

EFFECTS OF MEDIAN-FIN AMPUTATION ON FAST-START PERFORMANCE OF RAINBOW TROUT (*SALMO GAIRDNERI*)

By P. W. WEBB

*School of Natural Resources, The University of Michigan,
Ann Arbor, Michigan 48109*

(Received 30 December 1977)

SUMMARY

Fast-start performance of eight groups of rainbow trout with various fin-rays removed was measured to test the hydromechanical theory (Weihs, 1973) that large fins are required for acceleration. A trend towards decreasing performance was found for the following sequence of fin-ray amputations: control (pelvic rays amputated); dorsal fin; anal fin; dorsal lobe of caudal fin and ventral lobe of caudal fin; ventral lobe of caudal fin and anal fin; dorsal and ventral lobes of caudal fin; both caudal-fin lobes and anal fin. The series represents progressive reduction in fin and body area, as well as reduction in these areas where lateral movements are largest. Effects of fin amputation on performance were statistically significant ($P > 0.05$) in comparison with controls only for the last three groups lacking the caudal fin. The results confirm the hydromechanical theory, and lead to the conclusion that mechanically optimum lateral body profiles for fast-start and for steady (cruising and sprint) performance are mutually exclusive. This mechanical restriction can be circumvented only in bony fish, with the evolution of flexible, collapsible fins that permit major variation in lateral body profile.

INTRODUCTION

Breder (1926), Gray (1933) and Webb (1973) have shown that amputation of the caudal fin has little effect on steady cruising performance of fish swimming in the subcarangiform mode. Horak (1969) has also shown that amputation of other median fins has no effect on cruising performance. These observations have been interpreted in terms of the boundary-layer thinning hypothesis, whereby lateral body movements of a swimming fish alter boundary-layer flow such that net drag is increased in comparison with a non-flexing body (Lighthill, 1971). Under these circumstances the thrust advantage of increasing trailing-edge depth (Lighthill, 1970) is offset by the increase in drag that occurs with the increase in area with increased depth (Webb, 1973). This leads to the conclusion that the mechanical requirements for optimum steady swimming are maximization of trailing-edge depth together with minimization of caudal fin area (Webb, 1973, 1977). This condition is realized in scombroid fishes (Fierstine & Walters, 1968; Lighthill, 1970).

The lack of significant effect of caudal-fin amputation on steady swimming leads to the conclusion that the typical caudal fin of most fish cannot have evolved to

improve steady performance, cruising and sprinting (Webb, 1973). Hydromechanical theory predicts that large body and fin area should be advantageous for fast-start (acceleration) and turning performance (Weihs, 1972, 1973). In such activities, body and fin interactions typical of steady swimming are minimal (Lighthill, 1970), so that each propulsive segment independently contributes to thrust over the two body-movement cycles characteristic of a fast-start (Weihs, 1973). Therefore, the virtual mass of water accelerated by body movements should be maximized for all body segments, hence resulting in a large body and fin area. Furthermore, each discrete median fin generates lift forces contributing to thrust, so that large area is again advantageous.

If the hydromechanical theory for acceleration is correct, then it must be concluded that mechanically optimal lateral body profiles for fast-start (unsteady) performance and for cruising or sprint (steady) performance are mutually exclusive. This will present little problem for locomotor specialists such as *Esox*, a sprinter, and scombroids, cruisers. However, most swimming fish are locomotor generalists requiring a balance of unsteady and steady swimming capabilities. This in turn must require some lateral body-profile design compromise (Webb, 1977). Furthermore, in view of the negligible effect of caudal-fin amputation on steady swimming, the compromise is expected to favour acceleration. It is therefore clear that understanding of locomotor functional design in fish requires validation of the hypothesis that large body and fin area are required for good acceleration.

The following experiments were designed to test Weihs' (1973) theory. Confirmation is obtained, and some of the consequences for unsteady and steady swimming performance are discussed for a range of lateral body profiles typical of fish.

MATERIALS AND METHODS

Fish

Eighty cultured rainbow trout (*Salmo gairdneri*, Richardson), obtained from a local trout hatchery and acclimated to 15 °C, were selected for uniform size. Individual fish were assigned to one of eight groups by means of a random number process. Each fish was lightly anaesthetized with MS 222 and the fin-web of various fins was amputated just above the fin base. The eight groups were as follows (Fig. 1):

Group 1: control; intact with the exception of amputation of pelvic fin-rays.

Group 2: dorsal fin-rays amputated.

Group 3: anal fin-rays amputated.

Group 4: dorsal-lobe fin-rays of caudal-fin amputated.

Group 5: ventral-lobe fin-rays of caudal-fin amputated.

Group 6: ventral-lobe fin-rays of caudal-fin and anal fin-rays amputated.

