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WEBB SCALES FAST-START MANEUVERS
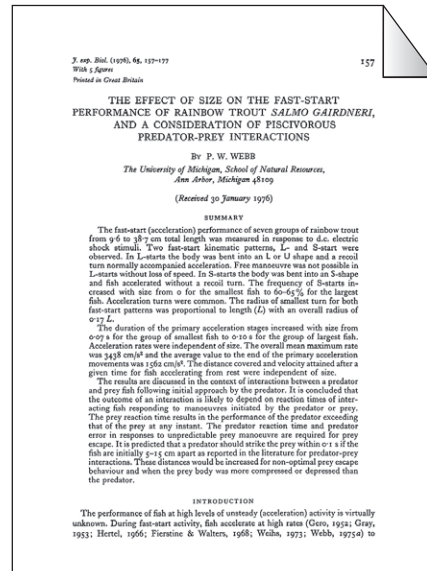
Paolo Domenici discusses Paul Webb's paper entitled 'The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator–prey interactions'.

A copy of the paper can be obtained from http://jeb.biologists.org/cgi/content/abstract/65/1/157

The aim of this classic paper by Paul Webb (Webb, 1976) was to investigate the effect of size on fast-start performance and to use the results in order to make some theoretical considerations on predator–prey interactions. Until the 1970s, most work on fish swimming had focused on steady conditions, with the goal of studying the relationship between the energetics, performance and kinematics of in-line swimming. Work by Richard Bainbridge in the late 1950s and early 1960s was fundamental in establishing the relationship between fish size, tail beat frequency, amplitude and speed [(Bainbridge, 1958); recently review by Webb (Webb, 2006)] as well as speed and stamina (Bainbridge, 1959; Bainbridge, 1962) while J. R. Brett's work (Brett, 1964) on salmonids provided the basis for the energetics of steady locomotion in fish, to which Webb himself provided a major contribution (Webb, 1971a; Webb, 1971b). Fundamental to these studies was the development of a number of experimental techniques such as swim tunnels and wheels that allowed researchers to monitor fish swimming continuously. Until the mid-1970s, however, very little was known about unsteady swimming in fishes, such as turning maneuvers and fast-starts. Yet, unsteady swimming is the basis of many fundamental behaviors in fish, from

catching prey and avoiding predators to social interactions.

Danny Weihs (Weihs, 1972; Weihs, 1973) provided the first hydrodynamic description of unsteady swimming (turning in 1972 and fast-start in 1973), based on the slender-body theory of Sir James Lighthill (Lighthill, 1969; Lighthill, 1971), adapted to deal with unsteady, curvilinear large-amplitude movement of the fish. However, it was only with a series of papers by Webb, starting in 1975, that the kinematics of fish fast-starts was systematically analyzed quantitatively (Webb, 1975). The 1975 paper was based on a comparative kinematic analysis of the acceleration performance of two species of fish. The subsequent paper (Webb, 1976) is discussed here and was the first paper on the scaling of fast-start performance. The high impact of this paper was due to the relevance of scaling in the predator–prey gambit, in which one of the main differences between the predator and the prey is their size. This is especially true in geometrically similar species, as is the case for many predator–prey pairs in fish. The experimental data presented in the paper were corroborated by theoretical considerations on predator–prey interactions. These considerations are an extension of a geometrical model of predator–prey interactions based on a seminal theoretical paper by Howard Howland – which investigated the relative importance of speed and maneuverability in predator–prey encounters (Howland, 1974) – and their strength lies in the use of experimental data acquired on the fast-start performance and kinematics of rainbow trout of various sizes.

Using a non-directional stimulus (a low-voltage electric shock), Webb induced fast-starts in seven size-sorted groups of rainbow trout (*Salmo gairdneri = Oncorhynchus mykiss*) ranging from 9.6 to 38.7 cm in total length. The fast-starts were recorded on film, and a number of kinematic variables, such as duration of each tail beat, distance covered, velocity, acceleration, and turning radius, were analyzed. In addition, Webb identified two types of fast-starts, which he originally called L-start (in later literature to be called C-start) and S-start. Webb recognized the diversity of fast-start patterns, which was the subject of many papers to come (Domenici and Blake, 1991; Gamperl et al., 1991; Hale, 2002; Harper and Blake, 1990). The issue of whether different kinematic patterns of fast-start may correspond to different neural control remains unresolved, although Hale has shown that, in pike, C-start and S-start escapes correspond to different muscle activation patterns,

suggesting differential neural activation (Hale, 2002).

