

## FAST-START PERFORMANCE AND BODY FORM IN SEVEN SPECIES OF TELEOST FISH

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### SUMMARY

Fast-start kinematics and performance were determined for *Etheostoma caeruleum*, *Cottus cognatus*, *Notropis cornutus*, *Lepomis macrochirus*, *Perca flavescens*, *Salmo gairdneri* and a hybrid *Esox* sp. at an acclimation and test temperature of 15 °C. Normal three-stage kinematic patterns were observed for all species. Fast-start movements were similar in all species, except *Lepomis*, which had slightly higher amplitudes than expected for its length. The duration of kinematic stages was a major variable among the seven species but was a linear function of length. Acceleration rates were not functions of size. Maximum acceleration rates ranged from 22.7 to 39.5 m.s<sup>-2</sup> with mean rates from 6.1 to 12.3 m.s<sup>-2</sup>, averaged to the completion of kinematic stage 2. Maximum velocity and distance covered in each fast-start stage varied among species but were related to length. Fast-start performance depended primarily on compromise between muscle mass as a percentage of body mass, and lateral body and fin profile. Optimal profiles provide large depth distant from the centre of mass to maximize thrust, and anterior depth enhancement to minimize recoil. The body form of *Lepomis* is considered optimal for multiple swimming modes.

### INTRODUCTION

Hydromechanical theory predicts that large thrust for good fast-start performance in fish is given by lateral profiles maximizing the mass of water accelerated by body movements along the whole body length. This is achieved by maximizing depth, and hence area, along the body (Weihs, 1973). Webb (1977) confirmed this prediction experimentally for trout by measuring fast-start performance of fish after amputation of the fin-rays from various combinations of median fins. He extended his results to show the relative performance of a variety of fish-like body profiles executing a given pattern of body movements. The biological significance of lateral profile (defined in terms of longitudinal depth distribution) is not known. This is largely because fast-start performance is not well known for any species, other than rainbow trout, *Salmo gairdneri* (Weihs, 1973; Webb, 1975*a*, 1976).

A few observations on other species have been made. None have been sufficiently complete for an evaluation of the importance of body structure on fast-start activity. Gero (1952), Gray (1953), Hertel (1966) and Fierstine & Walters (1968) have measured maximum acceleration rates of several species. Unfortunately, since acceleration rate

decreases with time (Weihs, 1973; Webb, 1975*a*; DuBois, Cavagna & Fox, 1976), these peak performance data bear little relationship to overall performance capabilities. Kinematics have been described qualitatively for several species (Hertel, 1966; Weihs, 1973; Webb, 1975*a*, 1976; Eaton, Bombardieri & Meyer, 1977). These studies suggest that acceleration performance may be similar among teleosts, irrespective of lateral body profile. This would challenge the biological significance of lateral body profiles predicted to be favourable for fast-starts and apparently correlating with the habits of fish (Webb, 1977). Alternatively, it seems more likely that other morphological, anatomical or kinematic parameters are equally important in affecting fast-start performance. Such parameters can be evaluated only by comparative studies.

The purpose of this study was therefore to evaluate the importance of body form on fast-start acceleration performance of fish. The relative importance of different kinematic patterns can be evaluated from Weihs' theory (1972, 1973). That of lateral body profile can be evaluated from both theory (Weihs, 1972, 1973) and observations (Webb, 1977). Therefore the importance of other components can be deduced by comparing acceleration kinematics and performance for fish with various lateral body profiles.

Other studies considering non-scombroid body form have based arguments on steady swimming performance (e.g. Greenway, 1965) or correlation between such parameters as mouth-form and food habits (e.g. Keast & D. Webb, 1966).

#### MATERIALS AND METHODS

##### *Fish*

Species were selected for experiments on the basis of their lateral body profiles and where possible more than one example of a particular form was studied (Fig. 1). *Etheostoma caeruleum* Storer (common name 'rainbow darter') and *Cottus cognatus* Richardson (slimy sculpin) were selected as having a large depth along most of the body length. This lateral profile is predicted to be optimal for developing thrust in a fast-start. These two species, together with *Perca flavescens* Mitchill (yellow perch), *Salmo gairdneri* Richardson (rainbow trout) and *Notropis cornutus* Mitchill (common shiner), represent a series towards less favourable profiles. This series was originally to have been extended with an eel. These fish were found to react to stimuli by retracting their heads rather than in an acceleration fast-start. The same response has been described for the eel-like *Mastacembelus loennbergi* (Eaton *et al.* 1977). *Esox* sp. was selected as representative of a specialized piscivorous predator. *Lepomis macrochirus* Rafinesque (bluegill) was selected as representative of the successful percoid body form common in many fish communities (Gosline, 1971). *Esox* and *Lepomis* also differ from the other more fusiform-bodied species in having elongated and truncated globose bodies respectively. Therefore a series such as *Esox*, *Salmo*, *Perca* and *Lepomis* would be expected to show differences in kinematics related to body form.

*Salmo* and *Esox* were obtained from local fish hatcheries. *Esox* used were tiger muskies, cultured from a cross between female *Esox lucius* Linnaeus and male *Esox masquinongy* Mitchell. Other species were seined from local streams and lakes.

