Energy efficiency and allometry of movement of swimming and flying animals

Rahul Bale, Max Hao, Amneet Pal Singh Bhalla, and Neelesh A. Patankar¹

Department of Mechanical Engineering, Northwestern University, Evanston, IL 60208

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Which animals use their energy better during movement? One metric to answer this question is the energy cost per unit distance per unit weight. Prior data show that this metric decreases with mass, which is considered to imply that massive animals are more efficient. Although useful, this metric also implies that two dynamically equivalent animals of different sizes will not be considered equally efficient. We resolve this longstanding issue by first determining the scaling of energy cost per unit distance traveled. The scale is found to be $M^{2/3}$ or $M^{1/2}$, where M is the animal mass. Second, we introduce an energy-consumption coefficient (C_E) defined as energy per unit distance traveled divided by this scale. C_E is a measure of efficiency of swimming and flying, analogous to how drag coefficient quantifies aerodynamic drag on vehicles. Derivation of the energy-cost scale reveals that the assumption that undulatory swimmers spend energy to overcome drag in the direction of swimming is inappropriate. We derive allometric scalings that capture trends in data of swimming and flying animals over 10–20 orders of magnitude by mass. The energy-consumption coefficient reveals that swimmers beyond a critical mass, and most fliers are almost equally efficient as if they are dynamically equivalent; increasingly massive animals are not more efficient according to the proposed metric. Distinct allometric scalings are discovered for large and small swimmers. Flying animals are found to require relatively more energy compared with swimmers.

cost of transport | Froude efficiency

Cost of transport (COT), defined as the energy spent per unit distance traveled, is often used as a measure of the energy efficiency of movement. However, a dimensionless efficiency measure enables comparison across animal sizes for which the scale of COT is required. The weight of the animal could be the scale to nondimensionalize COT (1, 2), but there is no basis in mechanics to do so. Here, we derive the scaling of COT. To that end, we note that it is frequently assumed that a swimming animal spends energy to overcome drag. The assertion that an animal spends power to overcome drag lacks direct evidence in undulatory propulsion. It is well known that animals swimming at low Reynolds number spend power in producing undulatory kinematics (3–5). Even at finite Reynolds numbers it is believed that swimming animals spend power to produce swimming kinematics (6). In this work we formally show that an undulatory swimmer spends power to produce the undulatory kinematics rather than to overcome drag. This result will be used to obtain the scaling of COT. This scale will be used to nondimensionalize COT, which is the new energy-consumption coefficient proposed here. Our analysis also leads to allometric scalings of different variables.

Power Spent During Swimming

Swimming animals achieve locomotion through the undulatory kinematics of their body. The undulations of the body are predominantly in a direction lateral to the direction of swimming (7–10). In consequence, we hypothesize that, during steady undulatory swimming, most of the power is spent by a swimming animal to generate movement in the lateral direction (P_{lat})

and very little or negligible power is spent to move in the anteroposterior direction of swimming (P_{antpos}). This implies $\bar{P}_{net} = \bar{P}_{antpos} + \bar{P}_{lat}$, where P_{net} is the total power and the overbar is the average over time. $\bar{P}_{antpos} = \overline{F_x u}$, where F_x is the axial force and u is the axial swimming speed. This implies

$$\bar{P}_{net} = \overline{F_x u} + \overline{F_x u'} + \bar{P}_{lat}, \quad [1]$$

where the swimming speed is written as the sum of a mean quantity ($\bar{u}$) and a fluctuation quantity (u') (see *SI Appendix, section S2* for derivations, and the sign convention is summarized at the end of this article). Because there is no net external force on a swimming body, $\bar{F}_x = 0$ during steady swimming. In addition, if $\overline{F_x u'}$ is found to be negligible in Eq. 1, then the hypothesis that all of the net power is spent to undulate laterally would be true. To test this we analyzed data from simulations of steady free-swimming larval zebrafish and black ghost knifefish. The simulations were based on experimentally obtained kinematics and the numerical solutions were validated with experimental data (*SI Appendix, section S1*). We computed each power term in Eq. 1 based on simulations. For the larval zebrafish, we found that $\overline{F_x u} = 0.0024$ erg/s (the value is not exactly 0 as expected due to computational errors) and that $\overline{F_x u'} = 0.0004$ erg/s is negligible compared with $\bar{P}_{net} = 1.67$ erg/s (Fig. 1). Thus, $\bar{P}_{net} \approx \bar{P}_{lat}$ (Fig. 1), i.e., the zebrafish spends practically all its power to undulate laterally. We got a similar result for the knifefish (Fig. 1).

