THE EFFECTS OF AN AIR/WATER SURFACE ON THE FAST-START PERFORMANCE OF RAINBOW TROUT (*ONCORHYNCHUS MYKISS*)

By PAUL W. WEBB

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

DOMINIQUE SIMS

Department of Biology, The University of Michigan, Ann Arbor, MI 48109, USA

AND WILLIAM W. SCHULTZ

*Department of Mechanical Engineering, The University of Michigan,
Ann Arbor, MI 48109, USA*

Summary

Fast-start performance of rainbow trout (mass 0.187 ± 0.022 kg; mean±2 s.e., $N=10$) was measured in water of various depths. Relative water depth was defined as z/B, where z is the water depth measured from the air/water surface to the longitudinal midline of the body and B is the span of the caudal fin, 0.062 ± 0.004 m. Relative water depths (at absolute depths) tested were; 0.31 (at 0.05 m), 1.11 (at 0.1 m), 1.92 (at 0.15 m), 2.73 (at 0.2 m) and 7.56 (at 0.5 m). Performance was defined in terms of the motion of the centre of mass as measured by the turning radius and the cumulative distance travelled in a given elapsed time. Turning radius was not affected by water depth and averaged 0.018 ± 0.003 m. Distance travelled was a positive function of water depth, although paired *t*-tests showed no significant effect of depth at 0.15 and 0.2 m after about 70 ms. Energy dispersion due to the formation of surface waves increased with decreasing relative water depth. The largest energy dispersion in wave formation at a relative water depth of 0.31 averaged about 70 % of the useful mechanical work performed in deep water. Energy dispersion in wave generation was negligible for relative water depths larger than approximately 3. Energy dispersion is similar to that for rigid streamlined bodies moving at constant speed.

Introduction

Amphibious animals and many solely aquatic animals move on or near the air/water surface. The higher oxygen content of the surface layer in poorly oxygenated waters and allochthonous food inputs attract many fish to the surface

(Moyle and Cech, 1988). Predators often displace small fish to shallow-water zones (Werner, 1986; Schlosser, 1987). Fish at or near the surface may be more vulnerable to predators, because they tend to be silhouetted to various degrees against the background spacelight (Bone and Marshall, 1982).

Swimming at or near the air/water surface creates surface waves. The energy required for their creation and propagation increases energy costs for propulsion (Hertel, 1966; Prange and Schmidt-Nielsen, 1970; Williams and Kooyman, 1985; Stephenson *et al.* 1989). Hertel (1966) has shown that drag may be elevated by a factor of up to five when a half-submerged rigid body moves at constant velocity. In view of the importance of acceleration in fitness-critical events such as predator–prey interactions, this study examines the performance consequences for fast-starts near an air/water surface.

Materials and methods

Experiments were performed on rainbow trout *Oncorhynchus mykiss* (=*Salmo gairdneri*) obtained from a local fish farm. Fish were held in 110 l tanks at 14.5°C in aerated water, and fed a maintenance diet of Purina Trout Chow. Fish were starved for 24 h before testing.

Individual fish were anaesthetized in $0.1 g l^{-1}$ tricaine methane sulphonate (MS222), and a small white thread was sewn on the ventral surface of the midline of the body at the estimated centre of mass. Fish were then transferred to a plateglass tank, measuring 0.5 m in length, breadth and depth.

A small tank size was used to ensure that the small displacements of the centre of mass would be seen as large movements on the projected film. However, the tank size might affect performance in two ways. First, the presence of walls may force turns earlier than would otherwise occur. Fish often combine turns and fast-starts and the same physical principles describe the mechanics of both (Weihs, 1972, 1973). Therefore, although chamber size might influence behaviour, it will not affect the evaluation of principles. Second, the wake may interact with the walls, increasing thrust. Simulation of the vortex sheet shed at the tail shows that the vorticity in a fast-start turn moves only 10–20 % of the body length (Q.-N. Zhou, W. W. Schultz and P. W. Webb, unpublished observations). Fish were always further from the walls than this distance.

