J. exp. Biol. 162, 157–166 (1992)
Printed in Great Britain © *The Company of Biologists Limited 1992*

IS THE HIGH COST OF BODY/CAUDAL FIN UNDULATORY SWIMMING DUE TO INCREASED FRICTION DRAG OR INERTIAL RECOIL?

BY PAUL W. WEBB

The University of Michigan, Department of Biology and School of Natural Resources, Ann Arbor, MI 48109-1115, USA

Accepted 21 August 1991

Summary

Deep-bodied fish, such as the bluegill sunfish (*Lepomis macrochirus*), are considered to have relatively larger wetted surface areas for their size than fusiform fish. On the basis of the boundary layer thinning hypothesis attributing high power requirements of undulatory swimming to enhanced friction drag, power (=drag) coefficients should be higher for such fish. Areas are typically normalized with total length, L, as L^2 for comparison among species. Bluegill had a wetted surface area of 0.65 L^2, compared with areas of about 0.41 L^2 for trout of similar mass. However, absolute areas and volume$^{2/3}$ of bluegill and trout were similar. Power requirements and power coefficients calculated from kinematics during steady swimming were lower for bluegill sunfish than for cruisers, such as trout, and power coefficients were also lower than those of accelerators, such as tiger musky. Large body depth also damps inertial recoil arising from the side force generated largely by the tail. Inertial energy losses appear to be more important contributors than friction to mechanical power requirements.

Introduction

Most studies of undulatory body and caudal fin swimming have focused on strong swimmers from pelagic or stream habitats (e.g. Brett, 1964; Beamish, 1970; Magnuson, 1978; Graham *et al.* 1990; Webb *et al.* 1984). Analysis of cruising and prolonged performance of such fishes has shown that mechanical power requirements of 'steady' swimming, where variation in speed is small, are 3–5 times greater than for an equivalent rigid reference (see Lighthill, 1975; Webb, 1975; Blake, 1983). The reference is typically a flat plate of equal area at the same Reynolds number, Re, where $Re=Lu/\nu$ and L is fish total length, u is swimming speed, and ν is the kinematic viscosity of water. Q. Bone suggested that the high cost of swimming might be attributed to boundary layer effects increasing friction drag, which was called 'boundary layer thinning' (Lighthill, 1971).

Inviscid models that simulate the pressure distribution around a swimming fish

Key words: swimming, recoil, drag, *Lepomis macrochirus*, bluegill.

also generate power coefficients elevated by a similar factor above those of a rigid reference (Lighthill, 1975; W. W. Schultz, personal communication). In some models, energy losses associated with undulatory self-propulsion can only be lost *via* inertial effects (W. W. Schultz, personal communication). One source of inertial energy loss is lateral recoil of the anterior of the body as a result of side forces generated by the tail (Lighthill, 1975, 1977).

Deep-bodied fish are considered to have relatively large surface areas of $0.6–0.7\,L^2$ compared to $0.4–0.5\,L^2$ for fusiform fish (Bainbridge, 1961; Webb, 1975, 1977). However, large body depth also damps recoil. Therefore, if enhanced friction drag is the major cause of high swimming costs in body/caudal fin undulatory propulsion, mechanical power requirements will be relatively higher for deep-bodied fish than for fusiform fish. Alternatively, such fish might have lower power requirements if body recoil were important. These alternatives are explored here using new observations on bluegill sunfish compared with data obtained using similar protocols for rainbow trout and to a lesser extent tiger musky (Webb, 1988*a*).

Materials and methods

Bluegill sunfish (*Lepomis macrochirus* Rafinesque) were obtained from the Michigan Department of Natural Resources Saline laboratory. They were held in 110-l tanks with continuous water replacement of 200 % per day. Dissolved oxygen levels were maintained close to air-saturation using air stones. Fish were fed a maintenance ration of worms and chopped fish. Fish used in the experiments averaged 15.6±0.9 cm (±2 S.E.; N=10) in total length and weighed 62.26±9.71 g.

