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Propeller efficiency and the spectrum of propulsor form with speed, from pike to tuna, vulture to swift.

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Code is available at https://doi.org/10.5281/zenodo.17791322. Further explanation and animated parameter sweeps at https://jimusherwoodresearch.com/wings-and-fins/.

Conflict of interest

I/We declare we have no competing interests

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Propeller efficiency and the spectrum of propulsor form with speed, from pike to tuna, vulture to swift.

Abstract

Tail fins, flukes, flapping wings and propellers are propulsors that generate thrust with foils. Efficient thrust production requires suitable foil design and operation. Simplified propeller theory allows the interactions between foil shape and kinematics to be addressed within the context of mechanical or 'propeller' efficiency. Efficient thrust at low forward speeds and/or high motor power is shown to require high foil area and/or lift coefficient. This offers an account for the relatively broad foils of the slow pike and birds requiring take-off at low speeds and high power. The efficiency benefit of high lift coefficients is consistent with the separated emarginate primaries forming multi-slat aerofoil sections observed not only in competent thermal soarers (vultures, storks etc.) but also many game birds. Efficient thrust at high speeds requires relatively small foil area and/or low lift coefficients, consistent with the simple, high aspect ratio foils of tuna and swifts. The spectrum of relatively high-area to low-area foils does not imply a compromise between acceleration and efficiency; both ends of the scale may result in efficient propulsors, with high thrust capacity for given power supply, but with differences in form relating simply to speed.

1. Introduction

Understanding the mechanical principles underlying the function of observed animal form and action may be helpful when considering a species' ecology and evolution, and is vital if sensible bioinspired design is to be attempted. Swimming and flying are energetically demanding activities with clear biomimetic potential in relation to water- and aircraft development. This paper exploits simplified propeller theory to address the relationship between mechanical efficiency – and so thrust capacity for given power and speed – with foil planform and section.

1.1 Fish

Fish are very diverse in form and have many functional demands including speed, manoeuvrability, stability, crypsis, economy and acceleration. Here, a single axis is addressed which might be termed the 'pike-tuna' axis (Figure 1a,b), with pike considered high-thrust, 'acceleration' specialists, and tuna high speed economy or 'cruising' specialists (Webb, 1984). By analogy with large planes that take off or land with extended flaps that produce a high wing area to generate sufficient aerodynamic forces at low speeds, the relatively broad, high-area tail fins of the pike may be considered suitable for high force production for acceleration at low speed. By

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analogy with modern gliders with very shallow glide angles, the relatively slender, high aspect ratio tuna tail fin might be viewed as adapted for high efficiency, with high lift to drag ratio. While such arguments are appealing, they are based on fixed-wing principles. Does this reasoning behind the ‘pike for acceleration v.s tuna for efficiency’ spectrum stand when considering the demands of oscillating the foils to provide thrust?

1.2 Birds

Fixed wing theory can be reasonably applied to soaring and gliding birds (Pennycuick 1989). The benefit of large-span, small-area – and so high aspect ratio – wings for gliding albatrosses appears inarguable: a high span allows a large, slow mass of air to be accelerated downward, so weight can be supported with low induced drag, while a small area results in low profile drag. A constraint to wingspan and a demand for very slow flight – perhaps allowing the ground to be surveyed, as with red kites, or for soaring in very, very tight circles – would account for lower aspect ratio wings. However, many soarers have broad wings that do not fit the previous two points: Pennycuick (1989, P.106) concludes: “*The vulture’s extremely broad wing is not ideal for any aspect of soaring* [when contrasted with a comparable petrel with narrow wings] *except climbing in very narrow thermals. One probably should look at other aspects of performance, such as take-off, to account for it”.* Fixed-wing theory alone therefore appears inadequate for explaining wing form and the spectrum from broad wings with separated, often highly emarginated primaries (Figure 1c) to high aspect ratio, simple planform wings of the fastest flapping fliers (Figure 1d).