The bottom of the observation tank was marked with a 0.1 m grid. The tank was maintained at 14.5°C. Two opposite sides of the tank were lined with aluminium window screen through which an electrical stimulus could be delivered to a fish to initiate a fast-start. The water depth in the tank was set at one of five levels, 0.05, 0.1, 0.15, 0.2 and 0.5 m. Trout were typically slightly negatively buoyant, and rested and accelerated at the bottom of the tank. Therefore, these nominal water depths were also the actual depths. After an acclimation period of at least 12 h, floodlights (1500 W) were turned on. Fish movements were monitored using a 45° mirror beneath the tank and a video recorder. When a fish was stationary and typically oriented parallel to the aluminium screens, a $0.01 V m^{-1}$ (d.c.) 0.25 ms

Table 1. *Morphological characteristics of rainbow trout used in experiments*

Total length (m)	0.263±0.030
Mass (kg)	0.187±0.022
Maximum depth of body and dorsal fin (m)	0.070±0.004
Maximum depth of caudal fin (m)	0.062±0.004
Distance of centre of mass from nose (m)	0.097±0.005

Data are mean±S.E., for 10 fish.

stimulus was given. This is below the threshold likely to cause injury to fish (Sharber *et al.* 1990). The stimulus initiated a fast-start which was recorded on ciné film at a framing rate of 250 Hz using a LoCam high-speed camera viewing the tank *via* the mirror. The film record included a timer signal at 100 Hz.

After recording the fast-start, the water was adjusted to a different depth, and fish were tested at this level after a further minimum of 12 h. Each fish was tested at all water depths. The sequence of depths was randomized.

At the end of an experiment, fish were removed and killed using MS222. Length and mass were measured. The depth of the caudal fin and the maximum depth of the body and dorsal fin were measured. After *rigor mortis* had developed, the centre of mass was determined by suspending the body from the caudal fin and then the dorsal fin. In each position, a plumbline was suspended adjacent to the fish, and its position marked on the body. The centre of mass was assumed to lie in the dorso-ventral plane at the intersection point of these plumblines. Morphometric data are summarized in Table 1.

Ciné film was analyzed frame-by-frame with images magnified by a factor from two to four. Two stages were defined in terms of the completion of the first and then the second lateral displacement of the trailing edge of the caudal fin. The duration of each stage was measured. The coordinates of the centre of mass, measured from the nose and/or the thread near this position, were determined using a Scientific Accessories Corporation acoustic digitizer with a nominal precision of 10^{-4} m. The distance travelled and the radius of the path of the centre of mass were calculated. The radius was determined by assuming that the positions between adjacent positions of the centre of mass marked chords on a turning circle. Perpendiculars bisecting these chords therefore intersected at the centre of the turning circle. The mean turning radius was determined through a fast-start up to the end of stage 2.

Results

Trout at all water depths responded to the electrical stimulus with typical C-starts, in which the body was bent into a C-shape during stage 1. The duration of stage 1 did not differ among trials, and the overall value was 62±6 ms
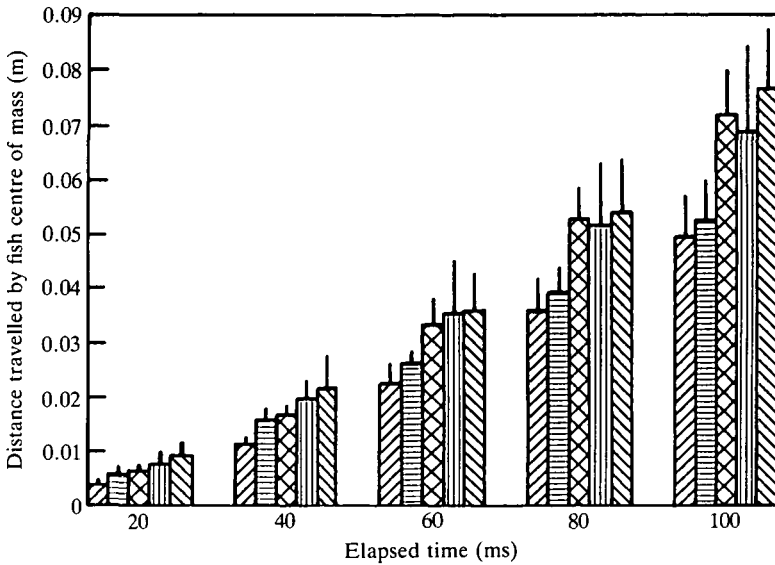
Fig. 1. Examples of the distance travelled in various elapsed times during a fast-start at five water depths. Water depth increases from left to right: 0.05, 0.1, 0.15, 0.2 and 0.5 m. These correspond to relative water depths of 0.31, 1.11, 1.92, 2.73 and 7.56. Vertical lines represent 2 s.e.

