quasi-propulsive efficiency is based on two separate experiments, one for a towed body (numerator, or useful work) and one for the self-propelled experiment (denominator, or expended energy); both experiments must refer to the same speed and the same duration of time over which performance is assessed, otherwise erroneous conclusions may be drawn.

One should also keep in mind that the mechanical efficiency, considered in this paper, is only the last link in a series of processes involved in swimming. As Ellerby (2010) explains in his short review of Webb's contributions, "For fish, just as with engineered vehicles, fuel consumption is the most obvious measure of power input." Fuel comes in the form of metabolic energy, and the efficiency of converting this chemical energy to mechanical energy plays an important role in the final measure of swimming efficiency, as hinted by the total power defined in (28).

Finally, the rationale presented in this paper to define the quasi-propulsive efficiency can also be used to choose proper fitness indicators for other problems. For instance, we showed that the net propulsive efficiency is a good measure of the ability for a propeller to efficiently accelerate the body. Section 5.3 describes a performance index, previously used in Tokić & Yue (2012), that is more general than the quasi-propulsive efficiency but is not an efficiency-like measure and is difficult to use in self-propelled cases.

Acknowledgments

This research was supported by the National Research Foundation Singapore through the Singapore MIT Alliance for Research and Technology's Center for Environmental Sensing and Modeling interdisciplinary research program. The authors also wish to acknowledge support from the MIT Sea Grant Program.

References

- Anderson, E. J., McGillis, W. R. & Grosenbaugh, M. A. (2001). The boundary layer of swimming fish, *Journal of Experimental Biology* **204**(1): 81–102.
URL: <http://jeb.biologists.org/content/204/1/81>
- Barrett, D. S., Triantafyllou, M. S., Yue, D. K. P., Grosenbaugh, M. A. & Wolfgang, M. J. (1999). Drag reduction in fish-like locomotion, *Journal of Fluid Mechanics* **392**: 183–212.
- Becker, L. E., Koehler, S. A. & Stone, H. A. (2003). On self-propulsion of micro-machines at low reynolds number: Purcell's three-link swimmer, *Journal of Fluid Mechanics* **490**: 15–35.

- Bergmann, M., Iollo, A. & Mittal, R. (2014). Effect of caudal fin flexibility on the propulsive efficiency of a fish-like swimmer, *Bioinspiration & Biomimetics* .
URL: <http://hal.inria.fr/hal-01059643>
- Borazjani, I. & Sotiropoulos, F. (2008). Numerical investigation of the hydrodynamics of carangiform swimming in the transitional and inertial flow regimes, *Journal of Experimental Biology* **211**(10): 1541–1558.
URL: <http://jeb.biologists.org/content/211/10/1541>
- Borazjani, I. & Sotiropoulos, F. (2009). Numerical investigation of the hydrodynamics of anguilliform swimming in the transitional and inertial flow regimes, *Journal of Experimental Biology* **212**(4): 576–592.
URL: <http://jeb.biologists.org/content/212/4/576>
- Borazjani, I. & Sotiropoulos, F. (2010). On the role of form and kinematics on the hydrodynamics of self-propelled body/caudal fin swimming, *The Journal of Experimental Biology* **213**(1): 89–107.
URL: <http://jeb.biologists.org/content/213/1/89>
- Comstock, J. A. G. o. A. (1967). *Principles of Naval Architecture*, revised edition edn, Society of Naval Architects and Marine Engineers.
- Domenici, P. & Blake, R. (1997). The kinematics and performance of fish fast-start swimming, *Journal of Experimental Biology* **200**(8): 1165–1178.
URL: <http://jeb.biologists.org/content/200/8/1165>
- Drucker, E. G. & Lauder, G. V. (1999). Locomotor forces on a swimming fish: three-dimensional vortex wake dynamics quantified using digital particle image velocimetry, *Journal of Experimental Biology* **202**(18): 2393–2412.
URL: <http://jeb.biologists.org/content/202/18/2393>
- Ehrenstein, U. & Eloy, C. (2013). Skin friction on a moving wall and its implications for swimming animals, *Journal of Fluid Mechanics* **718**: 321–346.
- Ellerby, D. J. (2010). How efficient is a fish?, *The Journal of Experimental Biology* **213**(22): 3765–3767.
URL: <http://jeb.biologists.org/content/213/22/3765>
- Eloy, C. (2013). On the best design for undulatory swimming, *Journal of Fluid Mechanics* **717**: 48–89.
- Fish, F. E. (2005). A porpoise for power, *Journal of Experimental Biology* **208**(6): 977–978.
URL: <http://jeb.biologists.org/content/208/6/977>

Fish, F. E. & Hui, C. A. (1991). Dolphin swimming a review, *Mammal Review* **21**(4): 181–195.