Experimental methods have been described in detail by Webb (1988*a*). Briefly, individual fish were selected at random from stock and swam overnight (18–20 h) at 5–10 cm s^{-1} in a flume (Vogel and LaBarbara, 1978) with a square observation section, 15 cm wide and 15 cm deep. Next day, locomotor kinematics and behavior were recorded on ciné film (200 frames s^{-1}) and video tape (60 fields s^{-1}) during an increasing velocity test with speed increments of approximately 5 cm s^{-1} every 2 min (Farlinger and Beamish, 1977). Film and tapes were subsequently analyzed frame-by-frame to record the following data for both the caudal fin trailing edge and the trailing edge of the median fins: frequency, amplitude, span and angle to the plane of lateral motion. The length of the propulsive wave and the amplitude distribution along the body length were measured. Sequences analyzed met the following criteria: there were at least five successive tail-beats, speed did not vary by more than 5 %, and fish were located at the center of the observation chamber.

Wetted surface area was 159±20 cm^2, measured at the end of an experiment as the sum of body and fin circumferences at 1 cm intervals along the body length. Myotomal muscle was dissected from the skeleton and skin and weighed, giving an average of 23.13±4.03 g.

Mechanical thrust power requirements, P, were calculated using the bulk

momentum form of Lighthill's large-amplitude modification of slender body theory (Lighthill, 1971):

$$P = MWwu - 0.5Mw^2u/\cos\theta, \quad (1)$$

where M is added mass per unit length$=\pi\rho B^2/4$, W is the root mean square average lateral speed of the trailing edge$=\pi fH/1.414$, w is the velocity given to the water$=W(1-u/c)$, u is the average swimming speed, θ is the angle of the trailing edge to the lateral plane of motion, ρ is the density of water, B is the trailing-edge span, f is tail-beat frequency, H is tail-beat amplitude, c is the speed of the propulsive wave, $f\lambda$, and λ is the length of propulsive wave.

Total power generation was the sum of that for the caudal fin trailing edge plus that of the non-re-entrant portion of the upstream median fins (Lighthill, 1975; Webb, 1988*a*).

Power coefficients, C_P, were calculated as:

$$C_P = P/0.5\rho Su^3, \quad (2)$$

where S is the wetted surface area of the fish.

Bluegill are compared with previously reported data on rainbow trout, *Oncorhynchus mykiss*, and tiger musky, *Esox* sp., both swimming in the subcarangiform mode (Webb, 1988*a*). To evaluate the basis for enhanced resistance during steady swimming, the critical comparisons are with trout, one of the most intensively studied fusiform species, since musky appear to have as yet unidentified mechanisms to reduce recoil energy losses.

Results

During steady caudal fin propulsion, bluegill tail-beat frequencies increased with swimming speed (Fig. 1). Frequencies were intermediate between those of trout and musky, but increased at a greater rate with swimming speed. Tail-beat amplitude increased slightly with swimming speed, but the slope was not significantly different from zero. The average tail-beat amplitude was 1.5±0.2 cm (0.1 L). The specific amplitude was lower than the value of 0.2 L commonly reported for fusiform cruising fish (Hunter and Zweifel, 1971; Webb, 1975; Blake, 1983), but was similar to that of 0.1 L for musky (Webb, 1988*a*).

The span of the caudal fin and the combined span of the dorsal and anal fins did not vary with swimming speed, and averaged 4.2±0.3 cm (0.27 L) and 6.1±0.4 cm (0.39 L), respectively. Fusiform fish typically have caudal fin spans of about 0.2–0.25 L (Webb, 1988*a*).

Values of $\cos\theta$ for the trailing edges of both the caudal fin and of the anterior median fins increased with swimming speed (Fig. 2) and were similar in magnitude to those reported for these fins of musky.