1.3 Propellers and fans

Biological and bio-inspired studies tend to treat the effects of foil properties and their oscillatory motions independently (e.g. Withers, 1981; Taylor et al., 2003; Xie et al., 2025). Propeller theory provides a framework for integrating these contributions to propulsive efficiency. Efficiency of thrust production is partly determined by lift to drag ratio (confusingly sometimes termed ‘aerodynamic efficiency’; this term only applies in fixed-wing analysis), which depends on aerofoil section, angle of incidence and planform. But in addition to this, efficiency depends on the tip speed ratio λ (see equation 1 below) which may also be expressed in terms of helix angle and has an equivalence for oscillating foils related to Strouhal number (Usherwood, 2025). Animals are observed to swim and fly under cruising conditions within a moderately conserved range of Strouhal numbers, consistent with high mechanical efficiency from propeller geometry, but somewhat lower than appears optimal from a purely mechanical perspective.

Propellers and fans range from very low aspect ratio, multibladed to very high aspect ratio, two- (rarely single-) bladed (which may also be expressed as high and low rotor solidity respectively). Far too many factors are important in propeller design to be covered here, and many of them have no biological relevance. For the present, it

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is sufficient to note that propellers on relatively slow vehicles (or fans) with relatively high power and constrained diameter tend to have broad blades, and may have complex geometries including sharp, swept leading edges (Figure 1e); and that propellers on relatively fast vehicles with relatively low power tend to have high aspect ratio blades with simpler planforms (Figure 1f).

2. Theoretical development

This analysis largely follows Usherwood, 2025 (see also William Froude, 1878). It assumes that the morphological and kinematic complexity of oscillating biological foils – fins, flukes and wings – can be sufficiently approximated by considering a single representative section. This assumption is less valid for very low aspect ratio and flexible fins (and is not suitable at all for eel-like or pectoral-fin propulsion) and proximal wing portions in level flight, where the foil is more responsible for weight support rather than propulsion. However, it is a useful assumption when considering discrete caudal fins, and bird wings during take-off, or the more distal wing sections in level flight. The representative section has forward velocity (-)*U* and a perpendicular plunging or flapping velocity (-)*V* (figure 2a), with

$$V = U\lambda, \tag{1}$$

meaning that

$$\varepsilon = \tan^{-1}(V/U) = \tan^{-1}(\lambda). \tag{2}$$

Lift *L* acts perpendicular to the resultant air velocity U_r (note that induced flows are not considered – this is effectively a single blade element simplification without actuator disc corrections); drag *D* acting on the foil acts in the direction of U_r . The magnitude of the lift force is determined by the air or water density ρ, foil lift coefficient C_L and area *S*:

$$L = \frac{\rho}{2} C_L S (U^2 + V^2) \tag{3}$$

The relationship between drag and lift is given by the lift to drag ratio *LDR* (initially assumed to constant, but developed later):

$$D = \frac{L}{LDR}. \tag{4}$$

Thrust *T* acts opposite to *U*, and the resisting force *R* that demands torque and power acts perpendicular to *T*, in the direction of *V*. From the trigonometry of Figure 2a:

$$T = L\sin(\epsilon) - D\cos(\epsilon); \tag{5}$$

$$R = L\cos(\epsilon) + D\sin(\epsilon). \tag{6}$$

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The useful mechanical power supplied P_{out} – which may overcome body drag or drive climb or an acceleration – is:

$$P_{\text{out}} = TU. \tag{7}$$

The mechanical power demanded P_{motor} due to the foil at V against the force R is:

$$P_{\text{motor}} = RV. \tag{8}$$

The ratio of P_{out} to P_{motor} is the mechanical (or 'propeller') efficiency η:

