

## THE EFFECT OF SOLID AND POROUS CHANNEL WALLS ON STEADY SWIMMING OF STEELHEAD TROUT *ONCORHYNCHUS MYKISS*

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### Summary

Kinematics and steady swimming performance were recorded for steelhead trout (approximately 12.2cm in total length) swimming in channels 4.5, 3 and 1.6cm wide in the centre of a flume 15cm wide. Channel walls were solid or porous. Tail-beat depth and the length of the propulsive wave were not affected by spacing of either solid or porous walls. The product of tail-beat frequency,  $F$ , and amplitude,  $H$ , was related to swimming speed,  $u$ , and to harmonic mean distance of the tail from the wall,  $z$ . For solid walls:

$$FH = 1.01(\pm 0.31)u^{0.67(\pm 0.09)}z^{(0.12 \pm 0.02)}$$

and for grid walls:

$$FH = 0.873(\pm 0.302)u^{0.74(\pm 0.08)}z^{0.064(\pm 0.024)},$$

where  $\pm 2$  S.E. are shown for regression coefficients. Thus, rates of working were smaller for fish swimming between solid walls, but the reduction due to wall effects decreased with increasing swimming speed. Porous grid walls had less effect on kinematics, except at low swimming speeds. Spacing of solid walls did not affect maximum tail-beat frequency, but maximum tail-beat amplitude decreased with smaller wall widths. Maximum tail-beat amplitude similarly decreased with spacing between grid walls, but maximum tail-beat frequency increased. Walls also reduced maximum swimming speed. Wall effects have not been adequately taken into account in most studies of fish swimming in flumes and fish wheels.

### Introduction

Current understanding of fish swimming mechanics hinges on hydromechanical models that assume fish swim in an unbounded fluid (Lighthill, 1975; Wu, 1977; Weihs, 1989). In practice, structure is a common and preferred feature of fish habitat (Hynes, 1970) that affects swimming behaviour and performance (Arnold and Weihs, 1978; Blake, 1979, 1983a,b; Webb, 1981, 1989; Webb *et al.* 1991).

Most studies of locomotor interactions with habitat structure for animals moving in fluids have focused on lift-based propulsors in ground effect (see Blake, 1983a, 1985; Norberg, 1986; Rayner, 1991). These ground effects result from interactions with the surface by the bound vortices on the lift-based propulsors and by reduction of the down-

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wash angle of the wake. The latter interaction is usually most important, resulting in lower induced drag, in turn reducing total locomotor power requirements. There is also a horizontal forward velocity component associated with the bound vortex on a wing that can offset this reduced power requirement when animals move close to the surface at low speeds (Rayner, 1991).

Many fish swim by lateral undulation of the caudal fin, with thrust produced primarily by acceleration reaction (Daniel and Webb, 1987). Ground effects can still occur from interactions between the flow around the tail and the substratum, but the interaction is likely to be small (Lighthill, 1975). However, vertical surfaces are also common habitat features, with stream margins, rock and boulder faces, and large woody debris representing walls. Flumes used to study swimming mechanics and energetics also have walls. A fish tail moving near such solid walls will experience a wall effect analogous to the ground effect associated with a reduction in the side-wash angle and reduced energy dissipation into the wake (Bell and Terhune, 1970; Hoerner, 1975). Therefore, fish swimming near solid walls could have reduced power requirements. Other walls occur in weed beds, but these are porous.

Performance may benefit from swimming near walls, but spacing between porous and solid walls in natural and experimental situations may be small enough to constrain locomotor movements. Such constraint may be sufficient to reduce thrust more than any benefits that might accrue from wall effects and thereby impair performance.

The purpose of this study was to determine the effect of solid and porous (grid) walls on fish steady swimming kinematics, mechanical power requirements and performance. Wall spacings were chosen not only to ensure that wall (=ground) effects would occur, but also to constrain tail-beat amplitude.

## Materials and methods

### *Fish*

Steelhead trout, *Oncorhynchus mykiss* (Walbaum), were obtained from a local hatchery and acclimated to the laboratory for at least 2 weeks before experiments were conducted. Fish were held at 15°C in 110l aerated tanks, with water replacement at 200% per day. Fish were fed a daily maintenance ration of trout chow.

### *Procedures*

Fish were tested at 15°C in channels with solid or grid walls delineated within a flume (Vogel and LaBarbara, 1978) with an observation section 15cm×15cm and 50cm long. I placed wide, medium and narrow channels in the centre of this flume, with wall spacings of 4.5, 3 and 1.6cm, respectively. These were approximately 37, 25 and 13% of the total length,  $L$ , of the fish. Tail-beat amplitudes, measured between extreme lateral positions of the caudal fin trailing edge, are typically about  $0.2L$ , so the wall spacings were about 185, 123 and 66% of the amplitude expected for fish swimming in unbounded water.