The length of the propulsive wave was independent of swimming speed and averaged 15.8±1.1 cm (1.01 L). The specific wavelength was larger than typical

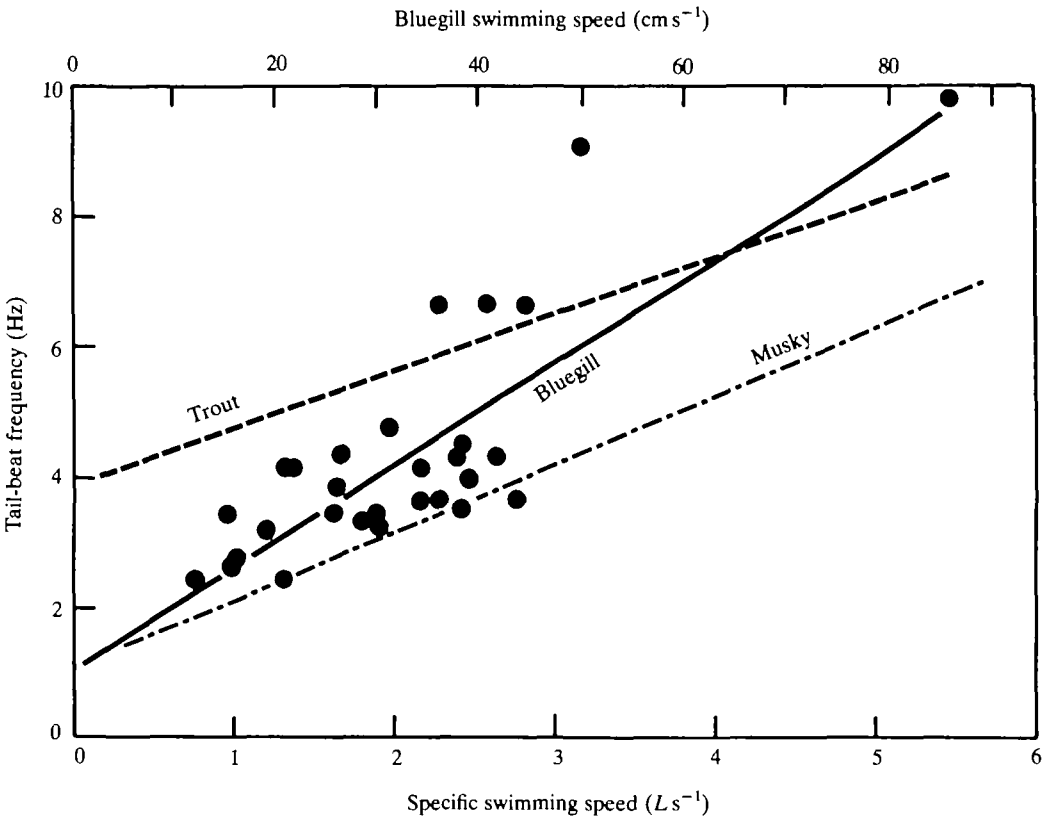

Fig. 1. The relationships between tail-beat frequency (f) and specific swimming speed (u/L, where L is body length and u is swimming speed) for bluegill during steady swimming. The best fitting linear regression equation for f (Hz) as a function of u ($\mathrm{cm\,s^{-1}}$) is: $f=1.61\pm0.84+0.082\pm0.042u$, $P<0.001$, where ±2 S.E. is shown for regression coefficients. Data for trout and musky are from Webb (1988*a*).

values of 0.7–0.8 L reported for fusiform subcarangiform fishes (Wardle, 1975; Videler and Wardle, 1978; Videler, 1981).

The amplitudes of lateral movement were smallest at a point located at 0.2 L, measured from the nose (Fig. 3), and increased anteriorly and posteriorly from this point (Bainbridge, 1963). However, amplitude did not increase continuously towards the tail, but increased slowly to a plateau in the region of the median fins before increasing rapidly over the caudal fin and tail to the maximum at the caudal fin trailing edge. This pattern is similar to that found in trout, but relative amplitudes of bluegill (normalized by the caudal fin trailing edge amplitude) were slightly lower (Fig. 3). Since trailing-edge amplitudes of bluegill were about half those of trout, absolute lateral movements along the entire body length were substantially lower than those of trout.