Webb found that the time required to complete the first muscle contraction (i.e. one tail beat) of a fast-start increases with fish size. This is in line with Clem Wardle's work (Wardle, 1975), which provided the basis for estimating the maximum swimming speed of fish based on the minimum contraction time of isolated muscle blocks. Webb's data show that both distance covered and velocity at the end of the first two half tail beats (stage 1 and 2) increased with size. For an ecologically relevant measure of performance, Webb introduced evaluation of swimming performance within a fixed time and found that, in this case, distance and speed were size independent, in line with the size independence of acceleration. This is a major finding because it implies, as Webb suggested, that predators may be unable, on the basis of swimming performance alone, to catch a geometrically similar, smaller prey. The situation would change if the interaction were prolonged (Guinet et al., 2007) since large fish can reach a higher speed than small fish if provided enough time, although this is a less common strategy and a challenging one to test in controlled conditions. Webb's work is particularly relevant for predator–prey interactions of relatively short duration, such as those often encountered in structurally complex environments (Domenici, 2003). Although later work has demonstrated that acceleration varies across developmental stages (i.e. as fish grow from larvae to juveniles) within one single species due to changes in body form and muscle contractile properties (Hale, 1999; Wakeling et al., 1999), when data from adults of various species are considered together, acceleration appears to be unaffected by size (Domenici, 2001; Vogel, 2008). Furthermore, Webb found that turning radius, a variable suggested to be a major determinant of predator–prey gambits, increases with size as a fixed proportion of length (0.17 length in trout), in line with theoretical predictions based on setting the centrifugal force acting on the fish equal to the force available for the turn (Howland, 1974). Hence, predators are likely to have lower maneuverability (i.e. larger turning radius) than their prey.

Despite all this, Webb argued, predators do catch their prey regularly in short-lived encounters. Therefore, there must be some other factors that play a role in determining the outcome of predator–prey interactions. Building on Howland's theoretical ideas, Webb introduced a number of factors that could play a role in determining the outcome of predator–prey interactions in modeled scenarios. Notably, these are factors that impinge upon various disciplines from biomechanics to behavior and neurobiology, such as the initial starting configurations (i.e. the relative orientation of predator to prey), the initial distance separating predators and prey, the duration of the acceleration, the delay time in prey response, and the prey turning radius. Based on the modeled scenarios, Webb concluded that the outcome of predator–prey interactions between geometrically similar fish depends more on reaction times than on swimming performance alone. The situation changes if predator and prey are geometrically different and, consequently, may have different swimming performance in terms of acceleration and maneuverability. This approach placed the kinematics of unsteady swimming within the larger context of predator–prey interactions, thereby providing a major contribution to creating a whole area of research that couples biomechanics to the study of predator–prey relationships. As the scaling of locomotion within the context of predator–prey interactions is receiving more and more attention in the literature (Dial et al., 2008; Higham, 2007; Vogel, 2008), Webb's general conclusion, that timing is a fundamental determinant of predator–prey encounters, has been largely confirmed by work on staged interactions (Fuiman et al., 2006; Scharf et al., 2003; Walker et al., 2005). Later work by Webb (Webb, 1982; Webb, 1986) considered the effect of predator morphology on the reaction distance of prey, further widening the scope of his investigations by linking ecomorphological considerations to behavioral ecology work (Dill, 1974).

As a PhD student in Robert Blake's laboratory at the University of British Columbia, where fast-starts were one of the main subjects of investigation (Frith and Blake, 1995; Harper and Blake, 1990), I quickly became fascinated with the relevance of fast-starts for predator–prey interactions, and it seemed to me that scaling was a promising area of investigation, both in terms of providing an ecologically relevant tool for comparing the swimming abilities of the predator and the prey, and the escape performance of prey of different sizes. Webb's integrative approach was also the inspirational key for my subsequent work on the scaling effects on a number of components of the escape response (reviewed in Domenici, 2010). In this respect, Webb's contribution goes beyond his actual experimental findings. Starting with the 1976 paper, Webb's work filled a major gap in the integrative approach to understanding predator and prey maneuvers, which necessitates a multidisciplinary approach. Webb started from a rigorous testing of kinematics and developed models of predator–prey scenarios by including considerations based on sensory biology, neurobiology, behavior and ecology. Webb's 1976 study is therefore a perfect example of biomechanics used as a tool for investigating the ecological relevance of locomotor performance, and as such it has all the ingredients necessary to appeal to researchers from a variety of backgrounds.

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REFERENCES

Bainbridge, R. (1958). The speed of swimming of fish as related to size and to the frequency and the amplitude of the tail beat. *J. Exp. Biol.* **35**, 109-133.

Bainbridge, R. (1959). Speed and stamina in three fish. *J. Exp. Biol.* **37**, 129-153.

Bainbridge, R. (1962). Training, speed and stamina in trout. *J. Exp. Biol.* **39**, 537-555.

Brett, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd. Can.* **21**, 1183-1226.

Dial, K. P., Greene, E. and Irschick, D. J. (2008). Allometry of behavior. *Trends Ecol. Evol.* **23**, 394-401.

Dill, L. M. (1974). Escape response of *Zebra danio* (*Brachydanio rerio*). 1. Stimulus for escape. *Anim. Behav.* **22**, 711-722.

Domenici, P. (2001). The scaling of locomotor performance in predator–prey encounters: from fish to killer whales. *Comp. Biochem. Physiol.* **131A**, 169-182.

Domenici, P. (2003). Habitat type, design and the swimming performance of fish. In *Vertebrate Biomechanics and Evolution* (ed. V. Bels, J. P. Gasc and A. Casinos), pp. 137-160. Oxford: Bios Scientific Publishers.