$$\eta = \frac{P_{\text{out}}}{P_{\text{motor}}} = \frac{TU}{RV}. \tag{9}$$

It should be noted that this mechanical efficiency is different from both Froude (sometimes 'ideal propulsive') efficiency as adopted in the engineering literature (Houghton et al., 2017) and metrics for economy. Froude efficiency (this relates to Robert Froude, son of William) describes the best theoretical mechanical efficiency that can be achieved for a propulsor of given dimensions, thrust, speed and fluid density; low span, high thrust and low fluid density has to result in low Froude efficiency because a high rate of energy must be put into the wake. This form of efficiency relates to induced flows and is not treated here other than indirectly in relation to *LDR* below. Confusingly, the term 'Froude efficiency' in the swimming literature, largely following Lighthill (1960), is equivalent to the mechanical efficiency of equation 9. The term 'economy' as often applied to studies of animal locomotion relates to the work demand for a given task – for instance, for a distance travelled. This metric is also not considered here – and so neither is steady-state swimming (a limitation of the approach) – as it requires that body drag is also addressed.

The mechanical efficiency of thrust production as adopted here (equation 9) is equivalent to the ratio of the output thrust (T_{out}=P_{out}/U) to the ideal, η =1, thrust (T_{ideal}=P_{motor}/U). While this is a mathematically trivial point, it means that viewing pike as adapted for acceleration and tuna adapted for efficiency may be misleading. A high thrust capacity – for a given forward speed and motor power – is the same thing as a high efficiency, and it may be that both pike and tuna are adapted towards both high thrust and high efficiency, but for low and high speeds respectively. True, pike may still be viewed as adapted for high acceleration; but this is synonymous with high efficiency given high motor power and low speed, and no compromise between acceleration and efficiency need be invoked.

Figure 2c show contour plots for efficiency as a function of U and $C_L.S$ assuming a constant power supply (calculated numerically by incrementing λ until the power limit is reached). Parameters used are broadly appropriate for a large bird in powerful downstroke: ρ =1.2 kg/m^3; *LDR* = 6; P_{motor}=100 W.

At high *LDR* the contribution of drag to power demand becomes small, so

$$R \approx L\cos(\epsilon) \tag{10}$$

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At high *LDR* optimal efficiency is found (as was developed previously for oscillating foils in relation to Strouhal number (Usherwood, 2025), and is a classic (Froude, 1878) and textbook result for propeller design (e.g. Barnard and Philpott, 1995)) when $V \approx U$. This allows a simple analytical approximation for the optimal foil properties $C_L.S$ as a function of power supply and speed. Combining equations 3, 6 and 8 (and noting $\cos(45°) = \frac{1}{\sqrt{2}}$):

$$P_{\mathrm{motor}} = RV \approx \frac{\rho}{2} C_{\mathrm{L}} S \, 2U^2 \frac{1}{\sqrt{2}} U \qquad (11)$$

which can be rearranged to give:

$$C_{\mathrm{L}} S \approx \frac{\sqrt{2} P_{\mathrm{motor}}}{\rho U^3} \qquad (12)$$

This analytical approximation for high *LDR* is displayed (Figure 2d) alongside optima derived numerically for a range of *LDR*.

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3. Discussion

The relationship described between efficiency and various kinematic and morphological parameters is not asserted as being novel: it is clearly understood in propeller and fan design. This paper is intended as an application of propeller principles to biology as a means of revealing aspects of form and function that cannot be simply addressed with extension of fixed-wing theory.

3.1 Form for low *U*

Foils with higher $C_L.S$ allow higher efficiency, or higher thrust for a given power, at low speeds.