The rate of working (power) of the body/caudal fin propulsive system increased with swimming speed (Fig. 4). Rates of working were lower than those for trout

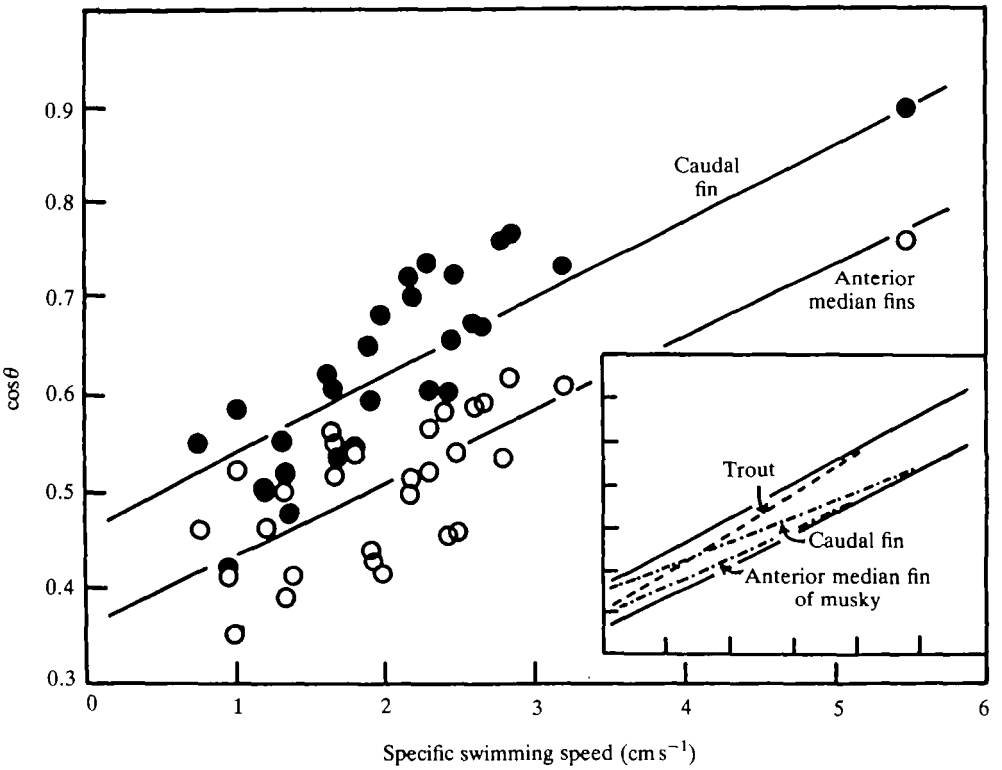

Fig. 2. The relationship between $\cos\theta$ at the caudal fin trailing edge and for the trailing edge of the anterior median fins. The best fitting linear regression equation for the caudal fin is: $\cos\theta=0.46\pm0.07+0.0051\pm0.002u$, $P<0.001$, and for the trailing edge of the median fins is: $\cos\theta=0.36\pm0.07+0.0048\pm0.003u$, $P<0.001$. The inset repeats the regression equations for bluegill (unlabeled solid lines) with the relationships for trout and musky (from Webb, 1988*a*).

and higher than those for musky (Webb, 1988*a*). Power coefficients (Fig. 5) were substantially lower for bluegill than for trout and musky at the same *Re*.

Discussion

The objective of this work was to determine whether mechanical power requirements were higher for a deep-bodied fish believed to have a relatively larger wetted surface area than for more fusiform fish. Relative area is usually expressed as factors of L^2 (Bainbridge, 1961). On the basis of this reference, the bluegill has a substantially larger wetted surface area of $0.65\,L^2$ compared with $0.41\,L^2$ for trout. However, the absolute wetted surface area of bluegill ($159\,\mathrm{cm}^2$) was similar to that of trout ($164\,\mathrm{cm}^2$). Volume$^{2/3}$ is sometimes used instead of wetted area (Au and Weihs, 1980). Bluegill and trout are close to neutral buoyancy, when mass$^{2/3}$ approximates volume$^{2/3}$. Bluegill and trout were similar in mass (62 and 69 g, respectively). Thus, both species would have similar values

