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JEB Classics

HOW EFFICIENT IS A FISH?
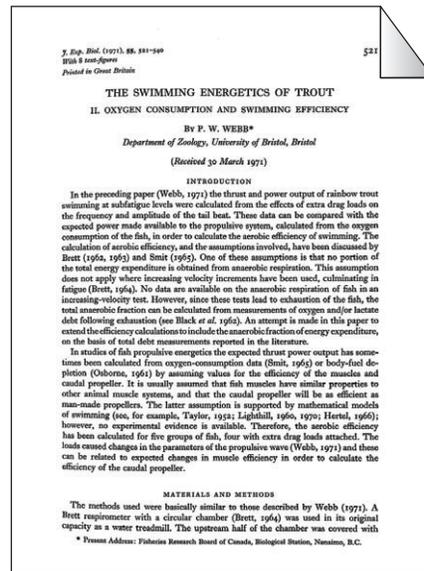
David Ellerby discusses Paul Webb's 1971 paper entitled 'The swimming energetics of Trout. II. Oxygen consumption and swimming efficiency'.

A copy of the paper can be obtained from http://jeb.biologists.org/cgi/content/abstract/55/2/521

Compared with other modes of locomotion, swimming is energetically inexpensive. The costs of moving a unit mass of swimming animal are lower than for animal flight or terrestrial locomotion, but higher than those of human-engineered vehicles (Schmidt-Nielsen, 1972). To understand why, the efficiencies of the underlying processes that convert metabolic energy into mechanical power need to be determined. In his 1971 study Paul Webb determined the efficiency of swimming trout by comparing metabolic rate data (the power input) with estimates of mechanical power output derived from added drag loads (Webb, 1971a) and mathematical modelling of momentum transfer to the wake based on tail kinematics (Lighthill, 1969; Lighthill, 1970). The paper isn't a classic because it gives us all the answers concerning swimming efficiency; we're still wrestling with the problems of quantifying fish thrust and the cost of its production (Schultz and Webb, 2002). For me its strength lies in the way it adopts a new approach to the problem: clarifying where the uncertainties lie; systematically addressing them; and combining distinct but complementary techniques to yield new information.

Webb's study descends directly from the earlier work of James Gray and Richard Bainbridge describing the nature of the propulsive movements of fish and how they are modulated with swimming speed (Gray, 1933a; Gray, 1933b; Gray, 1933c;

Bainbridge, 1958). Importantly though, Webb moves beyond this approach, integrating kinematic data with measures of energy expenditure (Fry and Hart, 1948; Blažka et al., 1960; Brett, 1962) and the use of mathematical models for estimating thrust production (Taylor, 1952; Lighthill, 1969; Lighthill, 1970). In doing so, Webb creates a classic model for integrative studies of animal locomotion; drawing together physiological and mechanical data obtained using the best available methods to gain a more complete picture of locomotor function.

In principle, measuring efficiency should be a straightforward prospect: simply identify, quantify and compare the inputs and outputs to and from a system. In practice, for swimmers (or for that matter any locomoting organism), there are many complicating factors. Swimming involves a series of interlinked processes whose combined efficiencies dictate how energy flows through the system: the efficiency of converting metabolic energy to muscle mechanical power; the efficiency of transferring the power to the water; and the proportion of this power that is available to generate thrust (Webb, 1975). As a consequence, definitions of efficiency and efficiency estimates are many and varied.

For fish, just as with engineered vehicles, fuel consumption is the most obvious measure of power input. For sustainable levels of exercise, oxygen consumption is a useful, if slightly indirect, indicator of this. Uncertainty lies in two main areas. First, the contributions of anaerobic energy expenditure, not indicated by oxygen consumption, may be unclear. Second, the energy expended supports a number of processes in addition to locomotion (Brett, 1962). This makes it difficult to establish just how much energy is being expended to support locomotion *per se*. Webb quantified the oxygen consumption of trout at a range of speeds, and with a range of drag loads (Webb, 1971a; Webb, 1971b), making his measurements in a recirculating swimming flume; essentially a fish treadmill. Although this is a standard piece of equipment for fish physiologists today, at the time that Webb made his measurements it had been developed relatively recently and only used in a few studies of energy expenditure (Blažka, 1960; Brett, 1962; Brett, 1963; Smit, 1965). Flumes allowed a greater degree of precision and control in studying fish swimming. Gray and Bainbridge had swum their fish in static tanks, or an annular 'fish wheel'. Flumes allow precise control of fish speed and produce relatively uniform and laminar flow conditions. They also overcome the problem of eternally swimming around a corner, something fish

have to do in 'fish wheels', which can elevate swimming costs (Weihs, 1981).