Here, $\bar{P}_{net}$ represents the mean power due to the interaction between the fluid and the swimmer's body. If there are negligible internal losses, the power generated by the muscles would be spent to produce lateral undulations, i.e., $\bar{P}_{musc} \approx \bar{P}_{net} \approx \bar{P}_{lat}$, where $\bar{P}_{musc}$ is the mean muscle power.

Significance

Is a whale or a tuna more efficient? The answer depends on the definition of efficiency. If one uses cost of transport, defined as the energy required to move unit distance, then the tuna wins. If energy of transporting unit mass over unit distance is used then the whale wins. We address this ambiguity by rationally deriving a new efficiency measure called the energy-consumption coefficient (C_E), which is a nondimensional measure of fuel consumption. C_E is a fundamental metric to quantify efficiency of self-propelled bodies analogous to the drag coefficient (C_d) to quantify aerodynamic shapes of vehicles. The analysis also leads to allometric scalings of frequency and velocity of swimming and flying organisms over more than 20 orders of magnitude of mass.

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¹To whom correspondence should be addressed. E-mail: n-patankar@northwestern.edu.

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Fig. 1. A comparison of the total power with the power due to fluctuating component of the swimming speed, and with the power spent in producing lateral undulations for (A) black ghost knifefish and (B) larval zebrafish.

A Comment on Froude Efficiency

The efficiency of swimming is often quantified by the Froude efficiency (11). It is defined as $\eta_F = \overline{D}\overline{u}/(\overline{T}\overline{u} + \overline{P}_{wake})$, where $\overline{P}_{wake}$ is the mean power in the wake of the swimmer. $\overline{D}$ and $\overline{T}$ are the mean drag and thrust forces, respectively. Although the wake power can be estimated (6, 7, 12, 13, 14), a drawback of using Froude efficiency is the ambiguity in the definition of drag and thrust because there is no unique method to estimate drag (15). Hence, cost of transport, which does not suffer from this drawback, is a suitable efficiency measure for swimming.

Energy-Consumption Coefficient

Metabolic and mechanical COT are two commonly used definitions of COT; the former is based on the metabolic power and the latter on the mechanical power spent by an animal. Here we focus on the mechanical COT, which is given by $COT = \overline{P}_{net}/\overline{u}$. COT is a dimensional quantity, whereas a dimensionless measure is preferred to enable comparison of efficiency of swimmers across species and length scales. To nondimensionalize COT we need to choose appropriate scales for $\overline{P}_{net}$ and $\overline{u}$.

We can choose the wave speed to nondimensionalize the swimming speed: $u' = u/(f\lambda)$, where the prime indicates a dimensionless quantity. f and λ are the frequency and wavelength of undulations, respectively. Note that using the body size or length L as the length scale would not fundamentally affect our results or the rationale for scaling. We choose λ because it is associated with the wave speed of undulations.

Because we have shown that the power is spent to produce lateral oscillations, the power of lateral undulations will be used to obtain the scaling of power. Additionally, it has been shown (7) that, for swimmers such as eels, trout, and bluegill sunfish, the axial oscillations during swimming are very small compared to lateral oscillations. This provides a kinematic basis to use the power of lateral undulations as the scale for power. The power scaling (P_l) for lateral undulations would be proportional to the lateral force (F_l) times the lateral speed (fa), i.e., $P_l \sim F_l(fa)$. In inertia-dominated flows $F_l \sim \rho(fa)^2 A_p$, where a is the amplitude of undulations, ρ is the density of the fluid, and A_p is the projected area of the swimmer's body in the lateral direction. The dimensionless power spent can be written as $P'_{net} = P_{net}/P_l$.