At low forward speeds, thrust can only be generated efficiently with a foil of high lift coefficient and/or area. For a given motor power, a foil with low $C_L.S$ would be driven with high *V*, deviating from the $V \approx U$ geometry required for high propeller efficiency (figure 2b). For a constrained span (the constraints to span are not considered here, and certainly contrast between fish, bird, fan and propeller), this results in a low aspect ratio foil typical of the pike tail fins; or broad-winged birds with explosive or highly loaded low-speed take-off ranging from pheasant to vulture to stork; or to a desk fan. A high lift coefficient is a complementary benefit with an effect equivalent to a high area. Desk fans have sharp, swept leading edges/tips that produce high-lift leading-edge / tip vortices with clear parallels to the leading-edge vortices described for a range of flapping (Ellington et al., 1996) and revolving foils (Usherwood and Ellington, 2002). By analogy to the fan, the multi-slat foils produced by separated and/or emarginate primaries during low-speed take-off may function to improve the efficiency – directly equivalent to increasing the thrust capacity for a given power – simply by increasing C_L of a flapping wing. Because emarginate primaries are very apparent in many successful thermal-soaring birds (vultures, eagles, storks etc.) they are sometimes viewed as analogues of winglets in aircraft, with the function of reducing induced drag (e.g. Cone, 1964, Tucker, 1993). However, it has long been recognised that the distribution of emarginate primaries does not correlate well with soaring (Graham, 1930; Saville, 1956; Brown, 1977, Van Oorschot et al., 2016) (and many birds are effective soarers without such primaries), and a role in high-powered take-off has been suggested . While there are alternative explanations for advantages of emarginate primaries during take-off (see particularly Graham, 1930), the propeller analysis indicates a simple benefit in terms of efficiency and therefore thrust and acceleration at low speeds.

3.2 Form for high *U*

Foils with lower $C_L.S$ allow higher efficiency, or higher thrust for a given power, at higher speeds.

At high forward speeds, operating a foil with high S and C_L would require it, for a given power, to flap or rotate relatively slowly because of the P_{motor} constraint (figure 2b), deviating from the optimum geometry for efficiency. Operating at a lower C_L would result in deviation from the optimal *LDR*: while a low angle of incidence would allow a lower C_L and enable a higher, more efficient velocity V, the concomitant reduction in *LDR* means that high efficiency is not possible with a simple kinematic change alone. This accounts for the relatively slender, high aspect ratio foils of tuna and swift, considered among the fastest swimmers and flapping fliers respectively. Foils with high *LDR*, even at the cost of lower operating C_L, might be predicted, consistent with windtunnel measurements of isolated bird wings (Withers, 1981).

3.3 Qualitative considerations for the spectrum between low-*U* and high-*U* foils

The development presented here begins by assuming any interaction between *LDR* and $C_L.S$ can be ignored. The influence of *LDR* on optimal $C_L.S$ as a function of U (Figure 2d) appears sufficiently minor to justify this as a starting point. It does suggest that the main relationship between increased speed and reduced $C_L.S$ is robust, but that it may not be quite as strong as indicated by equation 12. Slow-specialised, low aspect ratio foils with thick, cambered sections and with high-lift multi-slat devices would have lower *LDR*; fast-specialised high aspect ratio foils with thin, less cambered sections and simple planforms would have high *LDR*. The resulting interaction is shown qualitatively in Fig. 2d.

3.4 Conclusion

Pike and tuna caudal fins may be considered efficient propulsor designs suited to low and high speeds respectively, producing high thrust capacity for given power supply. This thrust capacity enables high acceleration of the pike at low speeds, and overcoming of body drag by tuna at high speeds. Relatively broad fins and wings with high lift coefficients (in the case of birds, potentially associated with separated

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and emarginate primaries), are efficient and therefore produce high thrust at low speeds despite reduced lift-drag ratios. Relatively slender, high-aspect ratio fins and wings are efficient at high forward speeds and do not benefit from elevated lift coefficients. The high lift-drag ratios afforded by high aspect ratio, moderate lift coefficient foils provide a supplementary contribution to efficiency; however, high aspect ratio and low operating C_L foils are found to be efficient at high speeds from propeller theory even without this contribution. Propeller theory explains aspects of fish and bird foil design that cannot be accounted for with fixed-wing aerodynamics and analogy with aeroplane wings.

Author contributions

Single author.

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Data and code accessibility

Code is available at https://doi.org/10.5281/zenodo.17791322. Further explanation and animated parameter sweeps at https://jimusherwoodresearch.com/wings-and-fins/.