The flume and the solid walls were made of Plexiglas. The grid was made of wires, 0.75mm in diameter, strung at 5mm intervals parallel to the water flow. The ends of frames holding the wires were outside the observation section in which the fish swam.

Smaller and more widely spaced wires would have been preferable, but fish invariably escaped through such walls. Thus, wire size and spacing were determined by the purely practical consideration of holding approximately 50% of the fish in the channel throughout an experiment.

I measured the flow patterns and mean flow speed in the channels created by each wall spacing from video recordings of neutrally buoyant particles over the entire range of speeds at which fish swam in the experiments.

Individual fish, starved for 24h, were placed in the flume and left overnight swimming at approximately  $1 \text{ L s}^{-1}$ . The following day, an increasing velocity test was performed with speed increments of approximately  $5 \text{ cm s}^{-1}$  every 2min until fish were fatigued. Fatigue was recognized as the inability of fish to swim off an electrified screen (3–5 V d.c.) delimiting the downstream end of the observation section.

The 2-min critical swimming speed,  $u_{\text{crit}}$  ( $\text{cm s}^{-1}$ ), was calculated as usual (Brett, 1964) from the speed increment,  $du$  ( $\text{cm s}^{-1}$ ), time increment,  $dt$  (min), the time to fatigue,  $t$  (min) and the speed,  $u_f$  ( $\text{cm s}^{-1}$ ), prior to that at which exhaustion occurred as:

$$u_{\text{crit}} = u_f + du(t/dt).$$

At the end of an experiment, fish were weighed and measured. There were no differences in length and mass of fish used in each test group (see Table 1; ANOVA,  $P < 0.001$ ).

Swimming movements, together with an in-line clock accurate to 0.01s, were recorded on video tape (Panasonic AG-1960) *via* a Panasonic Digital-5000 camera with a shutter speed of 1/1000s. Recordings were played back field-by-field (framing rate, 60Hz). Steady swimming, with at least five consecutive tail-beats without forward or backward movement of the nose, was analyzed to determine tail-beat frequency and amplitude, and caudal fin trailing edge depth. The length of the propulsive wave was recorded from overlapping mirror images of the body deformation. Control fish were only analyzed when swimming in the centre of the flume.

#### *Gap-span ratio*

The distance between a propulsor and the ground is non-dimensionalized as the gap/span ratio, where the gap,  $z$ , is the distance from the ground to the propulsor and the span,  $B$ , is the tip-to-tip length of the propulsor. The influence of the ground decreases non-linearly as the gap/span ratio increases (Reid, 1932; Lighthill, 1979; Rayner, 1991). Studies of ground effect have focused on fixed-wing aircraft, birds gliding or flying with minimal flapping (Withers and Tomcko, 1977; Blake, 1985; Norberg, 1986; Rayner, 1991), helicopters (Bramwell, 1976; Lighthill, 1979) and fish hovering while flapping their propulsors parallel to the ground, and hence acting in a manner analogous to helicopters (Blake, 1979, 1983b). Under these conditions, the gap/span ratio is constant.

During swimming in channels, the fish tail beats normal to the walls so that the gap/span ratio varies with time. Fish often swim close to a wall, when at one extreme lateral tail position there will be a large interaction with the near wall and a small interaction with the far wall. The strength of the interaction with the near wall will decrease as the tail moves away from the wall, simultaneously increasing for the far wall.

I chose to determine an average gap as the harmonic mean of the distances from each wall at the extremes of the tail beat, and from the centre line, crossed twice in each beat (see Fig. 1). This method takes into account the closest approach of the tail to the near wall,  $z_1$ , and the far wall,  $z_2$ , and the mean distance of the tail from the near wall,  $z_3$ , and from the far wall,  $z_4$ . The mean gap,  $z$  is;

$$z = (z_1 z_2 z_3 z_4)^{1/4} \quad (1)$$

The gap/span ratio was calculated from this value of  $z$  and the depth of the caudal fin trailing edge,  $B$ .

#### *Rate of working*

Ground effect is often expressed as a ratio of the rate of working in ground effect,  $P_g$ , and a reference out of ground effect (Hoerner, 1975; Rayner, 1991). Here the reference is  $P_{ref}$ , the rate of working for the control fish. The total rate of working,  $P$ , was computed after Wu (1977):

$$P \propto F^2 H^2 B^2 (1 - u/c), \quad (2)$$

where  $F$  is tail-beat frequency,  $H$  is tail-beat amplitude,  $B$  is caudal fin trailing edge depth,  $u$  is swimming speed and  $c$  is speed of the propulsive wave where  $c = F\lambda$  and  $\lambda$  is the length of the propulsive wave.