Fish were held in 200 l oval tanks, flushed continuously with water at 50 l/hr. Water was circulated in each tank by means of a submerged pump which generated

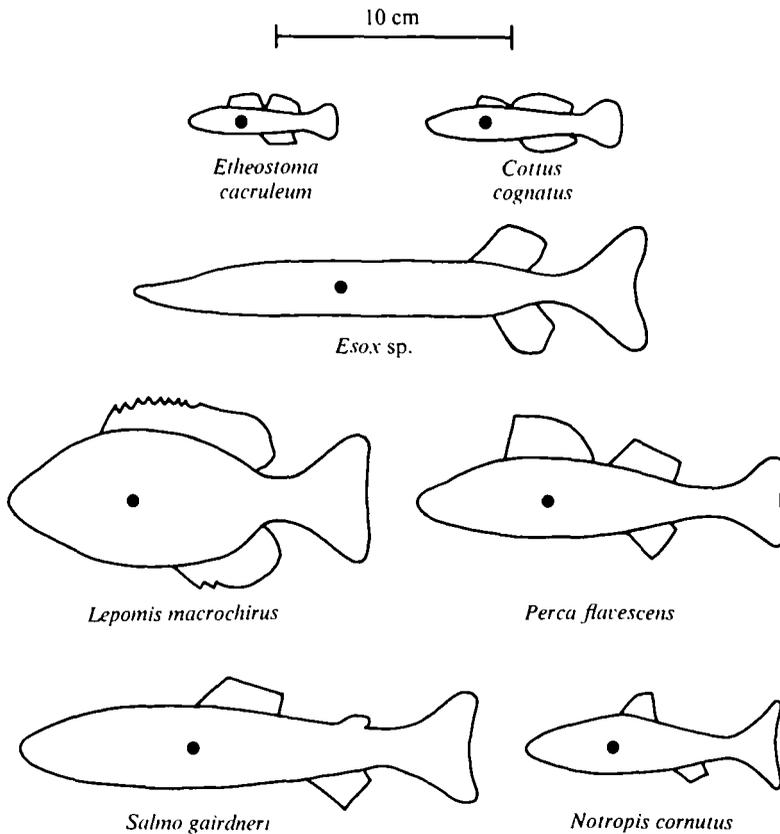


Fig. 1. Body and fin lateral profiles of the seven species of teleost fish used in measurements of fast-start performance. Outlines are composites of several individuals of each species, traced from movie films. The solid circles show the locations of the centre of mass for the stretched-straight body.

a mean current of approximately  $20 \text{ cm} \cdot \text{sec}^{-1}$ . Fish swam against this current. Cover, in the form of green water-filled bottles, was provided for *Esox*, *Lepomis*, and *Perca*.

All fish were acclimated to the experimental temperature of  $15^\circ \text{C}$  and were held at  $15.0 \pm 0.2^\circ \text{C}$  for at least 2 weeks prior to experiments. Dissolved oxygen levels were maintained close to air saturation by means of air stones. Fish were fed to excess once a day on Purina Trout Chow, except *Esox*, which was fed on live goldfish.

### Experimental procedure

Details of experimental procedures have been described elsewhere (Webb, 1976, 1977). Briefly, individual fish were starved for 2 days. Each fish was lightly anaesthetized and a white thread attached flush to the skin over the predicted centre of mass for the stretched-straight body. This served as a reference point to improve accuracy of subsequent film analysis. Each fish was placed in an observation chamber and left for 20 h prior to testing. Water was circulated through the chamber at a low rate to maintain dissolved oxygen levels close to air saturation. Two observation chambers were used. A chamber with dimensions 50 cm long, 50 cm wide and 10 cm

Table 1. *Morphometric characteristics of the seven species of teleost fish used to measure fast-start performance*

(Species are shown in order of increasing length. Means  $\pm$  2 s.e. are shown.)

	<i>Etheostoma caeruleum</i>	<i>Cottus cognatus</i>	<i>Notropis cornutus</i>	<i>Lepomis macrochirus</i>	<i>Perca flavescens</i>	<i>Salmo gairdneri</i>	<i>Esox</i> sp.
Total length, $L$ (cm).	$6.2 \pm 0.3$	$8.2 \pm 0.4$	$10.7 \pm 1.05$	$15.3 \pm 0.6$	$15.5 \pm 0.3$	$19.5 \pm 1.0$	$21.7 \pm 1.0$
Mass, $M$ (g)	$2.25 \pm 0.19$ (= $0.0094L^3$ )	$6.94 \pm 1.67$ (= $0.0126L^3$ )	$11.18 \pm 2.09$ (= $0.0091L^3$ )	$64.50 \pm 6.31$ (= $0.180L^3$ )	$33.48 \pm 1.44$ (= $0.0090L^3$ )	$69.90 \pm 5.00$ (= $0.0094L^3$ )	$41.80 \pm 3.65$ (= $0.0041L^3$ )
Muscle mass (g)	$0.86 \pm 0.12$ (= $0.382M$ )	$2.11 \pm 0.81$ (= $0.304M$ )	$4.50 \pm 1.03$ (= $0.403M$ )	$27.76 \pm 5.54$ (= $0.430M$ )	$15.59 \pm 1.19$ (= $0.466M$ )	$37.48 \pm 5.73$ (= $0.536M$ )	$23.12 \pm 2.05$ (= $0.553M$ )
Total wetted surface area, $S_w$ (cm <sup>2</sup> )	$16.4 \pm 0.8$ (= $0.43L^2$ )	$33.2 \pm 3.6$ (= $0.49L^2$ )	$46.9 \pm 7.4$ (= $0.41L^2$ )	$164.3 \pm 15.3$ (= $0.70L^2$ )	$107.6 \pm 8.6$ (= $0.45L^2$ )	$154.2 \pm 14.2$ (= $0.41L^2$ )	$130.8 \pm 14.6$ (= $0.28L^2$ )
Distance of centre of mass from nose (cm)	$2.2 \pm 0.1$ (= $0.35L$ )	$2.5 \pm 0.2$ (= $0.30L$ )	$3.7 \pm 0.4$ (= $0.35L$ )	$5.3 \pm 0.2$ (= $0.35L$ )	$5.6 \pm 0.1$ (= $0.36L$ )	$7.4 \pm 0.4$ (= $0.38L$ )	$8.8 \pm 0.3$ (= $0.41L$ )
$n$	7	8	10	10	10	10	10