(mean±2 s.e.). This was followed by stage 2, when the tail moved in the opposite direction, with the body ending in another C-shape or an S-shape. The time to the end of stage 2 also did not vary among trials, and was 126±11 ms.

Most fish began a glide during stage 2. In previous experiments, including those using fish of similar size and in a tank of similar dimensions (Webb, 1976), fish most commonly swam for at least several tail beats. The reason for the different behaviour in the present experiments is not known, but was not a function of water depth.

There were no differences in turning radius of the path of the centre of mass among trials (ANOVA $P<0.05$), and the overall mean value was 0.018±0.003 m.

The cumulative distance travelled in any elapsed time (Fig. 1) varied with water depth (ANOVA $P<0.05$), and at any elapsed time there was a significant relationship between water depth and distance travelled. These trends were strongest earlier in a fast-start. Thus, after about 70 ms, there were no significant differences in distance travelled in water depths of 0.15, 0.2 and 0.5 m (t-test; $P<0.05$).

Discussion

Moving near a surface affects both resistance and thrust. Most studies have

focused on the ground effect, which improves performance of lift-based systems near rigid planar surfaces (Reid, 1932; Hoerner, 1975; Blake, 1979; Lighthill, 1979). In contrast to the improved performance of lift-based devices moving near a rigid surface, swimming performance is reduced when moving near the air/water surface because the creation and propagation of surface waves disperses energy (Prange and Schmidt-Nielsen, 1970; Stephenson *et al.* 1989). The associated increase in drag depends on the relative depth, z/B, where z is the distance from the mean water surface to the longitudinal dorso-ventral centre-line of the object, and B is the depth, or span, of that object (Hertel, 1966). Thus, when z/B is zero, an object is half out of water.

The depth, or span, of a fish varies along the body length. The maximum depth of trout occurs at the position of the dorsal fin (Table 1). However, in a fast-start, the largest lateral excursions of the body, the greatest contributions to thrust and the most prominent surface waves are made by the caudal fin. Therefore, B is assumed to be the span of the trailing edge of the caudal fin. Since the trout swam at the bottom of the water column, z is the water depth in each trial. Therefore, relative depth took values (at trial water depths) of 0.31 (at 0.05 m), 1.11 (at 0.1 m), 1.92 (at 0.15 m), 2.73 (at 0.2 m) and 7.56 (at 0.5 m). Thus, fast-start performance was reduced in shallow water, with shallow water defined as a water depth of less than approximately 2–3 caudal fin spans (Fig. 1).

The energy dispersed as a result of wave generation can be estimated by assuming that all fish performed the same amount of work regardless of test water depth and that the added mass coefficient is not affected by accelerating near the air/water surface. The first assumption appears to be reasonable for an all-or-none startle response, when performance can be presumed to be maximized. The added mass coefficient is affected in acceleration near a boundary. However, the coefficient is small (Webb, 1982a) and acceleration reaction forces of both resistance and thrust would be expected to be affected equally. Thus, large changes in the acceleration reaction coefficient and performance appear improbable.

The work performed during the initial stages of a fast-start in the absence of an air/water boundary is primarily inertial, and frictional components due to water viscosity are negligible (Webb, 1982a). As a result, fast-start resistance forces associated with accelerations and decelerations are additive when performance at various water depths is most parsimoniously compared in terms of the average work performed. The average work performed by the control fish, W_c, in accelerating a mass, M, from rest over a distance, s_c, in time t is:

$$W_c = 2Ms_c^2t^{-2}, \tag{1}$$

where M is $(1+\alpha)M_f$, α is the added mass coefficient and M_f is the mass of the fish.