## **Results**

### *Gap*

The harmonic mean gap for the caudal fin trailing edge of the control fish swimming in the centre of the flume was 6.9cm, when  $z/B$  was 2.71 (Table 1). This gap decreased with decreasing channel width to 0.27cm ( $z/B=0.11$ ) for channels with both solid and grid walls.

### *Kinematics*

Both caudal fin trailing edge depth and the length of the propulsive wave were independent of swimming speed and of treatment (ANOVA,  $P < 0.001$ ), with mean values ( $\pm 2$  S.E.) of  $2.6 \pm 0.1$ cm and  $10.4 \pm 0.1$ cm respectively.

As with other studies of swimming kinematics, tail-beat frequency,  $F$ , increased linearly with speed in all treatments (Table 2), although consistent patterns between frequency and wall spacing were not apparent. Tail-beat amplitude,  $H$ , co-varied with tail-beat frequency and swimming speed within groups. Similar modulation of both frequency and amplitude with speed is observed in other species and populations, especially at lower swimming speeds (see Bainbridge, 1958; Webb, 1975; Webb *et al.* 1984; Videler and Wardle, 1991). In these situations, the product,  $FH$ , summarizes the principal kinematic changes with swimming speed (Webb, 1971; Wu, 1977; Webb *et al.* 1984).

The product  $FH$  decreased consistently as spacing decreased for solid walls. Since other kinematic variables were independent of treatment, this meant that fish worked less

Table 1. Mass, length, number of fish used, gap and mean gap/span ratio for steelhead trout swimming in channels of various widths

Group	Length (cm)	Mass (g)	<i>N</i>	Gap <i>z</i> (cm)	Mean <i>z/B</i>
Control	12.1±0.4	13.29±1.70	10	6.92±0.11	2.71
Solid walls					
Wide spacing	12.1±0.7	12.93±1.89	10	1.49±0.09	0.55
Medium spacing	12.3±0.3	14.59±1.63	10	0.84±0.05	0.33
Narrow spacing	12.2±0.6	13.40±2.43	10	0.27±0.03	0.11
Grid walls					
Wide spacing	12.2±0.5	13.65±1.51	10	1.75±0.06	0.69
Medium spacing	12.0±0.5	12.64±1.41	10	0.97±0.06	0.38
Narrow spacing	12.3±0.7	13.80±3.24	10	0.27±0.04	0.11

Data are means ±2 S.E.  
*B*, the tip-to-tip length of the propulsor; *z*, gap.

hard when swimming at a given speed near solid walls. Combining all data for experiments with solid walls and the control group gave the following relationship between *FH*, swimming speed, *u*, and gap, *z*:

$$FH = 1.01(\pm 0.31)u^{0.67(\pm 0.09)}z^{0.12(\pm 0.02)}, P < 0.01 \quad (3)$$

where ±2 S.E. are shown in parentheses.

A consistent pattern between the rate of change in *FH* and channel width was still not apparent from visual comparison of the data for treatment groups. However, a significant relationship was found between wall spacing, kinematics and swimming speed:

$$FH = 0.873(\pm 0.302)u^{0.74(\pm 0.08)}z^{-0.064(\pm 0.024)}, P < 0.01 \quad (4)$$

Differences in exponents for *u* and *z* in equations 3 and 4 were significant (ANCOVA,  $P < 0.01$ ). Thus, fish obtained benefits from wall effects when swimming at low speeds and greater benefits when swimming between solid walls than with grid walls. Equations 3 and 4 described the data well (Fig. 1), although observations on the solid wide-wall treatment tended to be somewhat higher than predicted from equation 3.

#### *Maximum tail-beat frequency and amplitude and critical swimming speed*

Maximum tail-beat frequency (Table 3) was independent of the gap between solid walls ( $P > 0.4$ ) but increased as gap decreased between grid walls ( $P < 0.05$ ). Maximum tail-beat amplitude (Table 3) was similarly constrained by solid and grid walls, decreasing as channel width declined ( $P < 0.05$ ).

The decrease in tail-beat amplitude with gap between solid walls without changes in tail-beat frequency would be expected to be associated with reduced swimming performance in an unbounded fluid. Reduced performance ( $P < 0.5$ ) was found for fish swimming in the channels with both solid and grid walls. Thus, wall effects and the

Table 2. Relationships between swimming speed,  $u$  ( $\text{cm s}^{-1}$ ), and tail-beat frequency,  $F$  (Hz), and the product  $FH$  of tail-beat frequency and tail-beat amplitude,  $H$  (cm), for fish swimming between solid and grid walls with various spacings