Table 2. *Fast-start kinematic parameters for seven species of teleost fish during kinematic stages 1 and 2*

(Species are shown in order of increasing length (Table 1). Means  $\pm$  2 s.e. are shown.)

	<i>Etheostoma caeruleum</i>	<i>Cottus cognatus</i>	<i>Notropis cornutus</i>	<i>Lepomis macrochirus</i>	<i>Perca flavescens</i>	<i>Salmo gairdneri</i>	<i>Esox</i> sp.
Amplitude coefficient	$0.14 \pm 0.02$	$0.016 \pm 0.06$	$0.16 \pm 0.03$	$0.16 \pm 0.03$	$0.17 \pm 0.03$	$0.17 \pm 0.03$	$0.14 \pm 0.03$
Curvature coefficient	$0.74 \pm 0.06$	$0.85 \pm 0.06$	$0.90 \pm 0.12$	$0.85 \pm 0.07$	$0.86 \pm 0.05$	$0.92 \pm 0.08$	$0.83 \pm 0.07$
Amplitude coefficient	$0.51 \pm 0.09$	$0.51 \pm 0.14$	$0.39 \pm 0.06$	$0.56 \pm 0.08$	$0.52 \pm 0.08$	$0.51 \pm 0.12$	$0.38 \pm 0.05$
Curvature coefficient	$0.82 \pm 0.07$	$0.89 \pm 0.04$	$0.87 \pm 0.09$	$0.86 \pm 0.07$	$0.86 \pm 0.07$	$0.92 \pm 0.07$	$0.85 \pm 0.05$
Centre of mass amplitude coefficient	$0.180 \pm 0.020$	$0.077 \pm 0.025$	$0.079 \pm 0.019$	$0.050 \pm 0.017$	$0.071 \pm 0.010$	$0.076 \pm 0.037$	$0.098 \pm 0.018$

deep was used to obtain records from the dorsal surface for analysis of acceleration performance. These dimensions do not restrict the fast-start performance of even the large fish because acceleration is high for a short period, and distances covered are small (Weihs, 1973; Webb, 1975*a*, 1976, 1977). A second chamber with dimensions 30 cm long, 10 cm wide and 10 cm deep was used to record changes in fin size. This chamber size restricts fast-start movements except when fish are orientated along the chamber length. Therefore acceleration performance was not calculated from these experiments.

Fast-start movements were recorded on movie film at a framing rate of 250 Hz, following an electric shock stimulus of 1.0 V. cm<sup>-1</sup> applied across the chamber length. Two tests were made for each fish with a 1 h recovery period between trials.

At the end of each experiment, fish were killed. Total body length (rostral tip of nose to caudal tip of the expanded tail), body mass, total myotomal muscle mass, total wetted surface area and the location of the centre of mass of the stretched-straight body were measured (Table 1).

Film records obtained using the large chamber were analysed frame by frame to observe kinematics and movements of the centre of mass of the stretched-straight body about which propulsive forces act (Weihs, 1972, 1973). Records were not analysed when a fish was considered too close to the walls of the chamber, or when the fish did not respond with a fast-start after stimulation. The latter occurred in some *Lepomis*.

It has been widely demonstrated that fast-start kinematic patterns are divisible into three stages defined by Weihs (1973). These stages are: a preparatory stroke (kinematic stage 1), a main propulsive stroke (kinematic stage 2) and a variable third stage (kinematic stage 3). In kinematic stage 3, fish behaviour varies from continued acceleration (usually at a greatly reduced rate), through continued swimming at uniform speed to deceleration glides. Kinematic stage 1 and 2 differ from kinematic stage 3, such that analysis of fast-start performance may be concentrated on these first two stages.