Group 7: dorsal- and ventral-lobe fin-rays of caudal fin amputated.

Group 8: dorsal and ventral fin-rays of caudal-fin and anal fin-rays amputated.

Pelvic fins were intact in groups 2–8. Dorsal and ventral caudal-fin lobes were amputated in groups 4 and 5 in case there was any difference in subsequent swimming patterns resulting from interactions between the observation tank bottom (see below and the ventral caudal-fin lobe).

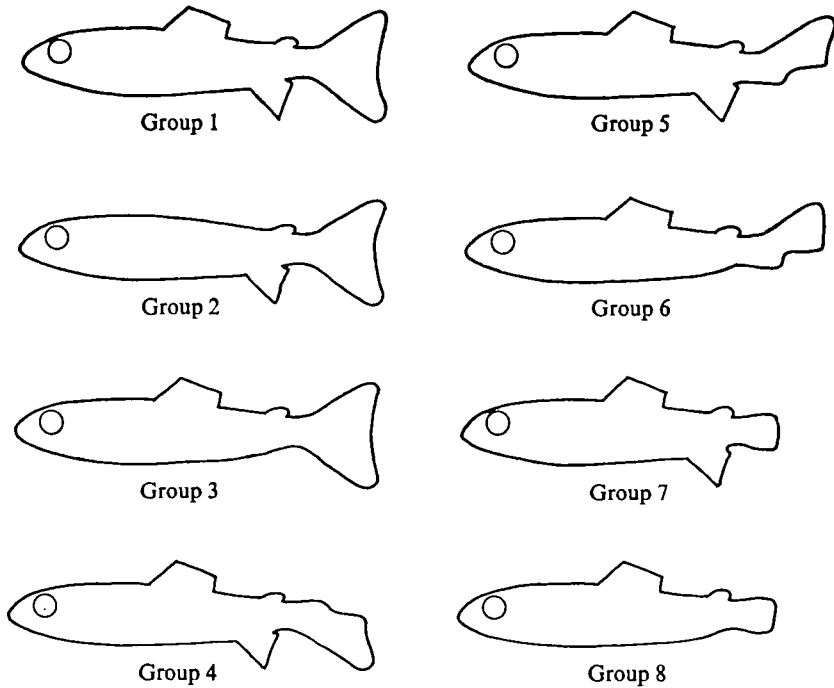


Fig. 1. Body and fin forms for the eight groups of fish used in experiments. Outlines are based on tracing made after the completion of each experiment.

The body and median fin patterns selected were chosen with the intention of evaluating the effect of fin distribution along the body (groups 1–5 and 8) and possible effects of fin interaction (groups 4 and 5, 6–8).

Fish were returned to holding tanks for a period of 2 weeks before experiments were started. This was to provide time for post-operation recovery in swimming behaviour. No mortalities occurred from the operation. Fish were held in groups of 20 in 200 l tanks flushed continuously with water at 50 l h^{-1} . Water circulated in each tank by means of a submerged pump which generated a mean current of about 20 cm s^{-1} in the area of the tank preferred by the fish. Fish swam continuously against this current.

Temperature was controlled at $15.0 \pm 0.2 \text{ }^\circ\text{C}$. Dissolved oxygen levels were maintained close to air saturation by means of airstones. Fish were fed to excess once a day on Purina Trout Chow.

Experimental procedure

Two series of experiments were performed. (1) Measurements of acceleration performance. (2) Measurements of changes in fin depth during acceleration. Fish treatment was the same in both series. Individual fish were starved for 2 days. Each was then lightly anaesthetized and a white bead (1 mm diameter) was attached flush to the skin above the predicted centre of mass for the stretched-straight body. This served as a reference point to facilitate accurate analysis of film and also to assist observation of changes in rolling stability resulting from fin amputation. After this

operation, each fish was placed in an observation chamber and was left undisturbed for 20 h prior to testing.

For the measurements of acceleration rate in the first series of experiments, observations were made in a square (50 × 50 cm and 10 cm deep) plexiglass observation chamber with a clear plexiglass lid. The dimensions of this chamber permitted unrestricted fast-start behaviour but it was not possible to obtain accurate records of the lateral view of the fish. Therefore changes in fin area, and body fin depth, were not obtained in these experiments. These latter observations were obtained in the second series of experiments using a different rectangular observation chamber (30 × 10 cm and 10 cm deep). The small size of the chamber constrained acceleration behaviour to some extent so the performance data were not considered accurate.

Fast start movements of fish were recorded at 250 frames/s following an electric shock stimulus of 1.0 V/cm applied across the longest axis of the chamber. A 45° mirror was used in recording the movements of fish in the first series of experiments. In the second series of experiments lateral and dorsal views were recorded using the smaller chamber. The film record included a stimulus marker and a 50 Hz timing record.