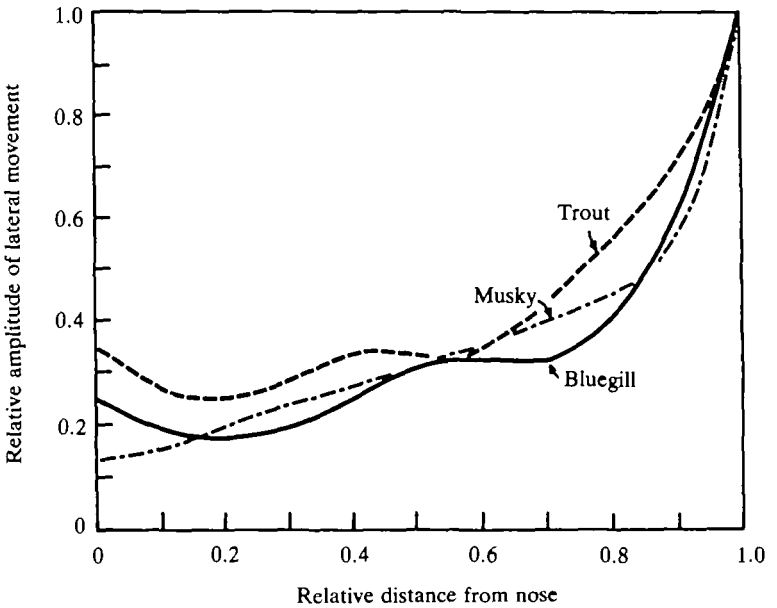

Fig. 3. Distribution of lateral amplitude along the body length. Amplitudes are normalized by the maximum amplitude measured at the caudal fin trailing edge. Position along the body length is normalized by total body length.

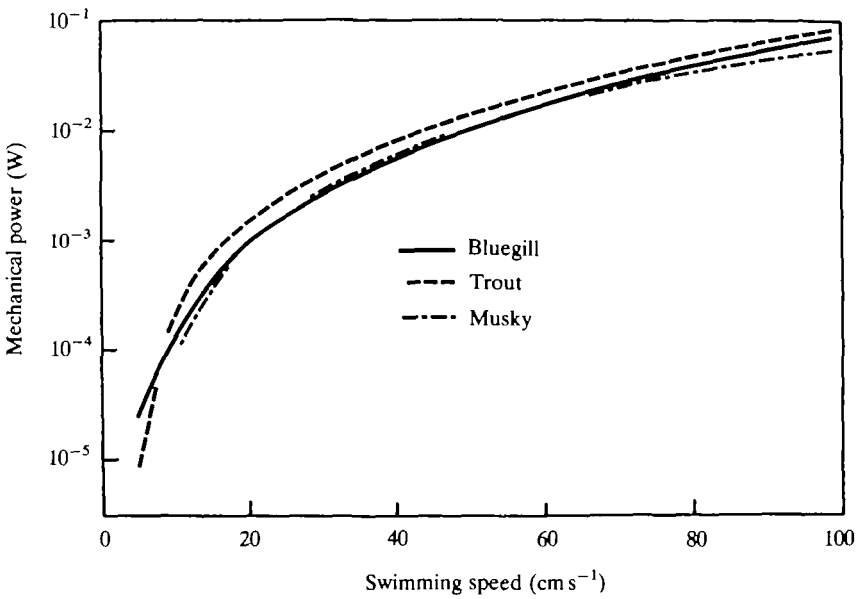

Fig. 4. Mechanical power requirements, calculated from Lighthill's large-amplitude slender-body theory shown as a function of swimming speed for bluegill, trout and musky.