It is convenient to express the energy dispersed in creating surface waves as a proportional loss relative to the maximum useful work performed by fish in the deepest water. The same fish were used for the whole range of water depths. Neglecting possible changes in the added mass coefficient, $2Mt^{-2}$ is constant for a

given value of t. Then the proportion of energy dispersed, W_d, compared to a fish in deep water is:

$$W_d = 1 - (s_t^2/s_c^2),$$ (2)

where s_t^2 is the distance travelled in shallower water.

The proportion of energy dispersed increased as relative water depth decreased (Fig. 2). Calculated energy dispersion in creating surface waves tended to be larger during the first 20 ms than for larger periods. There were no significant trends, suggesting that temporal integration of work done for time-dependent acceleration rates is required, supporting the use of averaged performance data.

About 70 % of the mechanical work used in propulsion for a fish in deep water was dispersed as waves when the dorsal surface of the trout was just out of water, corresponding to a relative water depth of 0.31. This is a common situation for large fish in shallow water, such as courting and redd-digging salmon. Energy dispersed in waves fell to zero at relative water depths greater than approximately 3.

Fig. 2 also shows the energy dispersed in wave formation for a non-flexing streamlined body of revolution moving at constant speed at various relative depths, calculated from data in Hertel (1966). The losses for accelerating trout span those for the rigid body moving at constant speed. For the rigid body,
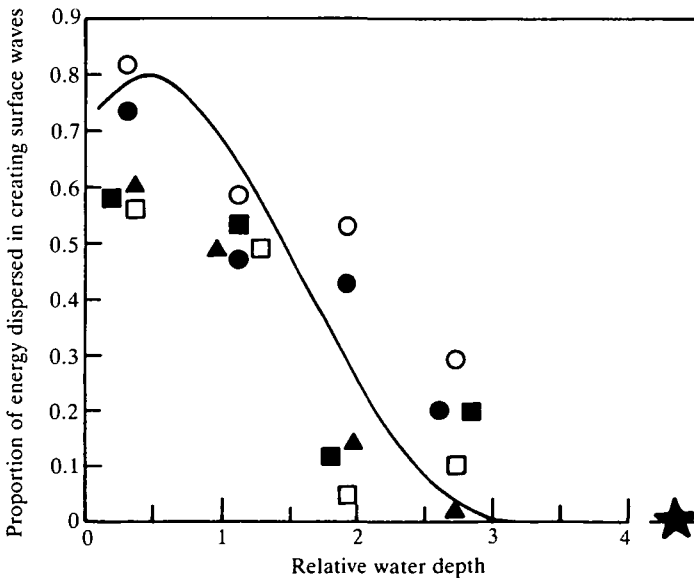

Fig. 2. The proportion of mean energy dispersed by surface waves after various elapsed times shown as a function of relative water depth. Wave energy losses are assumed to be negligible for fast-starts in 0.5 m of water. ○, mean energy losses to an elapsed time of 20 ms; ●, 40 ms; ▲, 60 ms; □, 80 ms; ■, 100 ms; solid line, a rigid body moving at constant velocity (from Hertel, 1966, page 227).

resistance increments due to moving near the air/water surface are negligible for relative depths in excess of 3.

Normal animal swimming behaviour comprises both state (velocity) and control (acceleration) variables (Daniel and Webb, 1987). The present results suggest that the energetic consequences of surface swimming are the same for both types of motions. Thus, swimming animals should avoid the water surface or, when they must swim at the surface, the exposed portion of the body should be as small as possible. However, Hertel (1966) showed that the resistance increment for a rigid body declined more rapidly with relative depth (distance) above the water surface than below it. Together with the reduced drag in air, the lower rate of energy dispersion in waves will contribute to energy-reducing behaviour such as porpoising (Au and Weihs, 1980) for animals that commonly move near the air/water surface.