Tail-beat frequency			
Control	$F = 2.31 + 0.097u$	$P < 0.001$	
	( $\pm 0.50$ ) ( $\pm 0.016$ )		
Solid walls			
Wide	$F = 1.52 + 0.157u$	$P = 0.001$	
	( $\pm 1.31$ ) ( $\pm 0.068$ )		
Medium	$F = 2.23 + 0.114u$	$P < 0.001$	
	( $\pm 0.91$ ) ( $\pm 0.030$ )		
Narrow	$F = 1.59 + 0.144u$	$P < 0.001$	
	( $\pm 0.98$ ) ( $\pm 0.034$ )		
Grid walls			
Wide	$F = 3.87 + 0.090u$	$P = 0.007$	
	( $\pm 1.98$ ) ( $\pm 0.056$ )		
Medium	$F = 2.42 + 0.127u$	$P < 0.001$	
	( $\pm 1.48$ ) ( $\pm 0.040$ )		
Narrow	$F = 2.85 + 0.135u$	$P < 0.001$	
	( $\pm 1.58$ ) ( $\pm 0.042$ )		
Tail-beat frequency $\times$ tail-beat amplitude			
Control	$FH = 3.03 + 0.300u$	$P < 0.001$	
	( $\pm 4.23$ ) ( $\pm 0.044$ )		
Solid walls			
Wide	$FH = 5.74 + 0.233u$	$P < 0.001$	
	( $\pm 5.26$ ) ( $\pm 0.079$ )		
Medium	$FH = 3.45 + 0.212u$	$P < 0.001$	
	( $\pm 4.02$ ) ( $\pm 0.061$ )		
Narrow	$FH = 2.21 + 0.182u$	$P < 0.001$	
	( $\pm 2.60$ ) ( $\pm 0.045$ )		
Grid walls			
Wide	$FH = 6.30 + 0.164u$	$P < 0.001$	
	( $\pm 2.49$ ) ( $\pm 0.074$ )		
Medium	$FH = 0.86 + 0.311u$	$P < 0.001$	
	( $\pm 3.64$ ) ( $\pm 0.034$ )		
Narrow	$FH = 3.07 + 0.220u$	$P < 0.001$	
	( $\pm 4.44$ ) ( $\pm 0.086$ )		

Means are shown with  $\pm 2\text{s.e.}$  in parentheses.

increasing tail-beat frequency with decreasing channel width between grid walls were insufficient to compensate performance for reduced amplitude.

#### Rates of working

The effect of gap/span ratio on the relative rate of working,  $P_g/P_{\text{ref}}$  varied with swimming speed for both solid and grid walls (Fig. 2). When channel walls were solid,  $P/P_{\text{ref}}$  increased non-linearly with  $z/B$ , as for ground effect. However, the reduction in  $P_g/P_{\text{ref}}$  at a given  $z/B$  decreased as swimming speed increased. A significant wall effect