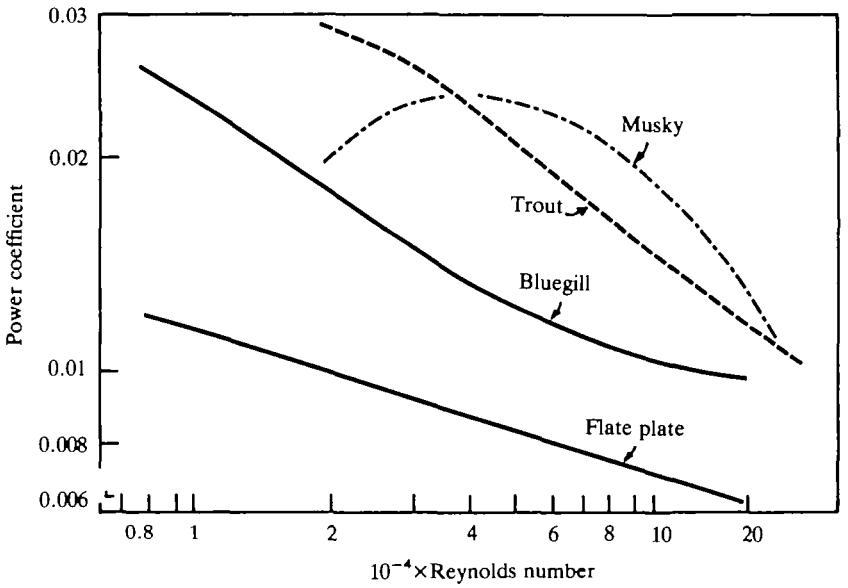

Fig. 5. The relationship between power coefficient and Reynolds number for bluegill, trout and musky. Drag coefficients are also shown for a rigid flat plate reference.

for volume$^{2/3}$. Defining a nondimensional relative area, S_V, based on absolute area and volume$^{2/3}$, as:

$$S_V = \text{wetted surface area/volume}^{2/3}, \tag{4}$$

gives a value of 10.1 for bluegill, similar to that of 9.7 for trout. Clearly, bluegill can be considered to have similar or different relative areas to those of trout depending on the frame of reference (Alexander, 1990).

This requires revision of the original hypothesis. Originally, higher power requirements were expected for the fish with the relatively larger surface area estimated from the traditional method of normalizing area with L^2. Since S_V is similar for trout and bluegill, both would now be expected to have the same rates of working and the same C_P at the same *Re*.

Comparisons between bluegill and trout might also be affected by the difference in lengths of the fish used in the experiments. Although both had similar areas, the area of trout extends over a longer downstream length than that of bluegill. The thickness of the boundary layer grows approximately with the square of distance from the nose (Schlichting, 1968). As a result, local drag coefficients tend to decrease with distance from the nose, and the average drag coefficient is lower for a longer body with the same wetted surface area as a shorter body. On this basis, trout might be expected to have lower power coefficients than bluegill.

Differences in length might also affect mean power coefficients if transition to turbulence occurred relatively closer to the nose of the longer fish. In practice, flumes used for studying fish swimming, including that used here, introduce micro-turbulent flow to provide rectilinear flow profiles. The intensity of turbulence

exceeds critical values for transition (Webb, 1975). In addition, swimming movements probably induce turbulent boundary layer flow (Webb, 1975). Therefore, it is unlikely that the differences in length of the fish used in these experiments would have a significant effect on power coefficients and thus affect the conclusions.

In practice, C_P was lower for bluegill than for trout, and rates of working for bluegill were 1.5 times lower on average than for trout. Thus, these results do not support the boundary layer thinning hypothesis, irrespective of how relative area is defined.

Lateral motions along the body of bluegill were also smaller than those of trout. This suggests that energy lost in lateral recoil movements of the anterior of the body may be lower for bluegill. Lighthill (1977) showed that the relative energy wastage in recoil for carangiform swimmers could be expressed as a ratio, ζ, between the maximum side force of the tail, F, and the lateral resistance forces of the anterior body.

$$\zeta = F/k\omega\rho B_{\max}{}^3 L\,, \tag{5}$$

where k is a constant, equal to 0.074 for carangiform swimmers, ω is the radian frequency, $2\pi f$, and $B_{\max}$ is the maximum span of the body and median fins.

Lighthill showed that energy wastage in recoil is large when ζ is large, but lateral recoil is effectively damped by the anterior virtual mass of the body when ζ is small.