Kinematic stages 1 and 2 constitute a kinematic phase 1, equivalent to the biphasic period of the Mauthner-initiated startle response (Eaton *et al.* 1977). Mechanics in phase 1 are described by large-amplitude fast-start hydromechanics for unsteady (time-dependent) motions (Weihs, 1972, 1973). Mechanics developed for steady swimming (e.g. Lighthill, 1970) are appropriate starting with kinematic stage 3 when swimming is sustained by cyclic lateral movements of the body and caudal fin. During such swimming movements, thrust is dominated by the trailing edge (Lighthill, 1970; Wu, 1971). Variation in lateral profile is expected to be a major component affecting thrust and performance only during acceleration in kinematic stages 1 and 2 (Weihs, 1973; Webb, 1977). These two stages cover the period when maximum acceleration rates occur. They also cover the crucial period in predator-prey interactions, even though distances covered and duration are small (Dill, 1973, 1974; Hurley & Hartline, 1974; Webb, 1976).

Although teleosts have similar fast-start patterns, this does not mean that kinematics are in fact the same for all species. Comparison of kinematics among species is problematic. Ideally, comparison should be based on the motion of each individual propulsive segment (*sensu* Gray, 1968) for each species, because each propulsive

segment contributes independently to thrust during a fast-start (Wiehs, 1973). A detailed analysis of all propulsive segments is obviously impractical.

In order to compare kinematics between the seven species, generalized parameters were measured for each stage. They were dimensionless coefficients for amplitude and body curvature measured from movements at the trailing edge. Duration of fast-start stages was also measured (see below). These were considered key measurements for the following reasons based on Weihs (1972, 1973).

(1) For any propulsive segment, the total force developed is proportional to its velocity<sup>2</sup>, determined by the amplitude in each kinematic stage and the time taken to complete each stage.

(2) The thrust component of the normal force acting on a propulsive segment depends on the angle subtended by each segment about the centre of mass. This will be related to body curvature about the centre of mass.

(3) The motion of a propulsive segment will be a function of that of the trailing edge for an inextensible body like a fish.

Amplitude was measured as the lateral displacement of the trailing edge relative to the axis of the body prior to a fast-start. Curvature was not measured directly. Instead the distance between the trailing edge and the centre of mass was measured. This approximates a cord of an arc described by the body centre-line. These measurements were divided by the length of the fish posterior to the centre of mass to obtain dimensionless amplitude and curvature coefficients. Normalization relative to the length of the body behind the centre of mass is appropriate because: (1) thrust forces are dominated by more caudal propulsive segments, (2) forces are resolved about the centre of mass, (3) the location of the centre of mass along the body was variable among species (see Table 1). An amplitude coefficient was also calculated for the lateral displacement of the centre of mass.

Fast-start performance was calculated from distance-time data for the centre of mass for the stretched-straight body. Velocity and acceleration rate were obtained from these data using moving point regression methods. Regressions were first obtained for moving overlapping blocks of five measurements of distance covered at successive 4 ms intervals. Velocity was then calculated from the regression equation for the mean of the time period sampled. Missing velocity values for the first and last two time intervals were estimated as described by Lanczos (1956). Acceleration rates were then calculated from the velocity-time data using the same moving-point regression method. Film records obtained using the small chamber were analysed frame by frame to observe changes in fin depth only.

Statistical comparisons between species were made using Duncan's New Multiple-Range Test (Steel & Torrie, 1960), and significant differences are declared at the 5% probability level.

All experiments were performed during the months of September to December inclusive.

## RESULTS

### *Fin movements*

In all species tested, the median fins were usually fully erected prior to accelerating or soon after acceleration had begun, as observed by Eaton *et al.* (1977) and Webb

Table 3. Results of statistical comparisons of data for fast-start kinematic parameters shown in Table 2 for seven species of teleost fishes

(Comparisons were made using Duncan's New Multiple-Range Test (Steel & Torrie, 1960). Lines underscore means that were not significantly different at the 5% level. Means calculated for each parameter are ranked to show statistical relations. Therefore columns do not correspond with any particular species. Species can be identified using Table 2. The significant differences found between species are discussed in the text.)

	Kinematic stage 1						
Amplitude coefficient	0.17	0.17	0.16	0.16	0.16	0.14	0.14
Curvature coefficient	0.92	0.90	0.86	0.85	0.85	0.83	0.74
	Kinematic stage 2						
Amplitude coefficient	0.56	0.52	0.51	0.51	0.51	0.39	0.38
Curvature coefficient	0.92	0.89	0.87	0.86	0.86	0.85	0.82
	Kinematic stages 1 and 2						
Centre of mass amplitude coefficient	0.180	0.098	0.086	0.079	0.077	0.071	0.050

Table 4. Fast-start velocities and acceleration rates of seven species of teleost fish up to the end of phase 1

(Data were calculated for the motion of the centre of mass measured for the stretched-straight body. Species are given in order of increasing length. Mean  $\pm$  2 s.e. are shown.)