Experiments were performed in summer months.

Film analysis

In the first series of experiments, film records were analysed frame by frame to observe fast-start kinematics and movements of the centre of the mass of the stretched-straight body about which propulsive forces act (Weihs, 1973). In the second series, film was analysed for changes in fin-span and depth. Data for distance covered by the stretched-straight body centre of mass with time were analysed using the moving-point method described by Lanczos (1956) to obtain swimming speeds and acceleration rates. Comparisons between groups of fish were made using Duncan's Multiple Range Test, and within groups using Student *t* test (Steel & Torrie, 1960). Times to the end kinematic stages 1 and 2 (Weihs, 1973) were recorded.

The experiments employed a framing rate four times that used earlier (Webb, 1975*a*, 1976*a*). The larger amount of data permitted better determinations of velocities and acceleration rates than previously possible. Therefore, comparisons were made between predictions from the simple linear regression (SLR) method used earlier and values for distance covered, velocity and acceleration rate obtained with the present more accurate method. No significant differences were obtained in distances covered with time, nor in velocity and acceleration rates for most points in time from the initiation of a fast-start. However, as previously noted (Webb, 1975*a*, 1976*a*) the SLR method over-smooths the changes in velocity and acceleration rate with time. This was substantiated with differences in velocity and acceleration being significantly different (5% level) from those predicted by the SLR method at some times intermediate between zero time and the time to the end of kinematic stage 1, and that time and the end of kinematic stage 2.

It is important to note that distance covered with time, the maximum speed attained and mean acceleration rates at the end of the principal acceleration stages (Webb, 1975*a*, 1976*a*) did not differ between the two methods. These are the key parameters defining over-all acceleration performance, and also the key parameters

Table 1. *Morphometric characteristics of the eight groups of rainbow trout used to determine the effects of fin amputation on fast-start performance (means \pm 2 S.E. are given)*

	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8
Total length (<i>L</i>) following surgery (cm)	18.4 \pm 1.7	17.7 \pm 1.6	17.4 \pm 1.5	18.9 \pm 1.0	17.4 \pm 1.6	17.0 \pm 1.5	16.1 \pm 1.5	16.9 \pm 0.9
Body mass (<i>M</i>) (g)	48.41 \pm 5.25	46.28 \pm 5.93	44.27 \pm 6.40	51.92 \pm 4.37	42.98 \pm 4.43	40.38 \pm 4.72	41.79 \pm 5.22	47.89 \pm 4.51
Muscle mass (g)	23.83 \pm 2.75	23.86 \pm 3.40	22.20 \pm 3.34	27.07 \pm 3.14	21.85 \pm 2.18	20.23 \pm 2.50	20.94 \pm 3.55	23.57 \pm 2.75
Total wetted surface area (cm ²)	126.9 \pm 19.3	117.4 \pm 18.4	113.3 \pm 21.1	124.1 \pm 12.2	110.7 \pm 16.6	101.8 \pm 15.8	102.4 \pm 18.1	109.9 \pm 14.8
Distance of centre of mass from nose (cm)	6.7 \pm 0.3	6.4 \pm 0.2	6.3 \pm 0.3	6.7 \pm 0.2	6.2 \pm 0.3	6.3 \pm 0.3	6.3 \pm 0.3	6.6 \pm 0.2
Number of fish	10	10	9	8	9	10	9	9

determining the behavioural significance of fast-starts. The improved data obtained from the current methods do not alter conclusions obtained from earlier experiments.

Morphometrics

At the end of an experiment each fish was blotted on a moist cloth to remove excess water, and weighed to the nearest 0.01 g. Total length was recorded to the nearest 0.1 cm both at the time of operation and at the end of an experiment. Outlines of the lateral profile of the fish were traced from which virtual mass (Lighthill, 1970) distribution along the body was calculated. Fin area was measured from these tracings using a planimeter. Body area was calculated from the body circumference measured at 1 cm intervals along the body using threads.

The centre of mass for the stretched-straight fish was obtained by suspending the fish from two positions against plumbines. The centre of mass was assumed to lie at the centre of the bilaterally symmetrical body at the point where the plumbines intersected.

All the myotomal muscle was dissected from the body and weighted. This weight did not include the skin.

Morphometric data are summarized in Table 1 for the eight groups of fish.

RESULTS

Kinematics

Typical fast-start kinematics (Weihs, 1973) were observed in all groups of fish with the L-start pattern (Webb, 1976a). There was an increased tendency for fish to roll with progressive removal of median fins indicating their importance in dynamic stability during normal propulsion. Kinematics were divisible into the usual three stages (Weihs, 1973) with the first two stages comprising a behavioural phase I during which fish accelerate to approach maximum speeds (Webb, 1975a). Results on acceleration performance are therefore reported to the end of kinematic stage 2 which covers the principal acceleration phase.