Wu (1977) showed that the force on the tail, F, including the lateral component, is related to swimming kinematics as:

$$F \propto f^2 H^2 B^2 (1 - u/c)\,. \tag{6}$$

Substituting equation 6 into equation 5 and simplifying:

$$\zeta \propto H^2 B^2 (1 - u/c)/B_{\max}{}^3 L\,. \tag{7}$$

Using equation 7, ζ for bluegill averaged 4.6 times that for trout over the range of swimming speeds where both swam steadily. This does not mean that power requirements of bluegill were one-quarter to one-fifth of those of trout, since recoil resistance is only one component of total resistance. However, if recoil energy costs are about 50 % of the total resistance of trout (Webb, 1988*a*), and if other frictional and inertial resistance components were the same for each species, then the power requirements for trout would be about 1.7 times those for bluegill. This is of the same order as the difference in power requirements.

It is important to recognize that the models used in this analysis are imprecise. Although the correlation between predictions of power requirements from slender-body theory and from biological expectations is remarkably good, calculated forces and power are probably only reliable to within an order of magnitude (Weihs, 1973; Yates, 1983; Webb, 1988*b*). Nevertheless, the various theories used in studying fish swimming appear to be reliable in ranking mechanical performance (Webb, 1988*b*). Similarly, Lighthill's analysis of recoil correctly applies only to carangiform fishes with a good separation of mass centers associated with thrust and inertial damping of recoil. Again, the model accurately

illustrates the principal factors of body/caudal fin morphology and function that are critical in determining recoil in other swimming modes where thrust generation is concentrated at the tail, as with bluegill and trout (Webb, 1988*a*). Therefore, in spite of considerable uncertainty about the actual values of thrust and resistance, this analysis strongly suggests that bluegill swimming power requirements are lower than those of trout. Furthermore, this is probably attributable to reduced recoil energy losses, this being a property of the deep-bodied shape.

The conclusion that enhanced friction drag is less important than is usually assumed is at variance with several interpretations of other experimental and comparative observations. For example, reduction in area by forked tails, culminating in the lunate tail of thunniform animals, has been considered to be a mechanism for minimizing friction drag in that region of the body where drag enhancement by boundary layer thinning would be greatest (Lighthill, 1975; Webb, 1982, 1984). However, as Lighthill has regularly pointed out (Lighthill, 1975), this will also reduce energy losses by reducing the side force and, hence, recoil. Similarly, Hunter and Zweifel (1971) found that tail-beat frequencies increased at different rates among fish species and this correlates with tail area. Thus, species with larger tail areas work harder at a given speed, which is consistent with a hypothesis of enhanced drag (Webb, 1982). Following Lighthill (1977), this trend could be explained by differences in energy wastage in recoil. Finally, prolonged swimming performance is virtually unaffected by caudal fin amputation in spite of the fact that this must reduce thrust (Webb, 1973). Since fin amputation reduces fin area, I originally suggested that the small effect of amputations on performance occurred because friction drag, enhanced by boundary layer thinning, was reduced by a similar amount to the reduction in thrust (Webb, 1973). These data are consistent with an alternative explanation, that energy losses following tail amputation occur through reduction of the side force and hence reduction of energy loss in recoil.

With the wisdom of hindsight, observations previously used to support the boundary layer thinning hypothesis fail to discriminate between hypotheses for resistance enhancement *via* drag and others, such as resistance enhancement by inertial energy losses. In contrast, the observations on deep-bodied bluegill suggest that the latter sources for the high costs of undulatory body/caudal fin propulsion should be given greater weighting in analyzing the functional morphology of aquatic vertebrates.

This work was supported by the National Science Foundation grants PCM-8401650 and DCB-8701923.

References

ALEXANDER, D. E. (1990). Drag coefficients of swimming animals: Effects of using different reference areas. *Biol. Bull. mar. biol. Lab., Woods Hole* **179**, 186–190.

AU, D. AND WEIHS, D. (1980). At high speeds dolphins save energy by leaping. *Nature* **284**, 348–350.