	<i>Etheostoma caeruleum</i>	<i>Cottus cognatus</i>	<i>Notropis cornutus</i>	<i>Lepomis macrochirus</i>	<i>Perca flavescens</i>	<i>Salmo gairdneri</i>	<i>Esox</i> sp.
Maximum velocity ( $m \cdot s^{-1}$ )	0.89 $\pm$ 0.13	0.77 $\pm$ 0.22	1.14 $\pm$ 0.14	1.30 $\pm$ 0.18	1.15 $\pm$ 0.11	1.58 $\pm$ 0.21	1.56 $\pm$ 0.18
Maximum acceleration rate ( $m \cdot s^{-2}$ )	32.3 $\pm$ 8.3	22.7 $\pm$ 6.2	28.7 $\pm$ 2.1	28.8 $\pm$ 12.4	23.9 $\pm$ 4.5	32.6 $\pm$ 8.5	39.5 $\pm$ 8.5
Mean acceleration rate ( $m \cdot s^{-2}$ )	10.3 $\pm$ 2.7	6.1 $\pm$ 2.6	11.0 $\pm$ 1.4	12.3 $\pm$ 2.5	9.3 $\pm$ 1.2	10.6 $\pm$ 2.3	10.4 $\pm$ 1.4

(1977). This is consistent with the requirement of large area in fast-starts (Weihs, 1973; Webb, 1977). Paired fins were adducted and pressed against the body during a fast-start. The timing of adduction during a fast-start was variable. There was no evidence that paired fin movements contributed significantly to acceleration.

### *Kinematics*

Typical fast-start patterns as described above were observed for the seven species of fish. Data for generalized fast-start kinematic parameters are shown in Tables 2 and 3.

No significant differences were found for the curvature coefficients in kinematic stages 1 and 2, nor for amplitude coefficients in kinematic stage 1 (Table 3). Differences were just significant for the extremes in amplitude coefficient during kinematic stage 2 for *Lepomis* and *Esox*. Thus, relatively larger amplitudes were achieved by *Lepomis* with a truncate body than by species with more elongate bodies. Motion of the centre of mass also varied among species but was generally only significantly different for the extremes of the range observed, for *Etheostoma* and *Esox* compared to *Lepomis*.

### *Time relations for distance covered, velocity and acceleration rate*

Distance covered, velocity and acceleration rates were determined for the centre of mass of the stretched-straight body. This approximates closely the instantaneous centre of mass of a swimming fish, the point about which propulsive forces act.\* Time relations for these parameters were more variable than previously observed for trout. Distance covered increased with time according to a power function as previously described (Weihs, 1973; Webb, 1975*a*, 1976, 1977) but there was commonly a change in the relationship from kinematic stage 1 to stage 2 (Fig. 2). Exponents were typically greater in kinematic stage 2 than in stage 1, contrasting with previous observations when a single function described both (Webb, 1975*a*, 1976). The exponents were still less than 2 showing that acceleration was not uniform and that acceleration rate decreased through each fast-start stage. Some discontinuity in thrust was indicated at the transition between kinematic stages. This was large only in the small fish *Etheostoma* and *Cottus*. These species had a large surface area relative to their mass. Under these circumstances kinetic energy would tend to be lower relative to drag so that some deceleration between caudal fin strokes would not be unexpected. Discontinuity was also observed in *Esox* (Fig. 2). In this species thrust is dominated by the large caudal fin and posteriorly located median fins, and would be discontinuous between fast-start strokes.

Velocity and acceleration rate varied as expected from the distance-time results. Velocity increased through a fast-start approaching maximum values toward the end

\* This convention has been routinely used by Weihs (1973) and Webb (1975*a*, 1976, 1977) in discussing fast-start mechanics, as described in those papers. A different convention has been adopted in studies on neurological factors involved in fast-starts (e.g. Eaton *et al.* 1977): responses are measured for the rostral tip of the head. The measurements of the rostral tip of the head include the net motion of the fish (as measured by the motion of the centre of mass) plus motions associated with lateral propulsive movements. These are large in kinematic stage 1 compared to the movements of the centre of mass (Weihs, 1973; Webb, 1975*a*). Later in a fast-start, the path of the centre of mass and the rostral tip of the head begin to overlap. Then kinematics and mechanics approach steady swimming patterns and the forward motion of the two motions are sufficiently similar that they can be interchanged. It is important to note that the various performance measures derived from the two conventions, associated with different lines of inquiry, are not intended to be equivalent, and cannot be equated.

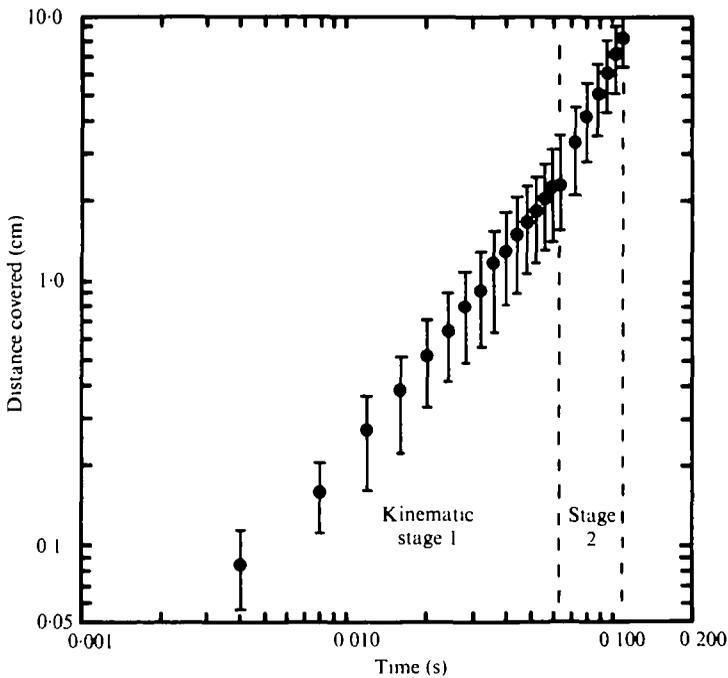


Fig. 2. An example for *Esox* of the relationship between distance covered with time during fast-starts. Vertical bars are  $\pm 2$  s.e. Alternate points only are shown in kinematic stage 2 for clarity.

of stage 2. Acceleration rate tended to decrease through a fast-start, maximum values occurring in kinematic stage 1. Discontinuities occurred in some fish between strokes.