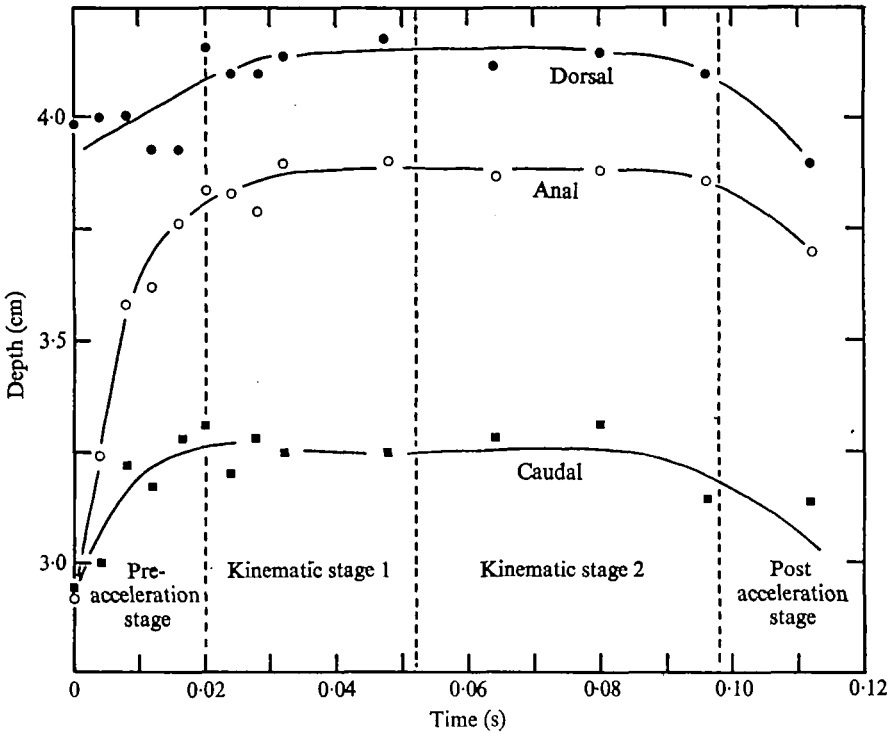


Fig. 2. Changes in body and fin depth at the dorsal, anal, and caudal fin positions with the time during acceleration from rest in rainbow trout.

Changes in body profile during fast-starts

Changes in median fin area and depth contribute to thrust by affecting lift forces and inertial forces in fast starts and turns (Weihs, 1972, 1973). The maximum depth of the various fins, and body included where appropriate, was used to monitor these changes (Fig. 2). The depth, and hence area, of the dorsal, anal and caudal fin increased prior to the start of acceleration of the body. The fin expansion started before acceleration and was almost complete before the body began to move. Fin and body depth remained at maximum values through kinematic stages 1 and 2. In the small fish chamber used to make these observations, fish usually shifted to a turning glide in kinematic stage 3, after the principal acceleration stages. During this stage, the fin and body depth was reduced, which would reduce drag during the glide, increasing the distance that could be covered.

Fast-start performance

Data on fast-start performance are summarized in Table 2. The duration of the principal acceleration movements was similar in all groups although differences between control group 1 and group 6 were just significantly different (5% level). Distance covered, velocity attained and mean acceleration rate up to the end of kinematic stage 2, and the maximum measured acceleration rates showed a trend toward decreasing performance through groups 1-8. This was associated with progressive removal of median fins. However, the differences among groups were not

Table 2. Fast-start performance parameters for the eight groups of fish to the end of kinematic stage 2 (mean values \pm S.E. are given)

	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8	Overall mean
Time (s)	0.115 ± 0.014	0.108 ± 0.011	0.109 ± 0.009	0.112 ± 0.013	0.107 ± 0.015	0.100 ± 0.016	0.111 ± 0.018	0.111 ± 0.015	0.108 ± 0.010
Distance covered (cm)	8.37 ± 0.96	7.96 ± 0.97	7.58 ± 0.91	7.75 ± 0.79	7.07 ± 0.66	6.29 ± 0.95	6.31 ± 0.65	5.94 ± 0.60	
Speed attained (cm/s)	132.5 ± 14.5	137.8 ± 17.3	144.0 ± 23.3	133.2 ± 16.6	120.9 ± 15.5	119.6 ± 13.1	114.7 ± 14.3	107.4 ± 8.1	
Maximum acceleration rate (cm/s ²)	2.04 ± 0.26 $\times 10^3$	2.43 ± 0.33 $\times 10^3$	2.66 ± 0.18 $\times 10^3$	2.46 ± 0.13 $\times 10^3$	1.94 ± 0.16 $\times 10^3$	2.62 ± 0.18 $\times 10^3$	2.43 ± 0.29 $\times 10^3$	2.02 ± 0.28 $\times 10^3$	
Mean acceleration rate (cm/s ²)	8.03 ± 0.81 $\times 10^3$	8.57 ± 0.90 $\times 10^3$	8.46 ± 0.91 $\times 10^3$	8.12 ± 0.80 $\times 10^3$	7.18 ± 0.91 $\times 10^3$	8.00 ± 0.84 $\times 10^3$	6.96 ± 0.75 $\times 10^3$	6.56 ± 0.80 $\times 10^3$	
Distance covered in 0.108 s (cm)	7.91 ± 0.67	7.96 ± 0.97	7.51 ± 0.88	7.24 ± 0.56	7.18 ± 0.93	6.87 ± 0.68	6.28 ± 0.65	5.83 ± 0.65	