BAINBRIDGE, R. (1961). Problems of fish locomotion. *Symp. zool. Soc., Lond.* **5**, 13–32.
BAINBRIDGE, R. (1963). Caudal fin and body movements in the propulsion of some fish. *J. exp. Biol.* **40**, 23–56.
BEAMISH, F. W. H. (1970). Oxygen consumption of largemouth bass, *Micropterus salmoides*, in relation to swimming speed and temperature. *Can. J. Zool.* **48**, 1221–1228.
BLAKE, R. W. (1983). *Fish Locomotion.* Cambridge: Cambridge University Press.
BRETT, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd Can.* **30**, 379–387.
FARLINGER, S. AND BEAMISH, F. W. H. (1977). Effects of time and velocity increment on the critical swimming speed of largemouth bass (*Micropterus salmoides*). *Trans. Am. Fish. Soc.* **106**, 436–439.
GRAHAM, J. B., DEWAR, H., LAI, N. C., LOWELL, W. R. AND ARCE, S. M. (1990). Aspects of shark swimming performance determined using a large water tunnel. *J. exp. Biol.* **151**, 175–192.
HUNTER, J. R. AND ZWEIFEL, J. R. (1971). Swimming speed, tail beat frequency, tail beat amplitude and size in jack mackerel, *Trachurus symmetricus*, and other fishes. *Fish. Bull.* **69**, 253–255.
LIGHTHILL, J. (1971). Large-amplitude elongated-body theory of fish locomotion. *Proc. R. Soc. Lond. B* **179**, 125–138.
LIGHTHILL, J. (1975). *Mathematical Biofluiddynamics.* Philadelphia, PA: Society for Industrial and Applied Mathematics.
LIGHTHILL, J. (1977). Mathematical theories of fish swimming. In *Fisheries Mathematics* (ed. J. H. Steele), pp. 131–144. New York: Academic Press.
MAGNUSON, J. J. (1978). Locomotion by scombrid fishes. In *Fish Physiology*, vol. VII (ed. W. S. Hoar and D. J. Randall), pp. 230–313. New York: Academic Press.
SCHLICHTING, H. (1968). *Boundary-Theory.* New York: McGraw-Hill.
VIDELER, J. J. (1981). Swimming movements, body structure and propulsion in cod *Gadus morhua*. *Symp. zool. Soc., Lond.* **48**, 1–27.
VIDELER, J. J. AND WARDLE, C. S. (1978). New kinematic data from high speed cine recordings of swimming cod (*Gadus morhua*). *Neth. J. Zool.* **28**, 465–484.
VOGEL, S. AND LABARBARA, M. (1978). Simple flow tanks for research and teaching. *BioSci.* **28**, 638–643.
WARDLE, C. S. (1975). Limit of fish swimming speed. *Nature* **255**, 725–727.
WEBB, P. W. (1973). Effects of partial caudal-fin amputation on the kinematics and metabolic rate of underyearling sockeye salmon (*Oncorhynchus nerka*) at steady swimming speeds. *J. exp. Biol.* **59**, 565–581.
WEBB, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 1–158.
WEBB, P. W. (1977). Effects of median-fin amputation on the fast-start performance of rainbow trout (*Salmo gairdneri*). *J. exp. Biol.* **68**, 123–135.
WEBB, P. W. (1982). Locomotor patterns in the evolution of actinopterygian fishes. *Am. Zool.* **22**, 329–342.
WEBB, P. W. (1984). Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.* **24**, 107–120.
WEBB, P. W. (1988*a*). 'Steady' swimming kinematics of tiger musky, an esociform accelerator, and rainbow trout, a generalist cruiser. *J. exp. Biol.* **138**, 51–69.
WEBB, P. W. (1988*b*). Simple physical principles and vertebrate aquatic locomotion. *Am. Zool.* **28**, 709–725.
WEBB, P. W., KOSTECKI, P. T. AND STEVENS, E. D. (1984). The effect of size and swimming speed on the locomotor kinematics of rainbow trout. *J. exp. Biol.* **109**, 77–95.
WEIHS, D. (1973). The mechanism of rapid start of slender fish. *Biorheology* **10**, 343–350.
WU, T. Y. (1977). Introduction to scaling of aquatic animal locomotion. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 203–232. New York: Academic Press.
YATES, G. T. (1983). Hydromechanics of body and caudal fin propulsion. In *Fish Biomechanics* (ed. P. W. Webb and D. Weihs), pp. 177–213. New York: Praeger.