URL: <http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2907.1991.tb00292.x/abstract>

Fish, F. & Lauder, G. (2006). Passive and active flow control by swimming fishes and mammals, *Annual Review of Fluid Mechanics* **38**(1): 193–224.

URL: <http://www.annualreviews.org/doi/abs/10.1146/annurev.fluid.38.050304.092201>

Gero, D. R. (1952). The hydrodynamic aspects of fish propulsion., *Fish propulsion* **1601**: 1–32. 32 p. : ill. ; 24 cm.

URL: <http://digitallibrary.amnh.org/dspace/handle/2246/4922>

Goldspink, R. M. A. . G. (ed.) (1977). *Swimming*, London: Chapman and Hall. 346pp, pp. 222–248.

Gray, J. (1936). Studies in animal locomotion VI. the propulsive powers of the dolphin, *J Exp Biol* **13**(2): 192–199.

URL: <http://jeb.biologists.org/content/13/2/192>

Hess, F. & Videler, J. J. (1984). Fast continuous swimming of saithe (*pollachius virens*): a dynamic analysis of bending moments and muscle power, *J Exp Biol* **109**(1): 229–251.

URL: <http://jeb.biologists.org/content/109/1/229>

Kagemoto, H. (2013). Why do fish have a fish-like geometry?, *Journal of Fluids Engineering* **136**(1): 011106–011106.

URL: <http://dx.doi.org/10.1115/1.4025646>

Kagemoto, H., Wolfgang, M. J., Yue, D. K. P. & Triantafyllou, M. S. (2000). Force and power estimation in fish-like locomotion using a vortex-lattice method, *J. Fluids Eng.* **122**(2): 239–253.

URL: <http://dx.doi.org/10.1115/1.483251>

Kern, S. & Koumoutsakos, P. (2006). Simulations of optimized anguilliform swimming, *Journal of Experimental Biology* **209**(24): 4841–4857.

URL: <http://jeb.biologists.org/content/209/24/4841>

Lighthill, M. J. (1971). Large-amplitude elongated-body theory of fish locomotion, *Proceedings of the Royal Society of London. Series B. Biological Sciences* **179**(1055): 125–138.

URL: <http://rspb.royalsocietypublishing.org/content/179/1055/125.short>

Liu, G., Yu, Y.-L. & Tong, B.-G. (2011). Flow control by means of a traveling curvature wave in fishlike escape responses, *Physical Review E* **84**(5): 056312.

URL: <http://link.aps.org/doi/10.1103/PhysRevE.84.056312>

- Liu, G., Yu, Y.-L. & Tong, B.-G. (2012). Optimal energy-utilization ratio for long-distance cruising of a model fish, *Physical Review E* **86**(1): 016308.
URL: <http://link.aps.org/doi/10.1103/PhysRevE.86.016308>
- Maertens, A. P. & Weymouth, G. D. (2014). Accurate Cartesian-grid simulations of near-body flows at intermediate Reynolds numbers, *Comput. Methods Appl. Mech. Engrg.* . In press.
- Pedley, T. J. & Hill, S. J. (1999). Large-amplitude undulatory fish swimming: fluid mechanics coupled to internal mechanics, *Journal of Experimental Biology* **202**(23): 3431–3438.
URL: <http://jeb.biologists.org/content/202/23/3431>
- Schultz, W. W. & Webb, P. W. (2002). Power requirements of swimming: Do new methods resolve old questions?, *Integrative and Comparative Biology* **42**(5): 1018–1025. ArticleType: research-article / Full publication date: Nov., 2002 / Copyright 2002 Oxford University Press.
URL: <http://www.jstor.org/stable/3884620>
- Shen, L., Zhang, X., Yue, D. K. P. & Triantafyllou, M. S. (2003). Turbulent flow over a flexible wall undergoing a streamwise travelling wave motion, *Journal of Fluid Mechanics* **484**: 197–221.
- Shirgaonkar, A. A., MacIver, M. A. & Patankar, N. A. (2009). A new mathematical formulation and fast algorithm for fully resolved simulation of self-propulsion, *Journal of Computational Physics* **228**(7): 2366–2390.
URL: <http://www.sciencedirect.com/science/article/pii/S0021999108006311>
- Smith, R. & Wright, J. (2004). Simulation of RoboTuna fluid dynamics using a new incompressible ALE method, *34th AIAA Fluid Dynamics Conference and Exhibit*, American Institute of Aeronautics and Astronautics.
URL: <http://arc.aiaa.org/doi/abs/10.2514/6.2004-2347>
- Taneda, S. (1977). Visual study of unsteady separated flows around bodies, *Progress in Aerospace Sciences* **17**: 287–348.
URL: <http://www.sciencedirect.com/science/article/pii/0376042176900117>
- Techet, A. H., Hover, F. S. & Triantafyllou, M. S. (2003). Separation and turbulence control in biomimetic flows, *Flow, Turbulence and Combustion* **71**(1-4): 105–118.
- Tokić, G. & Yue, D. K. P. (2012). Optimal shape and motion of undulatory swimming organisms, *Proc. R. Soc. B* **279**(1740): 3065–3074.
URL: <http://rspb.royalsocietypublishing.org/content/279/1740/3065>