The scaling of COT follows from the ratio of the scaling of power spent to the scaling of speed:

$$C_E = COT \frac{\lambda}{\rho a^3 f^2 A_p}, \quad [2]$$

where C_E is the dimensionless COT or the energy-consumption coefficient. A lower value of C_E is desirable because it indicates

lower energy consumption and therefore greater mechanical efficiency to move some distance. The utility of C_E is twofold. First, the scaling of COT gives insights into how various spatial and temporal parameters of a swimmer affect COT. These insights can be useful in the design of efficient underwater vehicles. Second, C_E enables comparison across species and length scales just like how the drag coefficient allows comparison of aerodynamic shapes across disparate length scales. Note that the form of Eq. 2 is very similar to the equation of drag coefficient, $C_d = D/(0.5\rho U^2 A)$, where C_d is the drag coefficient of a body, U is the speed of the body relative to the fluid, and A is the area normal to the fluid velocity. Thus, C_E can play the same role in quantifying energy consumption during propulsion as the drag coefficient does in quantifying drag on aircrafts, cars, and submarines. A typical trend of C_E vs. Reynolds number (Re) is similar to C_d vs. Re trend as demonstrated by simulations of zebrafish in *SI Appendix, section S4 and Fig. S8*.

Our next goal is to estimate C_E as a function of mass M , for swimming and flying animals. First we need to derive an allometric scaling for COT in terms of the mass of the animal ($COT \sim M^x$). To do this, mass scalings of all of the variables in Eq. 2 are required. The scalings of all of the variables except frequency are known [$A_p \sim M^{2/3}$, $\lambda \sim M^{1/3}$, $a \sim M^{1/3}$; (2)]. The allometric scaling of frequency is derived next.

Allometry of Movement

In this section we interrogate the allometric scaling of frequency, speed, and COT along with some additional variables.

The metabolic power, P_{met} , follows a scaling given by $P_{met} \sim M^\alpha$, where the value of α depends on the type of metabolic rate in question. The power generated by muscles of an animal moving its body at frequency f is given by $P_{musc} \sim Mf$ (16). The metabolic power is converted into the muscle power, which is then spent in doing work on the fluid (the required power). There will be some inefficiencies associated with the conversion from the metabolic to the muscle power, and from the muscle to the required power. As long as these inefficiencies do not strongly depend on the mass, the balance between the metabolic power and the required power can be used to estimate the allometric scaling of frequency.

Viscous forces dominate the inertia forces at low Re , whereas inertia forces dominate at high Re . The scaling of the power

Fig. 2. Theoretical scaling predictions for swimmers in the viscous and inertial regimes compared with data of different class and species of swimmers: (A) frequency scaling and (B) velocity scaling. Regression fits of the data are summarized in Table 1. Data sources: pentagrams (microorganisms) (29–33), squares (34), diamonds (35), and circles (2). For some microorganisms, the mass data were not available. In those cases the mass was computed using the body size and the water density assuming neutral buoyancy. Details of microorganism data can be found in *SI Appendix, Table S3*.

Fig. 3. Theoretical scaling predictions for flying animals compared with data of insects, bats, and birds: (A) frequency scaling and (B) velocity scaling. Regression fits of the data are summarized in Table 1. Data sources: triangles (insects) (34), pentagrams (bats) (34), circles (birds) (34), diamonds (birds) (36, 37), and squares (birds) (38).

required to undulate a swimmer's body is given by (SI Appendix, section S3)

$$P_l \sim \begin{cases} \mu(fa)^2 L, & \text{viscous forces dominate,} \\ \rho(fa)^3 A_p, & \text{inertia forces dominate,} \end{cases} \quad [3]$$

where μ is the viscosity of the fluid and L is a linear measure of the swimmer's size.

Consider the metabolic power $P_{met} \sim M^\alpha$. For the basal metabolic rate (BMR), the value of α has been reported to be either 3/4 (17–20) or 2/3 (21). Nagy (22) suggested the field metabolic rate (FMR) better reflects the real energy requirements than BMR. He notes that FMR was not significantly different from the scaling of BMR for birds and mammals (mammals: $\alpha = 0.73$, birds: $\alpha = 0.64$) (22). For most groups of animals, the scaling of routine metabolic rate with mass has little or no difference from that of BMR (see figure 7 in ref. 23) (24).

The power produced through the swimmer's metabolism must be at least same order as the power required to move the swimmer's body. Equating P_l to P_{met} , a scaling for frequency with respect to M is derived as (SI Appendix, section S5)

$$f \sim \begin{cases} M^{[-\frac{1}{6}, -\frac{1}{8}]}, & \text{viscous forces dominate,} \\ M^{[-\frac{1}{3}, -0.305]}, & \text{inertia forces dominate,} \end{cases} \quad [4]$$

where $[a, b]$ represents set of real numbers between the arguments a and b . We give a range of exponents because the value of α ranges from 2/3 to 3/4 in the literature. We can also arrive at the frequency scaling in the inertia regime using Hill's estimate of the muscle power $P_{musc} \sim Mf$ (16). To do so we equate the power produced by the muscles to the required power (Eq. 3), which gives $f \sim M^{-1/3}$. This agrees well with the frequency scaling in the inertia regime that was derived above based on the metabolic rate.