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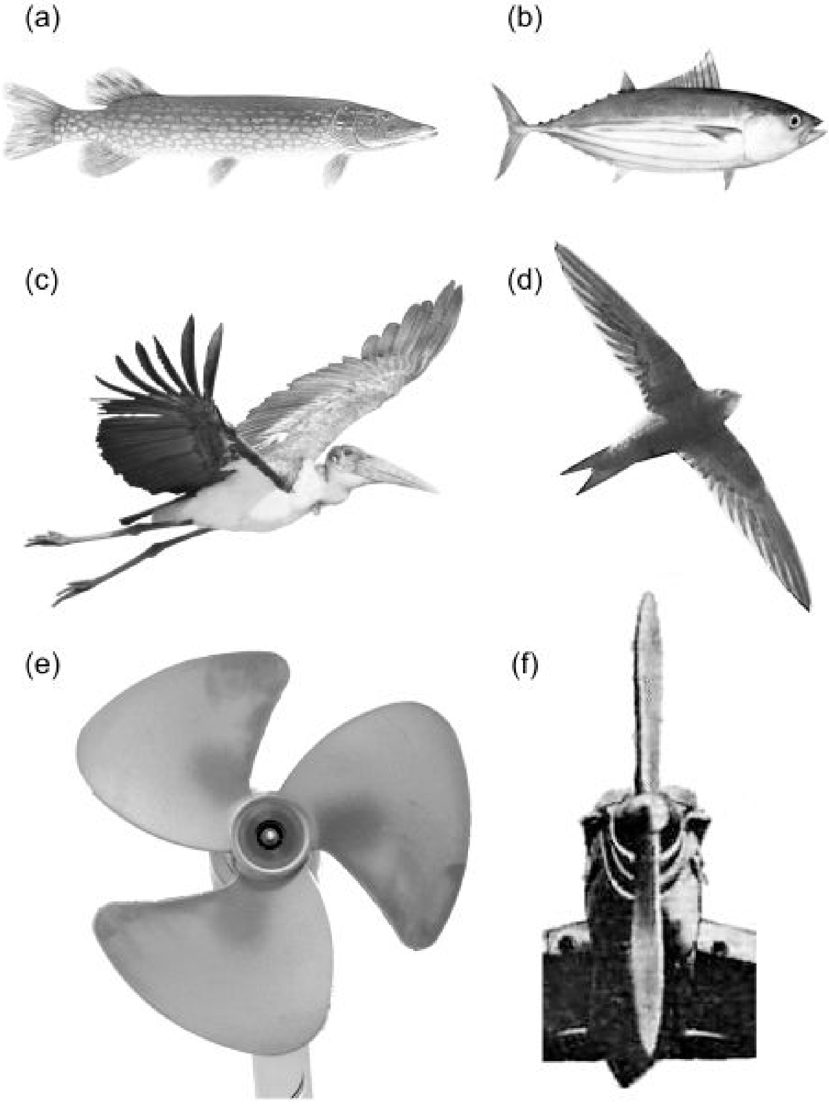

Figure 1

Figure 1 legend

Fish (northern pike (a), skipjack tuna (b)), bird (marabou stork (c), swift (d)) and rotor (desk fan (e), propeller of a Supermarine 224, a very early model of Spitfire, (f)) showing relatively broad, low aspect ratio propulsor foils related to slow progression (a, c, e) contrasting with narrow, high aspect ratio foils associated with higher speed swimming or flying (b, d, f).