statistically significant (5% level) except for comparisons between control group 1 and groups 6–8. These are the groups where reduction in fin area and virtual mass are associated with lateral body movements of greatest amplitude and hence greatest thrust.

Fast-start performance parameters are sensitive to small changes in the duration of kinetic stages. Therefore, comparisons between groups should be made for a given time interval for fish accelerating from rest (Webb, 1976a). Distance covered in a given time is of particular importance in fast-start activity such as predator-prey interactions and thus the most meaningful as well as the most convenient parameter for comparison among the eight groups. The over-all mean time to the end of kinematic stage 2 was 0.108 s. Values for the distance covered in this time (Table 2) showed the same general trends towards reduced performance through groups 1–8 as the other data.

DISCUSSION

Median fins and fast-start performance

The expansion of the dorsal, anal and caudal fins before the fish began to accelerate, and the reduction in area and depth after completion of acceleration movements indicates that large fins are important in generating thrust during a fast-start. This is predicted from Weihs' (1973) theory. The reduction in acceleration performance following amputation of the caudal fins provides empirical support and shows in particular that a large caudal fin is required for maximum acceleration performance.

The general trend towards reduced fast-start performance through groups 1–8 with progressive reduction in median fin area and local virtual mass suggests that the dorsal and anal fins are also important in generating thrust. This is implied by the area changes prior to acceleration. However, the observed performance changes following

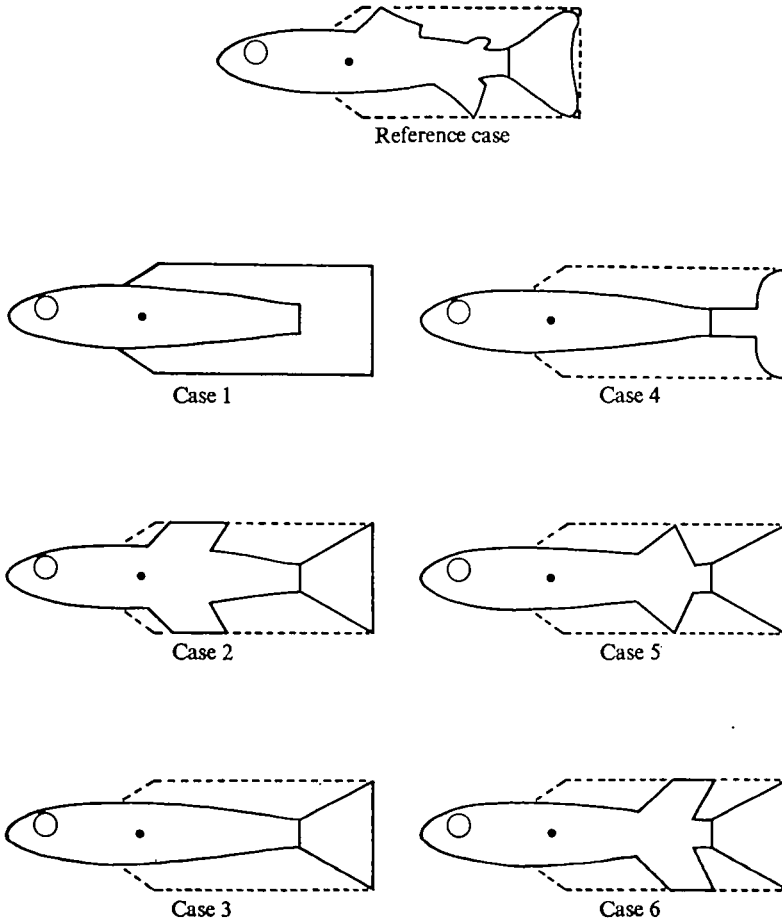


Fig. 3. Lateral body profiles used to evaluate the effects of body profile on unsteady and steady performance. The reference case shows the actual profile of control fish used. Anterior median fin areas in cases 2 and 6 are equal. The solid circle shows the centre of mass for the stretched-straight body.

amputation of the dorsal fin (group 1 *v.* group 2) and the anal fin (group 1 *v.* group 3 and group 7 *v.* 8) were small and not statistically significant. Therefore, thrust tends to be dominated by the caudal area, as in steady swimming, although less completely. The trends in performance data indicate that a fin distribution maximizing area caudally should maximize fast start performance, as expected from theory (Weihs, 1973).