Swimming speed u scales as $u \sim f\lambda$. By substituting the scaling of frequency into this equation, the scaling of speed is found to be

$$u \sim \begin{cases} M^{[\frac{1}{6}, \frac{5}{24}]}, & \text{viscous forces dominate,} \\ M^{[0, 0.03]}, & \text{inertia forces dominate.} \end{cases} \quad [5]$$

In Fig. 2A we compare theoretical predictions of the frequency scaling to data of swimming animals ranging from a bacterium to

a sperm whale. It is seen that small animals with mass between 10^{-15} to 10^{-2} kg follow our scaling predicted for the swimmers in the viscous regime. The theoretical scaling predicted in the inertial regime also compares well with the trend in frequency data of larger animals. A similar comparison of the speed scaling with speed data are shown in Fig. 2B. Many microanimals use cilia for locomotion. For such animals the speed scaling we derived for undulatory propulsion may not be applicable (Fig. 2B).

Flying animals flap their wings normal to the direction of flight. Hence, fliers too spend their power laterally like undulatory swimmers. The frequency and velocity scalings of flying animals are derived similar to that for swimming (SI Appendix, section S6) to give $f \sim M^{[-\frac{1}{3}, -0.305]}$ and $u \sim M^{[0, 0.03]}$. In Fig. 3 the wing-beat frequency and speed of three classes of fliers, namely, insects, bats (mammals), and birds, are plotted against the body mass. It is inertial scaling that is mostly relevant in case of flying.

Next, we interrogate whether the speed of animals observed in nature is energetically optimal. For this we consider the speed of locomotion (u) that minimizes gross cost of transport (GCOT) (24), where GCOT is based on gross power. The gross power is the sum of the basal metabolic power and the power for locomotion (SI Appendix, section S7). Note that COT, defined earlier, is based only upon the power for locomotion. The optimal speed that minimizes GCOT is derived to be (SI Appendix, section S7):

$$u_{opt} \sim \begin{cases} M^{[\frac{1}{6}, \frac{5}{24}]}, & \text{viscous forces dominate,} \\ M^{[0, 0.03]}, & \text{inertia forces dominate.} \end{cases} \quad [6]$$

These are the same scalings found in data (Figs. 2B and 3B), which suggests that animals move with speed scales that also minimize GCOT.

We also note that the Strouhal number, $St = \frac{fa}{u}$, of most swimming and flying animals does not change across species or with size (25). We used the frequency and speed scalings, derived above for $\alpha = 2/3$ and $\alpha = 3/4$, to obtain St scaling (SI Appendix, section S8). In both cases where $\alpha = 2/3$ and $\alpha = 3/4$, as expected St is found to be independent of mass.

Fig. 4. (A) Cost of transport of small and large swimming animals compared with the theoretical scalings in the viscous and inertial regimes, respectively. Data sources: triangles (mammalian swimmers) (2), diamonds (aquatic flight) (2), circles (fish) (2), squares (fish) (1). (B) Cost transport of flying animals compared with the theoretical scaling in the inertial regime. Data sources: Diamonds (bat) (2), triangles (birds) (2), circles (insects) (2), and squares (flying) (1). Regression fits of the data are summarized in Table 1.

Table 1. A summary of theoretical scaling and regression fit of frequency, speed, and cost of transport, and theoretical scaling of optimal speed and Strouhal number for aquatic and aerial locomotion