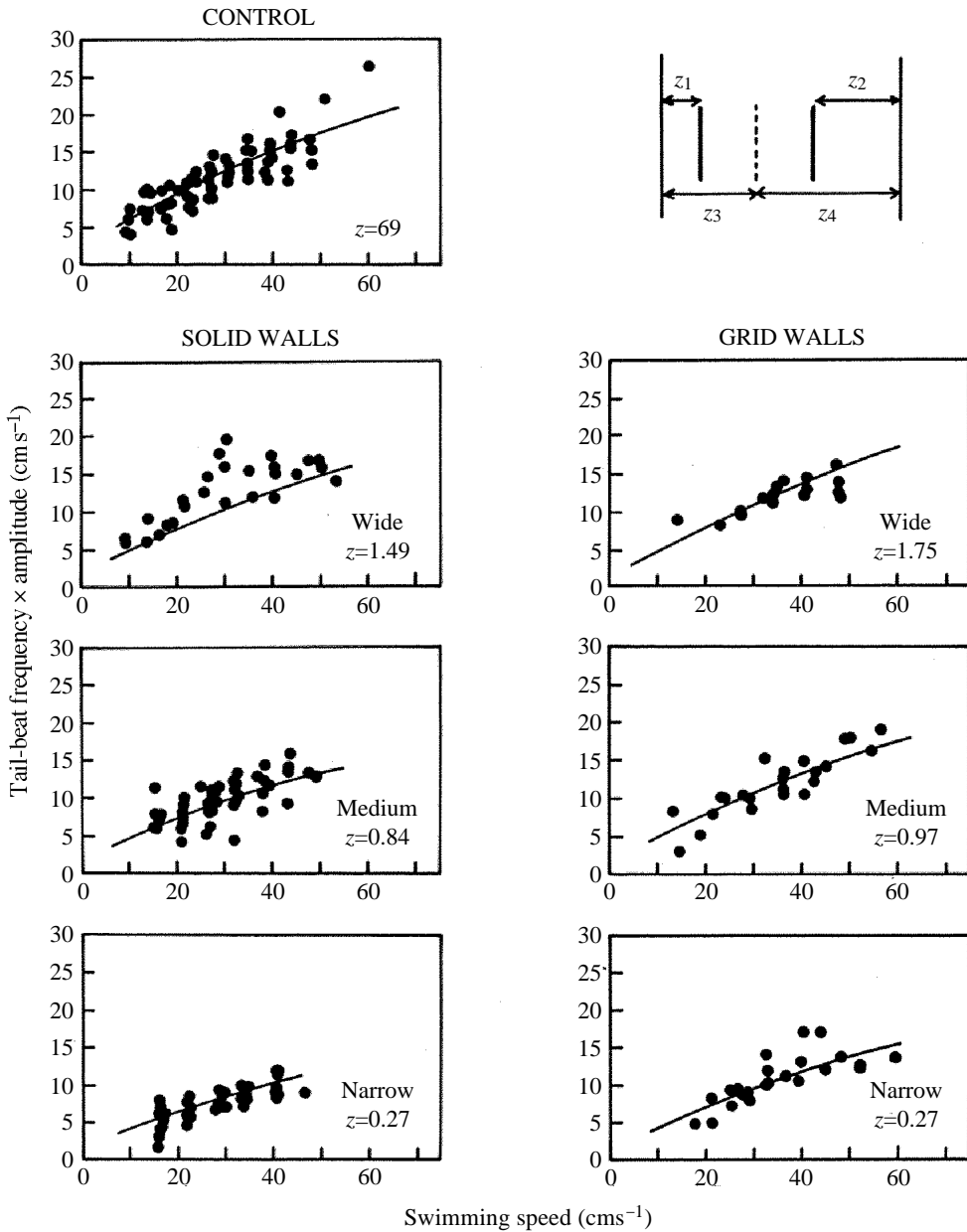


Fig. 1. Relationships between the product of tail-beat frequency and amplitude with swimming speed for steelhead trout swimming in channels between solid and grid walls. Solid lines are regression equations fitted to the data for all fish swimming between solid walls and the control fish (left-hand column) and for all fish swimming between grids and the control fish (right-hand column). Values of  $z$  are mean distances from the tail trailing edge to the walls, determined from the harmonic mean of  $z_1$ – $z_4$  as shown in the inset at the top of the right-hand column. The walls and the limits of the lateral motion of the tail are shown as vertical lines, and the mid-point of the tail beat as a dotted line.

Table 3. *Maximum tail-beat frequencies and amplitudes and critical swimming speeds for steelhead trout swimming between solid and grid walls with various spacings*

Group	Maximum tail-beat frequency (Hz)	Maximum tail-beat amplitude (cm)	Critical swimming speed (cm s <sup>-1</sup> )	N
Control	7.3±1.5	2.7±0.4	61.1±4.2	10
Solid walls				
Wide spacing	6.9±0.5	2.7±0.4	43.4±1.9	10
Medium spacing	6.7±0.8	2.0±0.3	50.8±4.1	10
Narrow spacing	7.2±0.9	1.5±0.2	47.2±7.8	10
Grid walls				
Wide spacing	7.7±1.5	2.1±0.4	45.5±9.3	7
Medium spacing	8.1±1.4	1.9±0.4	48.5±8.6	8
Narrow spacing	8.6±1.3	1.5±0.3	47.8±9.5	5

Data are means ±2s.e.

was only found for grid walls at low speeds, and  $P_g/P_{ref}$  was unaffected by wall spacing at higher swimming speeds.

### Discussion

Ground effect increases lift and reduces drag for negatively buoyant animals and fixed-wing aircraft moving near a horizontal surface (Rayner, 1991). Neutrally buoyant fish swimming between solid walls obtained similar advantages, especially at low swimming speeds, but performance was impaired as a result of constraints on the amplitude of locomotor movements.

Thus, the ratio  $P_g/P_{ref}$  for fish swimming between solid walls declined as the gap/span ratio decreased. However, the benefits of swimming near solid walls declined with swimming speed. Two factors were probably major contributors to this decline. First, as speed increases, the angle between the caudal fin trailing edge and the axis of forward progression decreases (Webb, 1988, 1992) and this will be associated with smaller side-wash angles. Second, Froude efficiency increases, reducing the relative energy loss to the wake interacting with the wall.

Reduced swimming performance probably resulted from reduced thrust due to constraint reducing tail-beat amplitude and perhaps limitations due to muscle dynamics. Thus, fish swimming between grid walls showed some increase in tail-beat frequency as wall width and amplitude decreased, but this was insufficient to compensate for reduced amplitude. Perhaps there is a minimum twitch time for red muscle that determines prolonged performance, as postulated by Wardle (1975) for sprint speeds.

The use of porous grid walls was conceived to differentiate possible consequences of wall constraint on performance from those due to hydrodynamic wall effects. Practical considerations of preventing escape necessitated a more substantial barrier than desirable.