The variance in the data is too high to detect fin interaction effects on fast-start performance.

Functional design for unsteady v. steady propulsion

The results from the present experiments confirm that large fins are required for good acceleration – that is, unsteady time-dependent propulsion. Previous experiments on individual fish have shown that a large caudal fin is not required for good cruising performance – that is, steady time-independent propulsion (Breder, 1926,

Table 3. Performance estimates for the lateral body profiles in Fig. 3 in fast-start cruising activity

(Performance estimates are normalized for comparative purposes with respect to the reference profile observed for the control group 1 fish.)

	Relative fast start (unsteady) performance	Relative cruising (steady) performance
Reference case	1.00	1.00
Case 1	1.57	0.85
Case 2	1.20	0.97
Case 3	0.84	1.04
Case 4	0.60	1.07
Case 5	0.96	1.00
Case 6	1.07	0.94

Gray, 1933; Webb, 1973). Instead, maximum steady performance is achieved in fish where the trailing-edge depth is maximized while caudal fin area is minimized (Lighthill, 1970; Webb, 1973), a situation realized by lunate-tail morphology (see Fierstine & Walters, 1968). Therefore the morphological correlates of high unsteady performance and high steady performance are in theory mutually exclusive (Webb, 1977). Normal activity of most fish involves both steady and unsteady locomotion so that they are locomotor generalists. These fish have presumably evolved a body form which compromises between requirements for steady propulsion and for unsteady propulsion. Since tail amputation has little effect on steady performance, it would seem likely that the compromise is towards improved acceleration performance at the cost of steady performance.

The effect of body form on unsteady and steady performance was evaluated for a set of lateral body profiles (Fig. 3) to determine the importance of functional-morphological compromise. Evaluations were based on calculations of forces acting on the body for each lateral profile in simulated fast-start and cruising kinematics.

(a) *Fast-start simulation* A typical fast-start sequence was selected and forces generated were calculated as described by Weihs (1972, 1973) from positions of the body centre-line at 0.004 s intervals. Thrust components about the centre of mass were calculated for inertial forces generated at positions 1 cm apart along the whole length of the body, assuming initially unit virtual mass at each position. Inertial thrust forces that would be generated by the body movements for the various lateral body profiles were simply obtained by multiplying the thrust calculated by each segment with unit virtual mass by the actual virtual mass. Lift forces for the dorsal, anal and caudal fins were calculated as appropriate, as described by Weihs (1972, 1973), taking into account various fin areas, aspect ratios and sweepback. The sum of the thrust forces for each position along the whole body length and the fin lift-forces where appropriate were averaged to the end of kinematic stage 2 to obtain the mean thrust force.

Thrust values for each profile were normalized with respect to a reference shape. The reference shape was the overall mean lateral body profile for the control group 1 fish used. Normalized results calculated in this way were used partly because the

Table 4. *Data sources used in the simulation of body movements during steady swimming*

Tail-beat frequency (f) at specific swimming speed (U/L)	$f = (0.339 + 0.540U/L) + f_0$	Hunter & Zweifel (1971)
Tail-beat frequency at zero speed (f_0) as a function of body length (L)	$f_0 = 0.630 - 0.474 \cdot \log L$	
Amplitude (A) of lateral movements of propulsive segments along the body	Measured from observations	Fig. 32 in Webb (1975b)
Lateral velocity of a propulsive segment (W)	$W = \pi \cdot f \cdot A / \sqrt{2}$	
Resultant velocity (W_R)	$W_R = \sqrt{(W^2 + U^2)}$	Webb (1975b)
Drag (D) for a propulsive segment	$D = \frac{1}{2} \cdot \rho \cdot S \cdot W_R^2 \cdot C_D$	
Wetted surface area (S) of a segment	Measured for fish used in the present experiments	
Drag coefficient (C_D)	$C_D = 0.768 \cdot W_R^{-0.473}$	Calculated from Webb (1973)
Caudal propeller efficiency (η_p)	$\eta_p = 1 - 0.5[(V-U)/V]$	Lighthill (1970)
Backward velocity of propulsive wave (V)	$V = f \cdot \lambda$	
Propulsive wave (λ)	Calculated	Fig. 4 in Webb (1976b)

theory remains approximate (Weihs, 1973), and also to facilitate comparison with steady cruising performance estimates which were calculated using different criteria. Normalized results are given in Table 3.