#### *Duration of fast-start stages*

Times to the end of kinematic stage 1 ( $T_1$ ) and stage 2 ( $T_2$ ) increased with size of the fish (Fig. 3). The relative durations of kinematic stage 1 versus kinematic stage 2 also varied with size (Fig. 3) such that kinematic stage 2 was relatively shorter in smaller fish than in larger fish. Best fit, least-square linear regressions were obtained for  $T_1$  and  $T_2$  as functions of length ( $L$ ):

$$T_1 = 0.0019 \cdot L + 0.026 \text{ s} \quad (R = 0.88), \quad (1)$$

$$T_2 = 0.0035 \cdot L + 0.043 \text{ s} \quad (R = 0.95). \quad (2)$$

This effect of size on the duration of the kinematic stages was greater than previously observed for trout (Webb, 1976).

#### *Performance*

Distance covered in a given time is the most accurate measure of net fast-start performance. It integrates variations in acceleration rate and is least subject to computational error and smoothing. Distance covered in kinematic stages 1 and 2 was

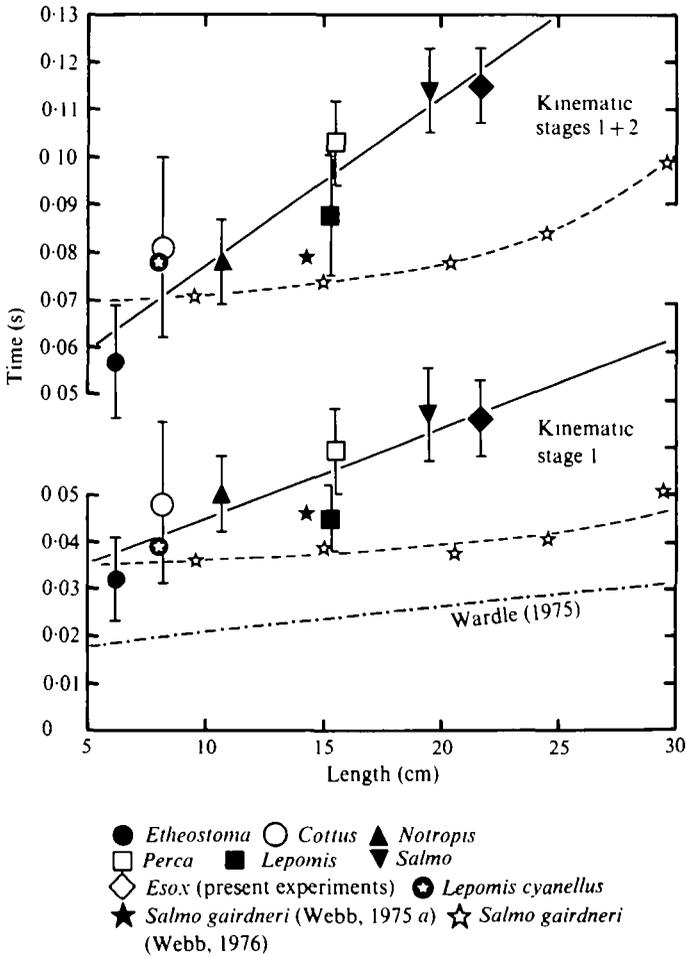


Fig. 3. The relationship between times to the end of kinematic stage 1 and phase 1 (stages 1 plus 2) and fish length for a variety of species. Vertical bars are  $\pm 2$  s.e. — Regression equation fitted to the interspecific data from the present study. ...., An eye-fitted curve to the intraspecific data for *S. gairdneri* from Webb (1976). — —, From Wardle (1975) for the contraction times of white muscle excised from various marine species and tested at 14 °C. Note that the ordinate is divided for clarity in separating kinematic stage 1 and kinematic stage 1 plus 2.

found to be related to length (Fig. 4). Power functions were found to provide the best fit to the data, when:

$$S_1 = 0.18 \cdot L^{0.94} \text{ cm} \quad (R = 0.91), \tag{3}$$

$$S_2 = 0.38 \cdot L^{1.01} \text{ cm} \quad (R = 0.98), \tag{4}$$

where  $S_1$  and  $S_2$  are the distances covered at the end of kinematic stages 1 and 2 respectively. The exponents of equations (3) and (4) are not distinguishable from unity. Therefore, distance covered with time essentially scales with length as did  $T_1$  and  $T_2$ .