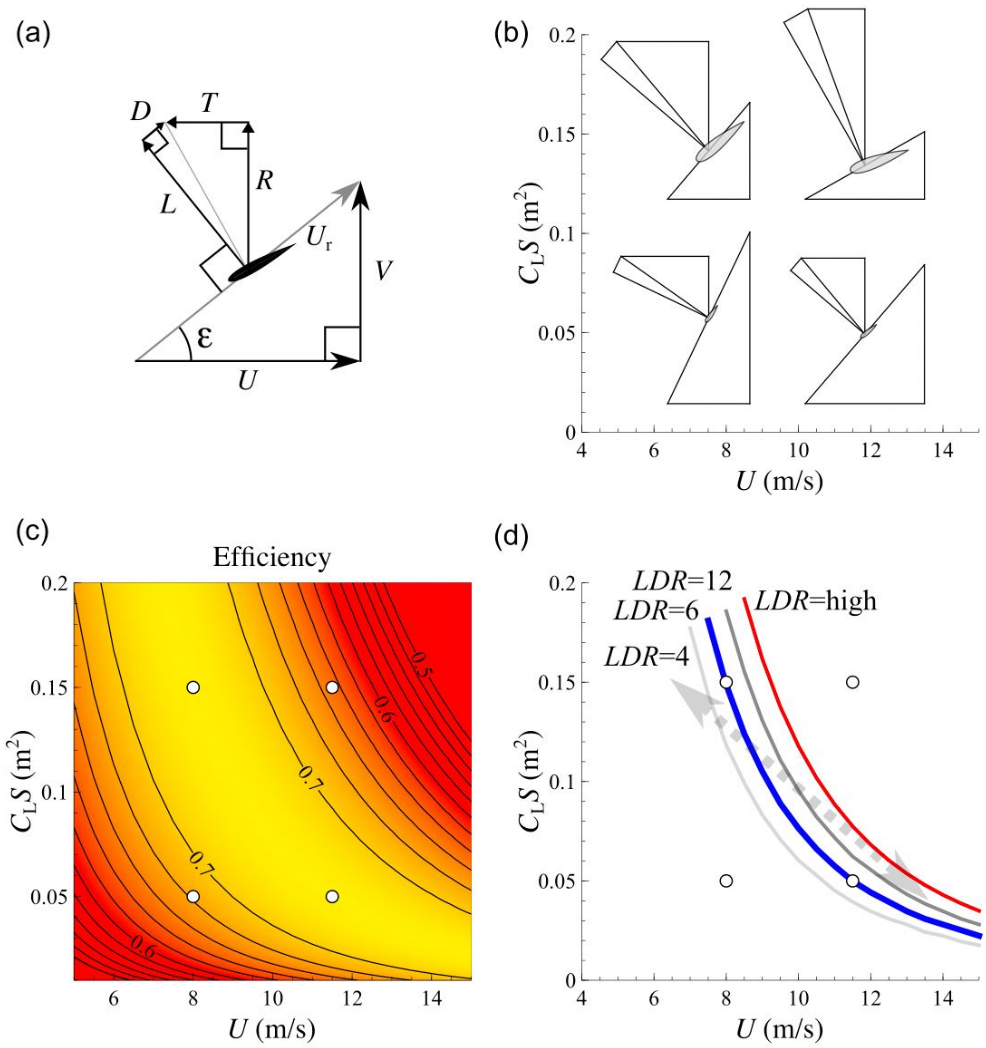

Figure 2

Figure 2 legend

Simplifying propeller geometry indicating symbols (see text) (a) and conditions for equal motor power for four combinations of speed *U* and $C_L.S$ (b). Efficiency at given power (100 W) and air density (1.2 kg/m^3) depends on *U*, $C_L.S$ and *LDR*; the surface for *LDR*=6 is shown (c). (The same plot for water, assuming a thousandfold greater density, would scale C_LS by 1/1000). Optima for a range of *LDR* (d) include the *LDR*=6 used on the surface plot (blue line) and the analytical relationship equation 12 for very high *LDR* (red line). White circles (c, d) relate to the four geometries (b); top left and bottom right are both maximally efficient for respective *U* (and $V \approx U$); bottom left has too small a foil and deviates from $V \approx U$ by excess *V* before the power constraint is hit; top right has too large a foil, and the power constraint prevents the foil from moving with sufficient *V* to achieve $V \approx U$. Grey dashed arrow (d) shows a qualitative interaction between $C_L.S$ and *LDR* for optimal $C_L.S$ across speed; low $C_L.S$ foils would be expected to have high *LDR*.