(b) *Cruising performance simulation.* For cruising performance the maximum speed attainable for each of the lateral body profiles was calculated. The speed was calculated using an iteration process, given a maximum muscle-power output and swimming drag that depended on body movements. The evaluation of the effect of lateral body form in steady swimming is thus estimated on the basis of drag rather than thrust. Drag estimates were used because thrust would be the same for all the body profiles. This follows because the depth of the caudal fin is as large as, or greater than, the body and fin depth anterior to the trailing edge (Lighthill, 1970). Therefore thrust-related vorticity shed upstream of the trailing edge would be absorbed at the leading edge of the caudal fin and would not contribute to the net thrust averaged over a propulsive cycle. At equilibrium, thrust and drag will, of course, be equal in steady swimming. It should also be noted that drag in acceleration is not known at the present time.

There is sufficient information to calculate drag for a cruising fish for theoretical body movements rather than using a selected, and hence possibly arbitrary, set of movements alone. Sources are indicated in Table 4. Drag was calculated for propulsive segments at 1 cm intervals along the body. The standard Newtonian equation for drag was assumed to apply, so that drag of each segment was proportional to the square of the resultant velocity (calculated from a segment's lateral and forward velocities) and a drag coefficient. The latter was determined from the effects of fin

amputation on thrust and drag at cruising speeds. Therefore drag calculations are expected to take into account the effects of propulsive movements on drag (Lighthill, 1971). Lateral velocities were obtained from data on tail-beat frequency and amplitude distribution along the body. Lateral movements were assumed to be simple harmonic.

Using these sources to simulate kinematics, the drag expected for each lateral body profile can be calculated for a given swimming speed. To evaluate the effect of the body profiles on performance, a maximum muscle power output was assigned of 8×10^5 ergs/s (1 erg = 10^{-7} joules). This value assumes use of red muscle representing 4% of the myotomal muscle plus some white muscle support (Hudson, 1973). Specific powers of red and white muscle were taken as 2×10^5 and 8×10^5 ergs $s^{-1} g^{-1}$ respectively (Bainbridge, 1961). Half the muscle was assumed to work at any instant. Power available to overcome drag, which must therefore equal thrust at the maximum steady speed, was calculated as the product of the assumed muscle power and caudal propeller efficiency. The speed was found where drag power was within 0.5% of the power available to overcome drag. Results from these calculations are shown in Table 3 again normalized with respect to the reference case.

(c) *Body form.* The most effective lateral body profile for the generation of thrust in fast-start movements is a shape that maximizes virtual mass along the whole body length (case 1). Since this shape also maximizes body area, and hence drag in cruising swimming, it has the poorest steady swimming capability. The body form is typical of cottids. These benthic fish have negligible amounts of red muscle, and their locomotor habits are typically short acceleration bursts. They are not known to swim steadily for any period of time.

Case 2 illustrates a situation where continuous large body depth is interrupted anterior to the caudal fin, a lateral body profile realized, for example, in Centrarchids. With this body shape, there is a possibility that the reduced virtual mass anterior to the caudal fin could be offset by lift forces generated by the anterior median fins. Acceleration capability was predicted to be good with this body form but the relatively large area again reduced cruising performance capability.

Cases 3 and 4 illustrate the lateral body form patterns approaching the specialized lunate tail situation considered optimal for cruising (Lighthill, 1970). In terms of lateral body profile alone, efficiency in cruising is made at the cost of acceleration performance. Superior thrust production in the carangiform mode with lunate tail (Lighthill, 1970) is not taken into account in this analysis. Thus the apparent moderate improvement in cruising capability in case 4 is undoubtedly an underestimate.

Cases 1-4 confirm that mechanical requirements for good unsteady and for good steady performance are not compatible. However, this conclusion makes the implicit assumption that body profile is unchanged during both fast-start and cruising activities. This is not the case for bony fish. These fish can retract their median fins during steady swimming, while extending them during fast-starts and turns. Therefore during unsteady propulsion, bony fish can approach cases 1 or 2 when the advantage of large body and fin area are realized. During steady propulsion the fish can approach case 3 with improved cruising capability. It is clear that this compromise is possible only with the evolution of highly flexible fins in bony fish. The greatest changes in lateral body profile are possible with truncate body forms, common among fish above the percid level of organization. Bony fish in reef communities represent the best examples

(Hobson, 1974). It is clear that the evolution of mobile fins in bony fish made possible important advantages in body and caudal fin swimming performance, in addition to the more widely recognized advantages in fin control and manoeuvre (e.g. Alexander, 1967; Gosline, 1971).