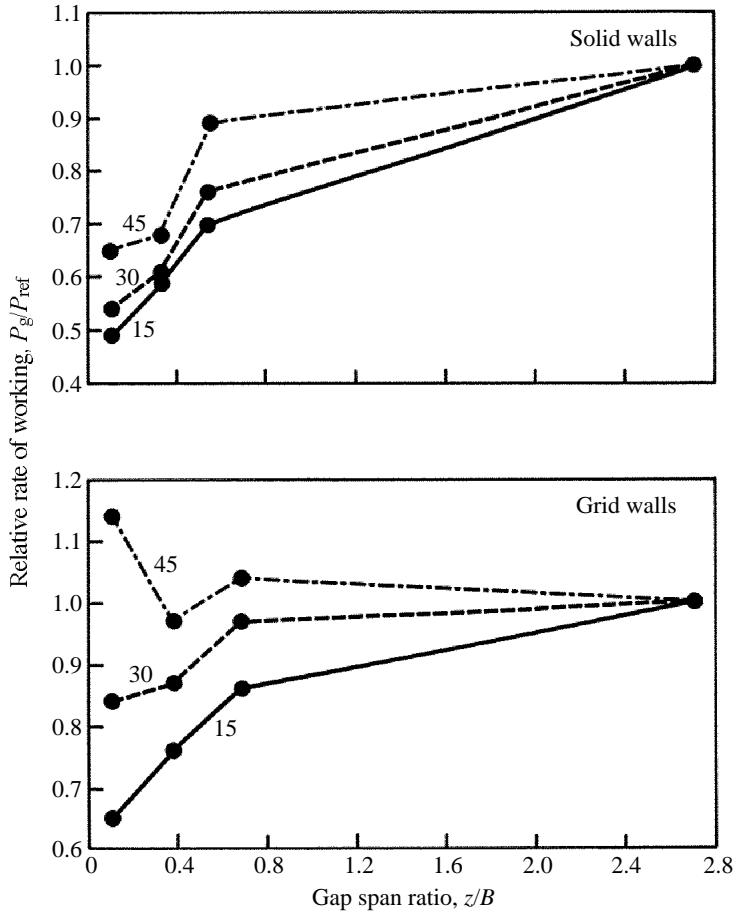


Fig. 2. The effect of gap/span ratio,  $z/B$ , on the relative rate of working,  $P_g/P_{ref}$  of steelhead trout. Effects are shown for three swimming speeds;  $15\text{ cm s}^{-1}$  (solid line),  $30\text{ cm s}^{-1}$  (dashed line) and  $45\text{ cm s}^{-1}$  (chain dashed line).

As a result, grid walls provided sufficient resistance to flow that rates of working were reduced for fish swimming near grids at low speeds (Fig. 2). Effects were smaller than for solid walls and decreased more rapidly at higher swimming speeds. Thus, it can be seen that narrow walls constraining body undulation do indeed reduce performance, and hydrodynamic effects with solid walls, although substantial, are insufficient to compensate.

Fish wheels and flumes have been critical instruments in the study of fish swimming mechanics and energetics (Alexander, 1983), and the results are presumed to apply to fish swimming in unbounded water. Indeed, solid blocking corrections are routinely made for this purpose (Webb, 1971; Beamish, 1978). Wake blocking and other wall effects have been thought negligible (Bell and Terhune, 1970; Webb, 1975) or have been ignored. Instead, the present results show that wall effects in flumes can be substantial.

The channel width of fish wheels and flumes is typically in the range 15–30 cm, in

which it is not uncommon to swim fish 30cm in total length. If tail-beat amplitude and depth are both  $0.2L$ , then  $z/B$  (harmonic mean) would be about 1 for such fish swimming in the centre of a flume 15cm wide. Based on Fig. 2, estimated rates of working would be between 70 and 90% of those in an unbounded fluid. If the fish swam with the tail 5mm from one wall,  $z/B$  would be 0.6, with energy expenditure underestimated at about 65–90%. Ground effects quickly decrease with increasing  $z/B$ , and are usually considered to become negligible when  $z/B > 3$  for propulsors that maintain a constant distance from the ground (Reid, 1932; Blake, 1983*b*). This value is reached by a fish 11.5cm in length swimming in the centre of a 15cm wide flume or a fish 23cm in length in a flume 30cm wide. Most studies of fish swimming in flumes have not reported distances from the walls, and in most situations it is not known whether data on fish near walls were used in the analysis. Therefore, results from such studies should be viewed with caution, especially those on fish swimming at low speeds.

The gap/span ratio for the reference fish used in the present experiments was 2.7, although the expectation was that it would exceed 3 for the size of fish used. Although I used a harmonic mean gap value, I presume a threshold of 3 is still appropriate. Thus, the control (reference) group probably experienced some wall effect. However, observations of hovering fish suggest the residual wall effect would have been of the order of 1% (Blake, 1979).