Distances covered by the various species were similar to those of trout of the same size (Fig. 4). The similarity occurred in spite of the lower slope of the relationship between length and duration for trout compared to that for the species studied here

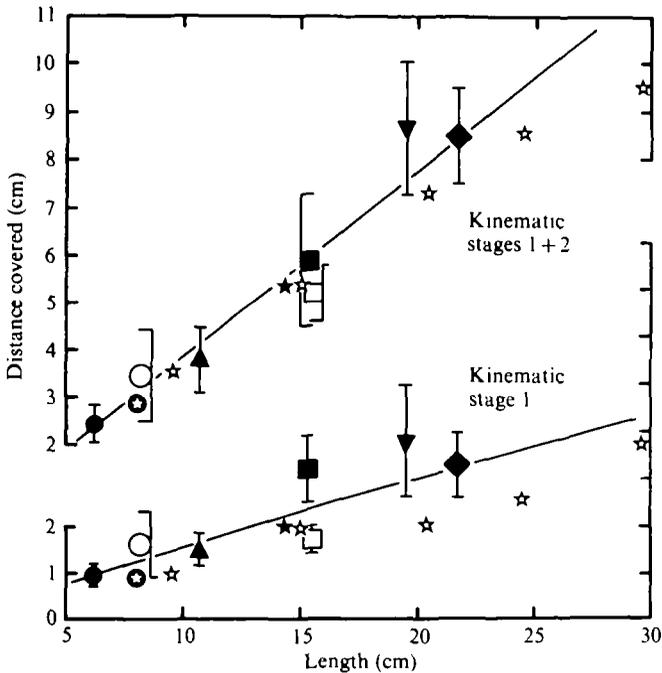


Fig. 4. The relationship between distance covered at the end of kinematic stage 1 and kinematic phase 1 (stages 1 plus 2) and fish length for a variety of species. Vertical bars are  $\pm 2$  s.e. For key, see Fig. 3. Note the ordinate is divided for clarity in separating kinematic stage 1 and kinematic stage 1 plus 2.

(Fig. 3). The trout, however, had an overall mean acceleration rate of  $15.6 \text{ m.s}^{-2}$  (Webb, 1976) compared to  $10.1 \text{ m.s}^{-2}$  for all the species used here. Thus there appears to be an inverse relationship between acceleration rate and the duration of a fast-start, such that distances covered are similar for fish of different species but similar size. It should also be noted with respect to trout that distance covered increases with the square of time for a given (uniform) acceleration rate, when effects of small differences in time will be magnified.

The performance similarity between the present interspecific observations and earlier intraspecific observations is important. In the present experiments, percentage muscle mass unexpectedly increased regularly with size (Table 1). Therefore it was possible that the relationship between distance covered and length was simply a result of the variations in relative muscle mass. The similarity of the relationships for trout and the present experiments show that the interspecific scaling of performance is not caused by relative muscle mass. Instead, performance is a function of the time required for completion of kinematic stages 1 and 2. The duration of such locomotory movements is well known to vary with size (e.g. Hill, 1950).

In previous studies (Webb, 1976, 1977), comparisons among groups of fish were made for acceleration over a given elapsed time because of the sensitivity of distance covered in relation to time. Results for distance covered in various time periods are shown in Fig. 5. There was relatively little difference in performance among the species studied, although *Perca* systematically covered least distance and *Lepomis* the greatest.

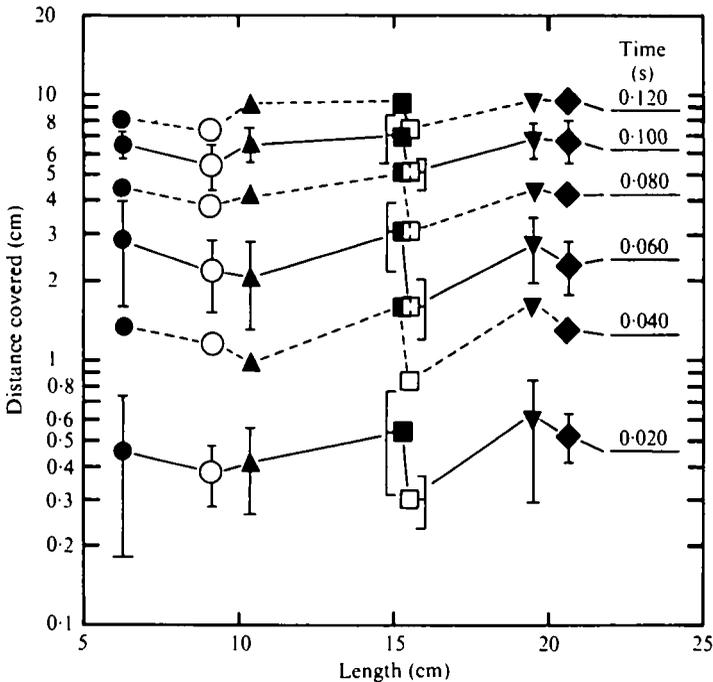


Fig. 5. The relationship between distance covered in various elapsed times and length for seven species of teleost fish. Horizontal lines at the right are the mean distances covered for the combined data for all the species studied, at the elapsed times (sec) for acceleration from rest shown directly above. Vertical bars are  $\pm 2$  S.E. and are shown for alternate times only, for clarity. For key, see Fig. 3.

