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BAINBRIDGE SETS THE STAGE ON SCALING IN FISH SWIMMING

[109]

THE SPEED OF SWIMMING OF FISH AS RELATED TO SIZE AND TO THE FREQUENCY AND AMPLITUDE OF THE TAIL BEAT

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INTRODUCTION

A fair number of values for the speed of swimming of a representative selection of fish species now exists in the literature. Many of the figures are only estimates; some are accurate measurements, but unfortunately even amongst these the absence of the all-important values of the weight or the length of the specimens concerned renders many of them of little use.

Stringham (1924) reviews and gives references to early work and Gray (1953) summarizes some later results and also gives figures of his own. The earliest recorded experiments seem to be those of Regnard (1893) who allowed small fish to swim in an annular rotating vessel, the speed of which could be controlled by a variable resistance and an electric motor. He rotated the vessel until the swimming fish could only just keep station and then recorded this as the maximum swimming speed. He makes no reference in his account to corrections for a lag between the speed of rotation of the water and that of the container, and in this respect his results may perhaps be suspect. Figures for by far the greatest selection of species are to be found in Magnan (1930). Besides dividing 172 species up into eight great groups according to the relationship between their speed of swimming and the square root of their length, he gives a table of values for eighteen species, recording amongst other things the length of the specimens used and their maximum speed of swimming. The methods he used comprise (i) timing the animal between two fixed points a known distance apart, (ii) using a special camera to make cine films of the animal swimming and calculating values from these, and (iii) attaching the animal to a speedometer by means of a thread, the speed at which this unrolled giving the fish's speed. He does not say which of these methods is used in any particular instance, or upon what distance of swimming any measurement is based, but regards all the figures as equally reliable. Dent (1927), in one of a series of papers, which deal exhaustively with the problem of constructing fish ladders for surmounting river obstacles, gives some measurements of the speed of various specimens swimming up passes of different design, and calculates from these figures their potential speed in open water. He also calculates the speed at which leaping fish must be moving when they leave the water. Lane (1941), in an entertaining popular article, refers to a device, made by H. E. Thompson and similar to that used in the last of

Paul Webb writes about Richard Bainbridge's 1958 Classic paper 'The Speed of Swimming of Fish as Related to Size and to the Frequency and Amplitude of the Tail Beat'.

This classic by Richard Bainbridge is the first of three data papers (Bainbridge, 1958; Bainbridge, 1960; Bainbridge, 1962) on the scaling of swimming motions and performance in fishes. When published, a quarter century had passed since the earlier key 1933 papers by James Gray (Gray, 1933a; Gray, 1933b; Gray, 1933c), recently reviewed (Lauder and Tytell, 2004), showing the body deformations necessary for propulsion. The intervening period saw a number of sallies probing the complexities of swimming, as described in Sir James Gray's summary of the state of the art in his 1968 book *Animal Locomotion*. Gray summarizes elegant studies on shark stability by John Harris, various resistive- and reactive-based models for fish propulsion, the ongoing fascination with maximum speed, and the uncertainties of the power balance between availability and apparent requirements. From Gray's review it was clear that further advances in the understanding of fish swimming would require methods for the systematic and accurate measurement of fish swimming motions in which key factors such as speed and size could be controlled. Bainbridge was among the first, starting in the late 1950s and early 1960s, to fill this vacuum.

In this 1958 paper, Bainbridge used natural variability in swimming speed (plus a little

bit of stimulation) to record tail-beat frequencies and amplitudes of three species of fishes swimming at various speeds in annular channels, dubbed 'fish wheels' (Fig. 1). Bainbridge improved on earlier designs of annular channels using ingenious gates to minimize slip and other uncontrolled water movements. He studied swimming using fishes from 4 to 30 cm in total length, close to an order of magnitude of fish length. As such, Bainbridge could extrapolate his results to larger-sized fishes. However, his fish did have to swim in circles, having to work harder than those swimming in straight lines (Weihs, 1981), so Bainbridge used two fish wheels with different diameters to reduce size effects of swimming in circles.

Bainbridge's paper is best known for the observations of *tail motions*, but his three-factor design studying effects of speed \times length \times species also remains remarkable in its scope. Bainbridge showed that the major factor controlling speed was modulation of tail-beat frequency, with a small effect of amplitude at lower speeds, results that have been confirmed for many additional species by other researchers using several different methods. For much of the swimming range, speed proves to be a linear function of tail-beat frequency, and the distance travelled per beat, or stride length, is essentially constant. Bainbridge further showed that size effects of tail-beat frequency and amplitude could be expressed in a common form by normalizing speed with body length, describing speed in body-lengths s^{-1} , or $L s^{-1}$. Remarkably, most of the variation in tail-beat patterns with speed, for all three species (dace *Leuciscus leuciscus*, goldfish *Carassius auratus*, and trout *Salmo irideus*=*Oncorhynchus mykiss*) could be expressed in a single equation, sometimes called Bainbridge's Equation:

$$U / L = 0.25[L(3F - 4)] ,$$

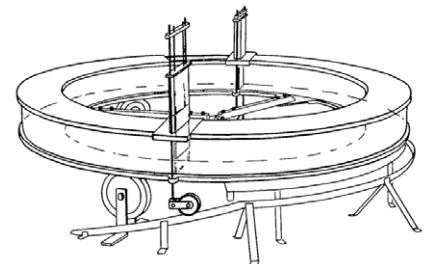


Fig. 1. Perspective view of the small fish wheel used by Bainbridge in his scaling studies. The fish swims on the extreme right where the vertical doors pass in the open position. The operator speeds up and slows down the wheel to keep the fish in the field of view of a fixed camera. Reproduced from Bainbridge, 1958.

where U =swimming speed (cm s^{-1}), L =total length (cm), and F =tail beat frequency (Hz). Expressing speed in body-lengths s^{-1} is still used in most studies on swimming to collapse size-related data. Bainbridge's results also shored up scattered observations suggesting larger fish achieve higher absolute speeds, but lower relative speeds expressed in $L \text{ s}^{-1}$. Knotty problems of how to improve representation of scaling into a single non-dimensional scaling function have largely been ducked since.

However, the Bainbridge Equation relating tail-beat frequency and speed did not pass through the origin, as the tail-beat frequency was modulated at lower speeds. Bainbridge found that tail-beat amplitude was also modulated at low swimming speeds. He thought that the product of amplitude and frequency would pass through the origin. This does not appear to be the case, but it is hard to induce fish to swim in any regular fashion at very low speed. Consequently, exactly what happens at low speeds is still not clear. Low-speed swimming appears to pose challenges for fishes, perhaps associated with stability (Webb, 2005).

Bainbridge's fish wheels followed a tradition dating at least as far back as the late 18th century of using annular channels to study fish swimming (Videler, 1993). Bainbridge used his fish wheels to examine 'steady swimming', speeds maintained for multiple similar tail beats. At the time Bainbridge was doing his work, new designs for straight water tunnels were being developed. These had advantages in that fish speed could be rigidly controlled for long enough to ensure that fish swam using many consecutive and similar tail beats and to estimate energy costs of swimming from rates of oxygen consumption (Blazka et al., 1960; Brett, 1963; Beamish, 1978). These flumes steered studies of steady swimming towards low, sustainable speeds, a trend that persists today. As a result, Bainbridge's results are especially notable, and still unique, because they show relationships between tail-beat frequency and amplitude in sprint swimming, the highest steady speeds maintained at best for a few tail beats.

Unfortunately, the conditions under which fish swam in the fish wheel could not be fully controlled. Consequently, maximum sprint speeds were probably not accurate and it is not clear to what degree fish might have been accelerating or decelerating at their highest observed speeds. However, the principles established by Bainbridge provide for indirect approaches to the question of limits to steady swimming performance. For example, given that tail-beat frequency is the major modulator of speed and that stride

length is constant at higher speeds, it has been suggested that maximum speed is ultimately limited by the twitch times of fish fast glycolytic (white) muscle. This can be measured, maximum tail-beat frequency inferred, and hence maximum speed estimated from the product of tail-beat frequency and stride length (Wardle, 1975).

This application of principles established by Bainbridge on maximum speed is just one example of the indirect consequences of his study. For me, a major impact came from the use of Bainbridge's results with models of fish swimming. James Lighthill's review of aquatic animal propulsion (Lighthill, 1969), which he developed with input from James Gray and Bainbridge (Crocker, 1999), included a simplified version of an elongated slender body model. This and subsequent models have been especially important for calculating mechanical power consumption from variables that Bainbridge demonstrated were readily measurable. Power estimates using data on tail-beat frequencies and amplitudes, improved knowledge of muscle power output and efficiency (Hill, 1950; Bainbridge, 1961), and measured rates of oxygen consumption all combined to give a picture of fish swimming energetics that has endured to today. Essentially, a convergence of results from different approaches show that swimming is expensive compared to transport costs of similar human engineering vehicles (Schmidt-Neilsen, 1972; Tucker, 1975). This has been attributed to high viscous-related energy losses along the body (boundary-layer thinning).

With the passing of almost 50 years since Bainbridge's study, efforts have been made by many to verify and understand the basis and consequences of such high locomotor costs, and another technological shift now appears to be taking place. Recent abilities to visualize flow using Particle Image Velocity (PIV) not only challenge postulated boundary-layer thinning (Anderson et al., 2001), but further suggest high costs relate more to kinetic energy lost in the wake (Schultz and Webb, 2002). In spite of such shifts, the generalizations showed by Bainbridge continue to contribute to thinking, and his results remain important in evaluating scaling aspects of such new ideas.

A PDF file of the original paper can be accessed online: <http://jeb.biologists.org/cgi/content/full/209/10/1789/DC1>
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