References

Barnard, R.H. and Philpott, D.R. (1995). Aircraft flight. A description of the physical principles of aircraft flight. 2nd edition. Pearson. ISBN 10: 0582236568 / ISBN 13: 9780582236561.

Brown, R.H.J. (1977). Discussion contribution. Separated primary feathers. In: Scale effects in animal locomotion. Edited by T.J. Pedley. Academic Press, London.

Cone, C.D., JR. (1964). The design of sailplanes for optimum thermal soaring performance. NASA technical note D-2052, 1-48.

Ellington, C.P., van den Berg, C., Willmott, A.P. and Thomas, A.L.R. (1996). Leading-edge vortices in insect flight. Nature 384, 626-630.

Froude, W. (1878). On the elementary relation between pitch, slip, and propulsive efficiency. Transactions of the Institution of Naval Architects. 19, 47-

Graham, R.R. (1930). Safety devices in wings of birds. British Birds 24, 34-47.

Houghton, E.L., Carpenter, P.W., Collicott, S.H., Valentine, D.T. (2017). Aerodynamics for engineering students, seventh edition. Elsevier. ISBN: 978-0-08-100194-3.

Lighthill, M.J. (1960). Note on the swimming of slender fish. J. Fluid Mech. 9, 305-317. Doi: 10.1017/S0022112060001110.

Pennycuick, C.J. (1989). Bird flight performance: a practical calculation manual. Oxford University Press, Oxford.

Saville, D.B.O. (1956). Adaptive evolution in the avian wing. Evolution. 11, 212-224.

Taylor, G.K., Nudds, R.L. and Thomas, A.L.R. (2003). Flying and swimming animals cruise at a Strouhal number tuned for high power efficiency. Nature. 425, 707-711. doi:10.1038/nature02000.

Tucker, V.A. (1993). Gliding birds: reduction of induced drag by wing tip slots between the primary feathers. J. Exp. Biol. 180, 285-310.

Usherwood, J.R. (2025). Limiting and optimal Strouhal numbers or tip speed ratios for cruising propulsion by fins, flukes, wings and propellers. J. R. Soc. Interface. Doi: 10.1098/rsif.2024.0730.

Usherwood, J. R. and Ellington, C. P. (2002). The aerodynamics of revolving wings. I. Model hawkmoth wings. J. Exp. Biol. 205, 1547–1564.

Van Oorschot, B.K., Mistick, E.A. and Tobalske, B.W. (2016). Aerodynamic consequences of wing morphing during emulated take-off and gliding in birds. J. Exp. Biol. 219, 3146-3154. DOI: 10.1242/jeb.136721

For Review Only

Webb, P.W. (1984). Form and function in fish swimming. Scientific American. 251, 72-83.

Withers, P.C. (1981). An aerodynamic analysis of bird wings as fixed aerofoils. J. Exp. Biol. 90, 143-162.

Xie, M., Pu, T., Zhoe, C., Guo, C., Zhang, Y. (2025). Effects of sweep angle and flexural stiffness of a tuna-like caudal fin on its swimming performance. Ocean engineering, 32. Doi: 10.1016/j.oceaneng.2025.120780.