I did not determine metabolic rate in these experiments. Relatively large water volumes are required in respirometers and flumes to ensure rectilinear flow lacking large-scale turbulence, whilst small fish were required to avoid wall effects for control fish. Thus, measuring metabolic rate would require fish to swim for very long periods at each test speed. During such long periods, fish swim throughout the volume of the observation section, making determination of a mean gap value difficult, and perhaps meaningless. Fish also use unsteady endurance-enhancing behaviour that increases in frequency as swimming speed increases (Webb, 1993). As a result, the mechanical approach used here was considered a more parsimonious and meaningful method to examine wall effects.

Nevertheless, wall effects probably affect reported relationships between metabolic rate and swimming speed, especially determination of standard metabolism by extrapolation of oxygen consumption/speed relationships to zero swimming speed. Variability in metabolic rate increases at low swimming speeds, and differences among individuals in the use of the wall effect may contribute to this variation. Brett (1964) suggested that standard metabolic rates should be obtained for a line bounding the lowest metabolic rates measured in an increasing velocity test, believing that excitement was the major cause of variation at lower swimming speeds. However, these may be fish that are more adept at using wall effect. Clearly closer attention must be paid to the behaviour of fish relative to the constraints and opportunities provided by flumes used for metabolic studies (Webb, 1993).

The foregoing discussion paints a fairly bleak picture of possible errors in standard methods that are fundamental to our present understanding of fish swimming mechanics and energetics. However, this picture may be too pessimistic. Swimming has been studied using many different methods for fish swimming in large tanks (e.g. Videler and Wardle, 1978, 1991), in the centre of large flumes (Webb *et al.* 1984), in fish wheels (Bainbridge,

1958; Bainbridge and Brown, 1958) and in various narrow flumes (e.g. Webb, 1975). The results are remarkably similar (Videler and Wardle, 1991). If wall effects were a major problem in previous flume studies, then data from fish swimming in large tanks would be very different from those for fish swimming in flumes and fish wheels. Such differences are not usually found. However, this lucky situation does not relieve future studies of accounting for wall effects. In future, more careful description of fish behaviour in experimental flumes or the selection of data for analysis that avoids free surface or wall problems is needed.

Walls are not only necessary artefacts of experimental situations, but wall-like structures abound in the natural fish habitat, where they influence behaviour. For example, stream fish swim near structures that not only provide regions of low flow but also an opportunity to swim more efficiently (Feldmeth and Jenkins, 1973; Fausch, 1984). Alternatively, highly structured habitats are well-known predator refuges within which predator success is typically reduced. Amongst weeds (porous walls), stem densities as low as  $50\text{ m}^{-2}$  (approximately 14cm between stems) can affect predation by piscivores 23–37cm in total length. As stem densities approached  $1000\text{ m}^{-2}$  (approximately 3cm between stems), largemouth bass shift from wide-ranging foraging to ambushing prey (Savino and Stein, 1982, 1989*a,b*). Studies on predation among structures have explained changes in terms of effects on predator and prey behaviour, but clearly mechanical factors could be major contributors to the outcome.

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## References

- ALEXANDER, R. McN. (1983). The history of fish biomechanics. In *Fish Biomechanics* (ed. P. W. Webb and D. Weihs), pp. 1–35. New York: Praeger.
- ARNOLD, G. P. AND WEIHS, D. (1978). The hydrodynamics of rheotaxis in the plaice (*Pleuronectes platessa*). *J. exp. Biol.* **75**, 147–169.
- BAINBRIDGE, R. (1958). The speed of swimming of fish related to size and to the frequency and amplitude of the tail beat. *J. exp. Biol.* **35**, 109–133.
- BAINBRIDGE, R. AND BROWN, R. H. J. (1958). An apparatus for the study of locomotion of fish. *J. exp. Biol.* **35**, 134–137.
- BEAMISH, F. W. H. (1978). Swimming capacity. In *Fish Physiology*, vol. 7, *Locomotion* (ed. W. S. Hoar and D. J. Randall), pp. 101–187. New York: Academic Press.
- BELL, W. H. AND TERHUNE, L. D. B. (1970). Water tunnel design for fisheries research. *Fish. Res. Bd Can. Tech. Rep.* **195**, 1–69.
- BLAKE, R. W. (1979). The energetics of hovering in the mandarin fish (*Synchropus picturatus*). *J. exp. Biol.* **82**, 25–33.
- BLAKE, R. W. (1983*a*). Mechanics of gliding birds with special reference to the influence of the ground effect. *J. Biomech.* **16**, 649–654.
- BLAKE, R. W. (1983*b*). *Fish Locomotion*. Cambridge: Cambridge University Press.
- BLAKE, R. W. (1985). A model of foraging efficiency and daily energy budget in the black skimmer (*Rynchops nigra*). *Can. J. Zool.* **63**, 42–48.
- BRAMWELL, A. R. S. (1976). *Helicopter Dynamics*. New York: Edward Arnold.
- BRETT, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd Can.* **21**, 1183–1226.