		Swimming		Flying
		Viscous	Inertia	Inertia
Frequency (f)	Regression	$f = 3.15M^{-0.1}$ $R^2 = 0.82$	$f = 3.28M^{-0.27}$ $R^2 = 0.88$	$f = 5.3M^{-0.23}$ $R^2 = 0.67$
	Theoretical	$f \sim M^{[-\frac{1}{6}, -\frac{1}{8}]}$	$f \sim M^{[-\frac{1}{3}, -0.3]}$	$f \sim M^{[-\frac{1}{3}, -0.3]}$
Speed (u)	Regression	$u = 0.47M^{0.15}$ $R^2 = 0.49$	Independent of mass	$u = 12.5M^{0.11}$ $R^2 = 0.67$
	Theoretical	$u \sim M^{[\frac{1}{6}, \frac{5}{24}]}$	$u \sim M^{[0, 0.03]}$	$u \sim M^{[0, 0.03]}$
COT	Regression	$COT = 0.76M^{0.57}$ $R^2 = 0.99$	$COT = 7.3M^{0.69}$ $R^2 = 0.98$	$COT = 5.4M^{0.685}$ $R^2 = 0.95$
	Theoretical	$u \sim M^{[0.5, 0.54]}$	$COT \sim M^{[\frac{2}{3}, 0.72]}$	$COT \sim M^{[\frac{2}{3}, 0.72]}$
Optimal speed (u_{opt})	Theoretical	$u \sim M^{[\frac{1}{6}, \frac{5}{24}]}$	$u \sim M^{[0, 0.03]}$	$u \sim M^{[0, 0.03]}$
Strouhal number (St)	Theoretical	C	C	C

C implies that the scaling is independent of mass.

The allometric scaling of COT can now be derived by substituting the mass scaling of the variables in Eq. 2 (*SI Appendix, section S9*):

$$COT \sim \begin{cases} M^{[\frac{1}{2}, 0.54]}, & \text{viscous forces dominate,} \\ M^{[\frac{2}{3}, 0.72]}, & \text{inertia forces dominate.} \end{cases} \quad [7]$$

Although two different metabolic rates were used to derive the scaling for COT, it can be seen that they lead to COT scalings that are not very different. The above scalings are compared with experimental data for COT of swimming and flying animals in Fig. 4.

The allometric scalings of COT, frequency, speed, optimal speed, and Strouhal number are summarized in Table 1. We see that the regression fit scaling is generally aligned with theoretical predictions. Specifically, the COT scaling is in excellent agreement with predictions. Additional effects may lead to deviations from predicted scalings; however, our analysis captures the primary mechanisms that cause the basic trends in a physically consistent framework.

C_E Applied to Swimming and Flying Animals

It follows from Eq. 2 that the energy-consumption coefficient $C_E = COT \frac{\rho_b^{2/9}}{k_m^{2/3} \rho^{1/3} M^{2/3}}$, where $\alpha = 2/3$ is used, ρ_b is the mean body density [ρ_b of swimming and flying animals is similar to water density; (26, 27)], and k_m is a constant in the metabolic rate equation $P_{met} = k_m M^\alpha$ (derivation in *SI Appendix, section S9*). By using experimentally available values of COT we get empirical measurements of C_E . In general, k_m is not known for the experimental data we found. Hence, we plot $\tilde{C}_E = k_m^{2/3} C_E$ in Fig. 5, which is based on experimental data. $k_m^{2/3}$ is expected to be $\mathcal{O}(1)$ and constant (*SI Appendix, section S9*) (22) therefore, $\tilde{C}_E$ provides same insights as C_E . Note that if $\alpha = 3/4$ were used for defining C_E above, the qualitative trend of C_E in Fig. 5 would not change.

Fig. 5 shows that swimming animals above 1 kg and almost all fliers show no meaningful trend in $\tilde{C}_E$ vs. M (*SI Appendix, section S9* for a discussion on how to convert this to a trend with respect to Re). Thus, COT scales as $M^{2/3}$ as predicted for the inertial regime. This implies that all fliers are almost equally efficient as if they are dynamically equivalent. The same is true of swimmers above 1 kg. Increasingly massive animals are not mechanically more efficient. $\tilde{C}_E \sim M^{-1/6}$ for swimmers with small mass [Re is

up to $\mathcal{O}(100)$], which is consistent with COT scaling of $M^{1/2}$ in the viscous regime (Eq. 7). This implies that small-mass swimmers are also dynamically equivalent and equally efficient, but according to the viscous scaling, $\tilde{C}_E$ for smaller swimmers is lower, which indicates more effective use of energy to move compared with massive swimmers. $\tilde{C}_E$ begins to transition from a lower value to a higher value around 10^{-2} kg, this transition ends around mass of 1 kg. Flying animals are found to require relatively more energy compared with swimmers. This is presumably because flying animals spend energy to not only move forward but also to overcome gravity.