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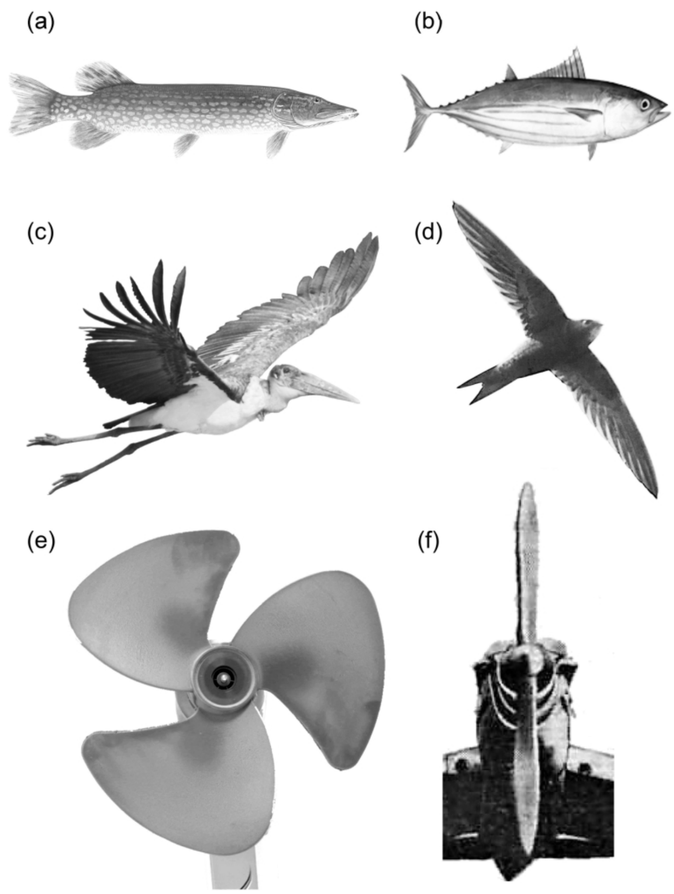

Figure 1

Fish (northern pike (a), skipjack tuna (b)), bird (marabou stork (c), swift (d)) and rotor (desk fan (e), propeller of a Supermarine 224, a very early model of Spitfire, (f)) showing relatively broad, low aspect ratio propulsor foils related to slow progression (a, c, e) contrasting with narrow, high aspect ratio foils associated with higher speed swimming or flying (b, d, f).

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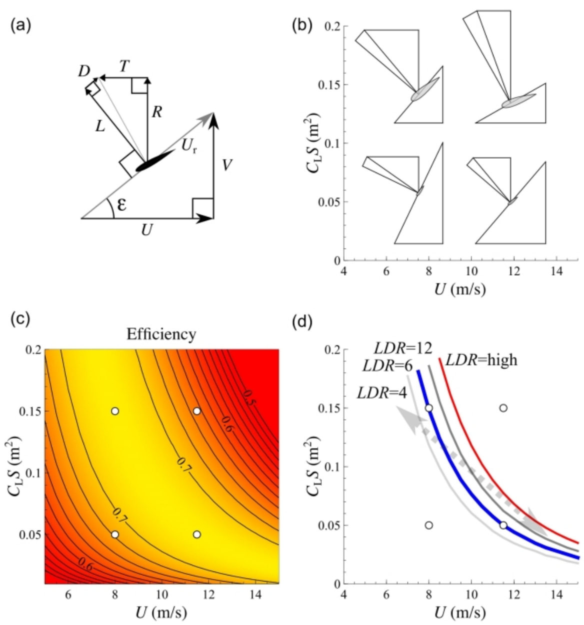

Figure 2

Simplifying propeller geometry indicating symbols (see text) (a) and conditions for equal motor power for four combinations of speed U and CL.S (b). Efficiency at given power (100 W) and air density (1.2 kg/m3) depends on U, CL.S and LDR; the surface for LDR=6 is shown (c). (The same plot for water, assuming a thousandfold greater density, would scale CLS by 1/1000). Optima for a range of LDR (d) include the LDR=6 used on the surface plot (blue line) and the analytical relationship equation 12 for very high LDR (red line). White circles (c, d) relate to the four geometries (b); top left and bottom right are both maximally efficient for respective U (and V≈U); bottom left has too small a foil and deviates from V≈U by excess V before the power constraint is hit; top right has too large a foil, and the power constraint prevents the foil from moving with sufficient V to achieve V≈U. Grey dashed arrow (d) shows a qualitative interaction between CL.S and LDR for optimal CL.S across speed; low CL.S foils would be expected to have high LDR.

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