Domenici, P. (2010). Escape responses in fish: kinematics, performance and behavior. In *Fish Locomotion: An Eco-ethological Perspective* (ed. P. Domenici and B. G. Kapoor), pp. 123-170. Enfield, NH, USA: Science Publishers.

Domenici, P. and Blake, R. W. (1991). The kinematics and performance of the escape response in the angelfish (*Pterophyllum eimekei*). *J. Exp. Biol.* **156**, 187-205.

Frith, H. R. and Blake, R. W. (1995). The mechanical power output and hydromechanical efficiency of northern pike (*Esox lucius*) fast-starts. *J. Exp. Biol.* **198**, 1863-1873.

Fuiman, L. A., Rose, K. A., Cowan, J. H. and Smith, E. P. (2006). Survival skills required for predator evasion by fish larvae and their relation to laboratory measures of performance. *Anim. Behav.* **71**, 1389-1399.

Gamperl, A. K., Schnurr, D. L. and Stevens, E. D. (1991). Effect of a sprint-training protocol on acceleration performance in rainbow-trout (*Salmo gairdneri*). *Can. J. Zool.* **69**, 578-582.

Guinet, C., Domenici, P., de Stephanis, R., Barrett-Lennard, L., Ford, J. K. B. and Verborgh, P. (2007). Killer whale predation on bluefin tuna: exploring the hypothesis of the endurance-exhaustion technique. *Ma. Ecol. Progr. Ser.* **347**, 111-119.

Hale, M. E. (1999). Locomotor mechanics during early life history: effects of size and ontogeny on fast-start performance of salmonid fishes. *J. Exp. Biol.* **202**, 1465-1479.

Hale, M. E. (2002). S- and C-start escape responses of the muskellunge (*Esox masquinongy*) require alternative neuromotor mechanisms. *J. Exp. Biol.* **205**, 2005-2016.

Harper, D. G. and Blake, R. W. (1990). Fast-start performance of rainbow trout *Salmo gairdneri* and northern pike *Esox lucius*. *J. Exp. Biol.* **150**, 321-342.

Higham, T. E. (2007). The integration of locomotion and prey capture in vertebrates: morphology, behavior, and performance. *Integr. Comp. Biol.* **47**, 82-95.

Howland, H. C. (1974). Optimal strategies for predator avoidance – relative importance of speed and maneuverability. *J. Theor. Biol.* **47**, 333-350.

Lighthill, M. J. (1969). Hydromechanics of aquatic animal propulsion. *Annu. Rev. Fluid Mech.* **1**, 413-446.

Lighthill, M. J. (1971). Large-amplitude elongated-body theory of fish locomotion. *Proc. R. Soc. Lond. Ser. B* **179**, 125-138.

Scharf, F. S., Buckel, J. A., McGinn, P. A. and Juanes, F. (2003). Vulnerability of marine forage fishes to piscivory: effects of prey behavior on susceptibility to attack and capture. *J. Exp. Mar. Biol. Ecol.* **294**, 41-59.

Vogel, S. (2008). Modes and scaling in aquatic locomotion. *Integr. Comp. Biol.* **48**, 702-712.

Wakeling, J. M., Kemp, K. M. and Johnston, I. A.

(1999). The biomechanics of fast-starts during ontogeny in the common carp *Cyprinus carpio. J. Exp. Biol.* **202**, 3057-3067.

Walker, J. A., Ghalambor, C. K., Griset, O. L., McKenney, D. and Reznick, D. N. (2005). Do faster starts increase the probability of evading predators? *Funct. Ecol.* **19**, 808-815.

Wardle, C. S. (1975). Limit of fish swimming speed. *Nature* **255**, 725-727.

Webb, P. W. (1971a). Swimming energetics of trout. 1. Thrust and power output at cruising speeds. *J. Exp. Biol.* **55**, 489-520.

Webb, P. W. (1971b). Swimming energetics of trout. 2. Oxygen consumption and swimming efficiency. *J. Exp. Biol.* **55**, 521-540.

Webb, P. W. (1975). Acceleration performance of rainbow trout *Salmo gairdneri* and green sunfish *Lepomis cyanellus. J. Exp. Biol.* **63**, 451-465.

Webb, P. W. (1976). The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator–prey interactions. *J. Exp. Biol.* **65**, 157-177.

Webb, P. W. (1982). Avoidance responses of fathead minnow to strikes by 4 teleost predators. *J. Comp. Physiol.* **147**, 371-378.

Webb, P. W. (1986). Effect of body form and response threshold on the vulnerability of 4 species of teleost prey attacked by largemouth bass (*Micropterus salmoides*). *Can. J. Fish. Aquat. Sci.* **43**, 763-771.

Webb, P. W. (2006). Bainbridge sets the scale on scaling in swimming fish. *J. Exp. Biol.* **209**, 1789-1790.

Weihs, D. (1972). A hydrodynamical analysis of fish turning maneuvers. *Proc. R. Soc. Lond. Ser. B* **182**, 59-72.

Weihs, D. (1973). The mechanism of rapid starting of slender fish. *Biorheology* **10**, 343-350.