The Re corresponding to the beginning and end of the transition of $\tilde{C}_E$ are around $\mathcal{O}(100)$ and $\mathcal{O}(10^3)$ (*SI Appendix, Fig. S9*), respectively. Note that the apparent transition in $\tilde{C}_E$ is not very different from the change in the trend of drag coefficient C_d for flow over a body. $C_d \sim 1/Re$ for low Re and $C_d \sim \text{constant}$ for large Re . C_d deviates significantly from a $1/Re$ trend to transition toward a constant value between Re of $\mathcal{O}(100)$ and $\mathcal{O}(10^3)$. Similarly, C_E transitions from $M^{-1/6}$ trend to a relatively constant value between the same Re . The transition in flying animals takes place between 10^{-6} and 10^{-4} kg. The dip in $\tilde{C}_E$ of flying animals,

Fig. 5. Energy-consumption coefficient $\tilde{C}_E = COT \frac{\rho_b^{2/9}}{k_m^{2/3} \rho^{1/3} M^{2/3}}$ of swimming and flying animals plotted against mass. Data for swimming and flying animals are colored red and blue, respectively. Data sources: red triangles (mammalian swimmers) (2), red diamonds (aquatic flight) (2), red circles (fish) (2), red squares (fish) (1), blue diamonds (bat) (2), blue triangles (birds) (2), blue circles (insects) (2), and blue squares (flying) (1).

as the mass decreases from 10^{-4} to 10^{-6} kg, is an indicator of the transition (Fig. 5). Similar to $\tilde{C}_E$ transition in swimming, Re corresponding to the transition in flying is also between $\mathcal{O}(100)$ and $\mathcal{O}(10^3)$ (SI Appendix, section S9.2). We also note that undulatory or flapping swimming ends and ciliary or flagellar swimming takes over for mass less than 10^{-6} kg (Fig. 2); the Re corresponding to this mass is between 10 and 20, which has been shown to be the critical Re for transition between ciliary and flapping swimming in *Clione antarctica* (28).

In summary, C_E provides insights into energy use to move some distance no matter how long it takes. If the time to cover a distance is important then a different metric such as the swimming speed scaled by the wave velocity could be relevant. Finally, we note that C_E and $\tilde{C}_E$ not only capture the non-dimensional trend of COT but also of COT per unit body length and of COT per unit body length per unit mass. In this sense the energy-consumption coefficient (C_E) is a fundamental non-

dimensional measure of energy use in swimming and flying (SI Appendix, section S9). We anticipate that the concept of energy-consumption coefficient will be applicable to terrestrial locomotion, automotive vehicles, and self-propelled vehicles in general.

Sign Convention

Swimming velocity is positive for swimmers swimming in the positive directions of the axes. Power spent by the swimmer on the fluid is positive. Forces presented in this work are the forces on the fluid by the swimmer. Thus, for a swimmer swimming along positive x direction drag force along x axis is positive.