Cases 2, 5 and 6 illustrate the importance of fin position and size on performance capability. The effects of anterior fin position and anterior fin size are relatively small as expected from the empirical observations presented here following dorsal and anal fin amputation. Horak (1969) has observed that amputation of anterior median fins has no effect on steady cruising performance. However, fins of larger depth and larger area, located more posteriorly, do result in improved fast-start performance, at moderate theoretical cost to steady performance. This disadvantage would, of course, be mitigated for bony fish. Although the effect of fin position appears small, it is clearly of selective advantage since the body shape is typical of specialized predators – for example, *Esox*.

The foregoing discussion indicates the relative importance of lateral body profile in generating thrust in fast-starts, and in reducing drag in cruising. It also shows the additional important locomotor advantages that occur with evolution of fin structure in bony fish.

However, the lateral body profile is only one body shape parameter pertinent to evaluating acceleration performance. A second parameter of equal if not greater importance is expected to be the percentage of the body represented by muscle mass which varies with body sectional shape (Webb, 1977). Ultimately, muscle mass must be limiting to acceleration, and small advantages or disadvantages of lateral body profile could be magnified by higher or lower percentages of muscle. Scombroids may offset an apparent poor lateral body profile with a higher muscle mass (Fierstine & Walters, 1968; Sumich, 1976, p. 221). There are currently inadequate data to evaluate this parameter.

This work was supported by the National Science Foundation grant number BMS7S-18423. Fish were provided by the Michigan Department of Natural Resources. Technical assistance was provided by Mr P. T. Kostecki.

REFERENCES

- ALEXANDER, R. MCN. (1967). *Functional Design in Fishes*. London: Hutchinson.
- BAINBRIDGE, R. (1961). Problems of fish locomotion. *Symp. Zool. Soc. Lond.* 5, 13–32.
- BREDER, C. M. (1926). The locomotion of fishes. *Zoologica, N.Y.* 4, 159–256.
- FIERSTINE, H. L. & WALTERS, V. (1968). Studies of locomotion and anatomy of scombroid fishes. *Mem. Sth Calif. Acad. Sci.* 6, 1–31.
- GOBLINE, W. A. (1971). *Functional Morphology and Classification of Teleostean Fishes*. Honolulu: The University Press of Hawaii.
- GRAY, J. (1933). Studies in animal locomotion. III. The propulsive mechanism of the whiting (*Gadus merlangus*). *J. exp. Biol.* 13, 192–9.
- HOBSON, E. S. (1974). Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish. Bull.* 72, 915–1031.
- HORAK, D. L. (1969). The effect of fin removal on stamina of hatchery-reared rainbow trout. *Prog. Fish Cult.* 31, 217–20.
- HUDSON, R. C. L. (1973). On the function of the white muscles in teleosts at intermediate swimming speeds. *J. exp. Biol.* 37, 509–22.
- HUNTER, J. R. & ZWEIFEL, J. R. (1971). Swimming speed, tail beat frequency, tail beat amplitude and size in jack mackerel, *Trachurus symmetricus*, and other fishes. *Fish. Bull. Calif.* 69, 253–66.

- LANCZOS, C. (1956). *Applied Analysis*. Englewood Cliffs, N.J.: Prentice Hall.
- LIGHTHILL, M. J. (1970). Aquatic animal propulsion of high hydrodynamic efficiency. *J. Fluid Mech.* **44**, 265-301.
- LIGHTHILL, M. J. (1971). Large-amplitude elongated-body theory of fish locomotion. *Proc. R. Soc. Lond. B* **179**, 125-38.
- STEEL, R. G. D. & TORRIE, J. R. (1960). *Principles and Procedures of Statistics*. New York: McGraw-Hill.
- SUMICH, J. L. (1976). *An Introduction to the Biology of Marine Life*. Dubuque, Iowa: W. C. Brown.
- 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**, 565-81.
- WEBB, P. W. (1975*a*). Acceleration performance of rainbow trout, *Salmo gairdneri*, and green sunfish, *Lepomis cyanellus*. *J. exp. Biol.* **63**, 451-65.
- WEBB, P. W. (1975*b*). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 1-159.
- WEBB, P. W. (1976*a*). 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**, 157-77.
- WEBB, P. W. (1976*b*). Effects of size and performance on energetics of fish. In *Biodynamics of Animal Locomotion* (ed. T. J. Pedley), pp. 315-331. New York: Academic Press.
- WEBB, P. W. (1977). Hydrodynamics; non-scombroid fish. In *Fish Physiology*, vol. 7 (ed. W. S. Hoar and D. J. Randall). New York: Academic Press. (In the Press.)
- WEIHRS, D. (1972). A hydrodynamic analysis of fish turning manoeuvres. *Proc. R. Soc. Lond. B* **182**, 59-72.
- WEIHRS, D. (1973). The mechanism of rapid starting of slender fish. *Biorheology* **10**, 343-50.