Fast-starts are important components of strikes by fish piscivores and escape manoeuvres by their prey (Webb, 1982*b*). Such predator–prey interactions are examples of interception games, where the general solution for an interceptor (predator) is to minimize the duration of an interaction. This minimizes the chance of prey reaching cover (Webb, 1986). Time minimization is usually achieved by maximizing speed and acceleration rate. Predators typically have linear dimensions five or more times larger than their prey (Popova, 1978). Therefore, water that is shallow relative to a predator will be deep relative to the prey. As a result, shallow water should reduce predator strike performance, increasing the duration of a predator–prey interaction and thereby shifting the chances of success towards the prey. Studies of fish distributions in streams and lakes show that fish of various sizes are not uniformly distributed (Werner, 1986; Schlosser, 1987; Angermeier and Schlosser, 1989). Small fish are commonly displaced to shallower areas, such as the littoral zones of lakes, stream margins and riffles. Often these are not the preferred areas for the small fish (Schlosser, 1987). Thus, the shallow water may act as a refuge for the prey.

References

ANGERMEIER, P. L. AND SCHLOSSER, I. J. (1989). Species–area relationships for stream fishes. *Ecology* **70**, 1450–1462.

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

BLAKE, R. W. (1979). The energetics of hovering in mandarin fish (*Synchropus picturatus*). *J. exp. Biol.* **82**, 25–33.

BONE, Q. AND MARSHALL, N. B. (1982). *Biology of Fishes.* London: Blackie.

DANIEL, T. AND WEBB, P. W. (1987). Physical determinants of locomotion. In *Comparative Physiology: Life in Water and on Land* (ed. P. DeJours, L. Bolis, C. R. Taylor and E. R. Weibel), pp. 343–369. Fidia Research Series IX. Padova: Liviana Press.

HERTEL, H. (1966). *Structure, Form and Movement.* New York: Reinhold Publ. Corp.

HOERNER, S. F. (1975). *Fluid-Dynamic Lift*. Brick Town, NJ: Hoerner Fluid Dynamics.

LIGHTHILL, M. (1979). A simple fluid-flow model of ground effect in hovering. *J. Fluid Mech.* **93**, 781–797.

MOYLE, P. B. AND CECH, J. J. (1988). *An Introduction to Ichthyology*. Englewood Cliffs, NJ: Prentice-Hall.

POPOVA, O. A. (1978). The role of predaceous fish in ecosystems. In *Ecology of Freshwater Fish Production* (ed. S. D. Gerking), pp. 215–249. Oxford: Blackwell.

PRANGE, H. D. AND SCHMIDT-NIELSEN, K. (1970). The metabolic cost of swimming in ducks. *J. exp. Biol.* **53**, 763–777.

REID, E. G. (1932). *Applied Wing Theory*. New York: McGraw-Hill.

SCHLOSSER, I. J. (1987). The role of predation in age- and size-related habitat use by stream fishes. *Ecology* **68**, 651–659.

SHARBER, N. G., CAROTHERS, S. W. AND SHARBER, J. P. (1990). Electrofishing-induced spinal injury in rainbow trout. *N. Am. J. Fish. Mgmt* (in press).

STEPHENSON, R., LOVVORN, J. R., HEIEIS, M. R. A., JONES, D. R. AND BLAKE, R. W. (1989). A hydrodynamical estimate of the power requirements of diving and surface swimming in lesser scaup (*Aythya affinis*). *J. exp. Biol.* **147**, 507–519.

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

WEBB, P. W. (1982a). Fast-start resistance of trout. *J. exp. Biol.* **96**, 93–106.

WEBB, P. W. (1982b). Avoidance responses of fathead minnow to strikes by four teleost predators. *J. comp. Physiol.* **147**A, 371–378.

WEBB, P. W. (1986). Locomotion and predator–prey relationships. In *Predator–Prey Relationships* (ed. M. E. Feder and G. V. Lauder), pp. 24–41. Chicago, IL: University of Chicago Press.

WEIHS, D. (1972). A hydrodynamical analysis of fish turning manoeuvres. *Proc. R. Soc.* B **182**, 59–72.

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

WERNER, E. E. (1986). Species interactions in freshwater fish communities. In *Community Ecology* (ed. J. Diamond and T. J. Case), pp. 344–358. New York: Harper & Row.

WILLIAMS, T. M. AND KOOYMAN, G. L. (1985). Swimming performance and hydrodynamic characteristics of harbor seals, *Phoca vitulina*. *Physiol. Zool.* **58**, 576–589.