- Tytell, E. D. (2004). The hydrodynamics of eel swimming II. effect of swimming speed, *Journal of Experimental Biology* **207**(19): 3265–3279.
URL: <http://jeb.biologists.org/content/207/19/3265>
- Tytell, E. D., Borazjani, I., Sotiropoulos, F., Baker, T. V., Anderson, E. J. & Lauder, G. V. (2010). Disentangling the functional roles of morphology and motion in the swimming of fish, *Integrative and Comparative Biology* **50**(6): 1140–1154.
URL: <http://icb.oxfordjournals.org/content/50/6/1140>
- Tytell, E. D. & Lauder, G. V. (2004). The hydrodynamics of eel swimming i. wake structure, *Journal of Experimental Biology* **207**(11): 1825–1841.
URL: <http://jeb.biologists.org/content/207/11/1825>
- van Rees, W. M., Gazzola, M. & Koumoutsakos, P. (2013). Optimal shapes for anguilliform swimmers at intermediate reynolds numbers, *Journal of Fluid Mechanics* **722**: null–null.
- Videler, J. (1981). Swimming movements, body structure and propulsion in cod gadus morhua, *Symp. Zool. Soc. Lond*, Vol. 48, pp. 1–27.
- Videler, J. J. & Hess, F. (1984). Fast continuous swimming of two pelagic predators, saithe (*pollachius virens*) and mackerel (*scomber scombrus*): a kinematic analysis, *Journal of Experimental Biology* **109**(1): 209–228.
URL: <http://jeb.biologists.org/content/109/1/209>
- Webb, P. W. (1975). *Hydrodynamics and energetics of fish propulsion*, Dept. of the Environment Fisheries and Marine Service.
- Weymouth, G. D. & Yue, D. K.-P. (2011). Boundary data immersion method for Cartesian-grid simulations of fluid-body interaction problems, *J. Comput. Phys.* **230**(16): 6233–6247.
URL: <http://www.sciencedirect.com/science/article/pii/S0021999111002610>
- Wolfgang, M. J., Anderson, J. M., Grosenbaugh, M. A., Yue, D. K. & Triantafyllou, M. S. (1999). Near-body flow dynamics in swimming fish, *The Journal of Experimental Biology* **202**(17): 2303–2327.
URL: <http://jeb.biologists.org/content/202/17/2303>
- Wu, T. Y.-T. (1961). Swimming of a waving plate, *Journal of Fluid Mechanics* **10**(03): 321–344.
- Wu, T. Y.-T. (1971). Hydromechanics of swimming propulsion. part 1. swimming of a two-dimensional flexible plate at variable forward speeds in an inviscid fluid, *Journal of Fluid Mechanics* **46**(2): 337–355.
URL: <http://resolver.caltech.edu/CaltechAUTHORS:WUTjfm71a>

Zhu, Q., Wolfgang, M. J., Yue, D. K. P. & Triantafyllou, M. S. (2002). Three-dimensional flow structures and vorticity control in fish-like swimming, *Journal of Fluid Mechanics* **468**: 1–28.