The next challenge concerns the output side of the efficiency calculation. How much mechanical power is required? Previous attempts to quantify this had relied on 'dead drag' experiments (literally towing a dead fish and measuring the power required) or theoretical estimates of drag that treated the fish as a rigid body (Brett, 1963; Smit, 1965). Dead fish and rigid models provide poor power estimates as they involve flow conditions very different from those experienced by an undulating fish (Triantafyllou, 1999; Anderson et al., 2000). Webb used an innovative approach, inferring swimming power from the kinematic effects of adding a range of drag loads to the swimming trout (Webb, 1971a). The loads were flat grids or plates, attached to the back of the fish so their faces were presented perpendicular to the flow. Loading increased the frequency (f) and amplitude (A) of the tail beat as the fish worked harder to overcome the added drag. Variation in f and A could therefore be used as an indicator of mechanical power output modulation, the range of variation defining a 'mechanical scope' for the fish. Webb established a relationship between the magnitude of the added load and the additional effort relative to this mechanical scope. He inferred that for a given speed, the drag load that was needed to double the mechanical scope would equal the drag of the unloaded fish, from which the unloaded mechanical power output was calculated. Manipulations to increase the work done during locomotion can, however, present problems, as the costs of moving the additional load may not be directly equivalent to those of moving the unloaded animal (Marsh et al., 2006). Despite this, Webb's 'added drag' derived estimates were comparable to those derived from mathematical models of power production (Lighthill, 1969; Lighthill, 1970).

Webb's efficiency data were significant as they represented the first realistic values obtained using estimates of mechanical power output derived from a swimming fish. Overall efficiency approached 15% at the upper end of the sustainable speed range (Fig. 1). This was a major step forward from estimates based on 'dead drag', where under some circumstances the estimated mechanical power requirement exceeded that available based on metabolic measurements (Brett, 1963).

Since Webb's work, additional techniques have become available with the potential to enhance our understanding of swimming power and efficiency. Through particle image velocimetry, flows around and behind swimming fish have been visualized, and their velocity and momentum quantified (e.g. Müller et al., 1997; Anderson et al., 2000; Tytell and Lauder, 2004). Increased computing power has allowed the development and application of complex computational fluid dynamic models (e.g. Carling et al., 1998; Wolfgang et al., 1999; Zhu et al., 2002; Borazjani and Sotiropoulos, 2008). A combination of physiological techniques have determined the patterns of activity and length change in the power producing muscles, and have been applied *in vitro* to measure muscle work and power outputs (e.g. Altringham et al., 1993; Rome et al., 1993). There is also improved understanding of the efficiency with which muscle converts metabolic energy into mechanical power (reviewed by Smith et al., 2005).

Although earlier work can now be augmented by these new physiological techniques and analytical tools, the flow of energy through a swimming fish from metabolism to wake momentum, or through any locomotor system, is still not fully understood. In large part, this is because integrative studies of locomotion remain rare. Different types of data are seldom collected under comparable circumstances in any given species, limiting the extent to which they can be combined. The lasting value of Webb's integrative, efficiency studies is that they exemplify this approach at its best, drawing together very different techniques to achieve a more thorough understanding of a system as a whole.

David J. Ellerby
Wellesley College
**dellerby@wellesley.edu**
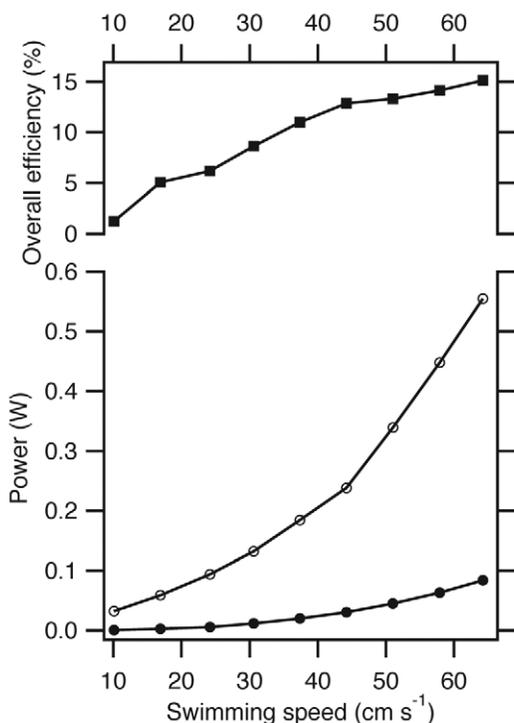
Fig. 1. Estimated metabolic power input (open circles), mechanical power output (closed circles), and overall efficiency (squares) of swimming rainbow trout (*Oncorhynchus mykiss*). Data re-plotted from Webb (Webb, 1971b). Overall efficiency is power output expressed as a percentage of power input.

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