- DANIEL, T. L. AND WEBB, P. W. (1987). Physics, design and locomotor performance. In *Comparative Physiology: Life in Water and on Land* (ed. P. Dejours, L. Bolis, C. R. Taylor and E. R. Weibel), pp. 343–369. New York: Liviana Press, Springer-Verlag.
- FAUSCH, K. D. (1984). Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Can. J. Zool.* **62**, 441–451.
- FELDMETH, C. R. AND JENKINS, T. M. (1973). An estimate of energy expenditure by rainbow trout (*Salmo gairdneri*) in a small mountain stream. *J. Fish. Res. Bd Can.* **30**, 1755–1759.
- HOERNER, S. F. (1975). *Fluid-dynamic Lift*. Brick Town, NJ: Hoerner Fluid Dynamics.
- HYNES, H. B. N. (1970). *The Ecology of Running Waters*. Toronto: Toronto University Press.
- LIGHTHILL, M. J. (1975). *Mathematical Biofluidynamics*. Philadelphia, PA: Soc. Industrial Applied Mathematics.
- LIGHTHILL, M. J. (1979). A simple fluid-flow model of ground effect on hovering. *J. Fluid Mech.* **93**, 781–797.
- NORBERG, U. M. (1986). *Vertebrate Flight*. New York: Springer-Verlag.
- RAYNER, J. M. V. (1991). On the aerodynamics of animal flight in ground effect. *Phil. Trans. R. Soc. Lond.* **334**, 119–128.
- REID, E. G. (1932). *Applied Wing Theory*. New York: McGraw-Hill.
- SAVINO, J. F. AND STEIN, R. A. (1982). Predator–prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Trans. Am. Fish. Soc.* **111**, 255–266.
- SAVINO, J. F. AND STEIN, R. A. (1989a). Behavior of fish predators and their prey: habitat choice between open water and dense vegetation. *Envl Biol. Fish* **24**, 287–294.
- SAVINO, J. F. AND STEIN, R. A. (1989b). Behavioural interactions between fish predators and their prey: effects of plant density. *Anim. Behav.* **37**, 311–321.
- VIDELER, J. J. AND WARDLE, C. S. (1978). New kinematic data from high speed cine film recordings of swimming cod (*Gadus morhua*). *Neth. J. Zool.* **28**, 465–484.
- VIDELER, J. J. AND WARDLE, C. S. (1991). Fish swimming stride by stride: speed limits and endurance. *Rev. Fish Biol. Fisheries* **1**, 23–40.
- VOGEL, S. AND LABBARBARA, 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. (1971). The swimming energetics of trout. II. Oxygen consumption and swimming efficiency. *J. exp. Biol.* **55**, 521–540.
- WEBB, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 1–159.
- WEBB, P. W. (1981). The effect of the bottom on the fast start of a flatfish, *Citharichthys stigmaeus*. *Fish. Bull. (U.S.)* **79**, 271–276.
- WEBB, P. W. (1988). ‘Steady’ swimming kinematics of tiger musky, an esociform accelerator and rainbow trout, a generalist cruiser. *J. exp. Biol.* **138**, 51–69.
- WEBB, P. W. (1989). Station holding by three species of benthic fishes. *J. exp. Biol.* **145**, 303–320.
- WEBB, P. W. (1992). Is the high cost of body/caudal fin undulatory swimming due to increased friction drag or inertial recoil? *J. exp. Biol.* **162**, 157–166.
- WEBB, P. W. (1993). Exercise performance of fish. In *Comparative Vertebrate Exercise Physiology* (ed. J. H. Jones). Orlando, FL: Academic Press. (in press).
- WEBB, P. W., KOSTECKI, P. T. AND STEVENS, E. D. (1984). The effect of size and swimming speed on locomotor kinematics of rainbow trout. *J. exp. Biol.* **109**, 77–95.
- WEBB, P. W., SIMS, D. AND SCHULTZ, W. W. (1991). The effect of an air/water interface on the fast-start performance of rainbow trout (*Oncorhynchus mykiss*). *J. exp. Biol.* **155**, 219–226.
- WEIHS, D. (1989). Design features and mechanics of axial locomotion in fish. *Am. Zool.* **29**, 151–160.
- WITHERS, P. C. AND TOMCKO, P. L. (1977). The significance of ground effect to the aerodynamic cost of flight and energetics of the black skimmer (*Rhyncops niger*). *J. exp. Biol.* **70**, 13–26.
- WU, T. Y. (1977). Introduction to the scaling of aquatic animal locomotion. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 203–232. New York: Academic Press.