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- Schmidt-Nielsen K (1972) Locomotion: Energy cost of swimming, flying, and running. *Science* 177(4045):222–228.
- Videler JJ (1993) *Fish Swimming* (Springer, London), Vol 10.
- Lauga E (2007) Floppy swimming: Viscous locomotion of actuated elastica. *Phys Rev E Stat Nonlin Soft Matter Phys* 75(4 Pt 1):041916.
- Lauga E, Powers TR (2009) The hydrodynamics of swimming microorganisms. *Rep Prog Phys* 72:096601.
- Purcell EM (1997) The efficiency of propulsion by a rotating flagellum. *Proc Natl Acad Sci USA* 94(21):11307–11311.
- Borazjani I, Sotiropoulos F (2010) On the role of form and kinematics on the hydrodynamics of self-propelled body/caudal fin swimming. *J Exp Biol* 213(1):89–107.
- Tytell ED (2007) Do trout swim better than eels? Challenges for estimating performance based on the wake of self-propelled bodies. *Exp Fluids* 43:701–712.
- Tytell ED, Lauder GV (2004) The hydrodynamics of eel swimming: I. Wake structure. *J Exp Biol* 207(Pt 11):1825–1841.
- Videler JJ, Hess F (1984) Fast continuous swimming of two pelagic predators, saithe (pollachius virens) and mackerel (scomber scombrus): A kinematic analysis. *J Exp Biol* 109:209–228.
- Pedley TJ, Hill SJ (1999) Large-amplitude undulatory fish swimming: Fluid mechanics coupled to internal mechanics. *J Exp Biol* 202(Pt 23):3431–3438.
- Lighthill MJ (1960) Note on the swimming of slender fish. *J Fluid Mech* 9:305–317.
- Tytell ED, et al. (2010) Disentangling the functional roles of morphology and motion in the swimming of fish. *Integr Comp Biol* 50(6):1140–1154.
- Tytell ED, Lauder GV (2004) The hydrodynamics of eel swimming II. Effect of swimming speed. *J Exp Biol* 207(Pt 19):3265–3279.
- Webb PW (1975) Hydrodynamics and energetics of fish propulsion. *Bull Fish Res Board Can* 190:1–159.
- Schultz WW, Webb PW (2002) Power requirements of swimming: Do new methods resolve old questions? *Integr Comp Biol* 42(5):1018–1025.
- Hill AV (1950) The dimensions of animals and their muscular dynamics. *Sci Prog* 38:209–230.
- Brody S (1945) *Bioenergetics and Growth* (Reinhold, New York).
- Kleiber M (1961) *The Fire of Life. An Introduction to Animal Energetics* (Wiley, New York).
- Hemmingsen A (1960) *Energy metabolism as related to body size and respiratory surfaces and its evolution*. (Steno Memorial Hospital and Nordinsk Insulin Laboratorium, Gentofte, Denmark).
- Kozłowski J, Konarzewski M, Gawelczyk AT (2003) Cell size as a link between non-coding DNA and metabolic rate scaling. *Proc Natl Acad Sci USA* 100(24):14080–14085.
- White CR, Seymour RS (2003) Mammalian basal metabolic rate is proportional to body mass^{2/3}. *Proc Natl Acad Sci USA* 100(7):4046–4049.
- Nagy KA (2005) Field metabolic rate and body size. *J Exp Biol* 208(Pt 9):1621–1625.
- Brett JR (1972) The metabolic demand for oxygen in fish, particularly salmonids, and a comparison with other vertebrates. *Respir Physiol* 14(1):151–170.
- Tucker VA (1970) Energetic cost of locomotion in animals. *Comp Biochem Physiol* 34(4):841–846.
- Taylor GK, Nudds RL, Thomas AL (2003) Flying and swimming animals cruise at a Strouhal number tuned for high power efficiency. *Nature* 425(6959):707–711.
- Davenport J (1999) Swimbladder volume and body density in an armoured benthic fish, the streaked gurnard. *J Fish Biol* 55:527–534.
- Hamerschock DM, Seamans TW, Bernhardt GE (1995) Determination of body density for 12 bird species. *Ibis* 137:424–428.
- Childress S, Dudley R (2004) Transition from ciliary to flapping mode in a swimming mollusc: Flapping flight as a bifurcation in Re_m . *J Fluid Mech* 498:257–288.
- Nakaoka Y, Tanaka H, Oosawa F (1984) Ca²⁺-dependent regulation of beat frequency of cilia in Paramecium. *J Cell Sci* 65:223–231.
- Ueyama S, Katsumaru H, Suzuki T, Nakaoka Y (2005) Halteria grandinella: A rapid swimming ciliate with a high frequency of ciliary beating. *Cell Motil Cytoskeleton* 60(4):214–221.
- Drewes CD, Fournier CR (1993) Helical swimming in a freshwater oligochaete. *Biol Bull* 185:1–19.
- Matsumoto GI (1991) Swimming movements of ctenophores, and the mechanics of propulsion by ctenophore rows. *Hydrobiologia* 216–217:319–325.
- Magariyama Y, et al. (1995) Simultaneous measurement of bacterial flagellar rotation rate and swimming speed. *Biophys J* 69(5):2154–2162.
- Bejan A, Marden JH (2006) Unifying constructal theory for scale effects in running, swimming and flying. *J Exp Biol* 209(Pt 2):238–248.
- Sato K, et al. (2007) Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proc Biol Sci* 274(1609):471–477.
- Pennycuik CJ (1990) Predicting wingbeat frequency and wavelength of birds. *J Exp Biol* 150:171–185.
- Pennycuik C (1996) Wingbeat frequency of birds in steady cruising flight: New data and improved predictions. *J Exp Biol* 199(Pt 7):1613–1618.
- Sato K, et al. (2009) Scaling of soaring seabirds and implications for flight abilities of giant pterosaurs. *PLoS ONE* 4(4):e5400.