Maximum velocities, maximum acceleration rates and mean acceleration rates were also measured and are summarized up to the end of kinematic stage 2 in Table 4. Velocities were scaled with length and were similar to those of trout of similar length at the end of kinematic stage 2 (Webb, 1976). They were lower than those reported by Eaton *et al.* (1977). This was because these authors measured velocities for the rostral tip of the head (see footnote). Mean acceleration rates varied as expected from the distances covered, with those fish covering least distance to the end of kinematic stage 2 having the lowest mean acceleration rates. However, *Cottus* was significantly different from *Notropis* and *Esox*, at the extremes of the observed range. Maximum acceleration rates were measured because they indicate the magnitude of maximum thrust developed (Gray, 1953, 1957). Values were typical of those reported for other fish (Gero, 1952; Gray, 1953; Hertel, 1966; Fierstine & Walter, 1968; Weihs, 1973; Webb, 1975a, 1976, 1977).

#### DISCUSSION

The results show that there was little variation in fast-start kinematics among the species tested and little difference in performance measured for fish accelerating from rest for a given elapsed time. Observed differences were related to the duration of fast-start stages which were correlated with size. This similarity in performance

occurred even though the selected variation in lateral body profile was large, such that differences in performance related to this component of body form could be expected. This raises the question; why are the performance differences so small? The answer relates to variation in percent muscle mass and to longitudinal body-depth distribution patterns making up the lateral body profile.

Evaluation of the various body forms will be made mainly with reference to trout, which are relatively unspecialized in terms of body form and locomotion, and their fast-start relations with size are known (Webb, 1976).

#### *Percentage muscle mass*

Fish contain a large proportion of white muscle designed for high activity levels (e.g. Alexander, 1967), typically acceleration and sprint swimming that follows acceleration to high speed. Therefore, variation in muscle mass would be expected to affect fast-start performance. Performance would be improved when the muscle mass is large relative to the body mass to be accelerated; that is, performance should be increased by high percentages of muscle. The results suggest that there is a relationship between body profiles favourable for good fast-start performance and a low percentage muscle mass, such that potential advantages of each cancel out. For example, in comparison with trout, *Cottus* and *Etheostoma* have lateral body profiles with median fins that enhance depth over most of the body length (Fig. 1). Such profiles would be expected to improve fast-start performance, but such improved performance was not observed. Both species have a substantially lower percentage muscle mass than trout. In addition, mean performance of *Cottus* was somewhat lower than *Etheostoma*. It can be shown that the ratio of distances covered in a given time by these two species is similar to the inverse of the ratio of their percent muscle masses. Similarly, *Notropis* and *Salmo* have similar body forms, except that *Notropis* has a larger caudal fin ( $0.18S_w$ ) compared to trout ( $0.13S_w$ ). Therefore, *Notropis* would be expected to develop greater thrust in a fast-start and cover a greater distance in a given time. Again this is not observed, and it is found that the ratio of caudal-fin areas of the two species is similar to the inverse of the ratio of percent muscle mass.

#### *Longitudinal depth distribution*

Although large depth along the length of the body is required for good fast-start performance (Weihs, 1973; Webb, 1977), the optimum arrangement is expected when large depth is correlated with large amplitude body movements. Then large depth, and hence large virtual mass, will be correlated with high lateral velocities, maximizing thrust (Weihs, 1973). Since amplitude of body movements increases with distance from the centre of mass (see figures in Hertel, 1966; Weihs, 1973; Webb, 1975a; Eaton *et al.* 1977), large depth should be distributed as far as possible from the centre of mass to maximize thrust. If depth is not favourably distributed in this way, then large area may not give improved fast-start performance.

*Perca* is an example of this situation. In comparison with trout, *Perca* has a larger area but smaller percentage muscle mass. Together these would be expected to give a fast-start performance similar to trout. In practice the performance was the lowest of all species tested (Fig. 5). The larger area of *Perca* is associated with enhanced depth the spiny first dorsal fin over the centre of mass, and the second dorsal and anal fins

which are relatively far forward towards the centre of mass. The caudal fin is relatively small ( $0.12S_w$ ). Thus the apparent thrust advantages of the larger depth and area in *Perca* are reduced by poor longitudinal depth distribution.

The same arguments would apply to *Lepomis* with a shorter body than *Perca*. However, *Lepomis* has a particularly large depth along the whole length of the body. The caudal fin is also large (Fig. 1). The very large depth, together with relatively higher amplitude lateral movements compared to more fusiform species, offset the apparent disadvantage of concentration of depth about the centre of mass for *Lepomis*.

The large-amplitude lateral movements characteristic of fast-starts generate large lateral forces that result in recoil of the centre of mass (Weihs, 1973). Such recoil movements can be energetically very wasteful (Lighthill, 1970). Fast-start performance would be reduced if such energy losses were large, and therefore recoil movements of the centre of mass should be minimized. Lighthill (1970) showed that a more rostral location of anterior median fins, together with large anterior body depth and mass, is a mechanism to reduce recoil movements for fish swimming in the lunate tail mode. Similar arguments would apply to fast-starts. Therefore, although depth should be concentrated at a distance from the centre of mass to enhance thrust, this advantage could be lost if sufficient mass and/or depth is not maintained at the centre of mass to reduce recoil.

Thus *Esox* would be expected to have superior performance compared to other species because of the concentration of large depth and area posteriorly and the high percentage muscle mass. Again, performance was not exceptional. *Esox* lack any anterior depth or mass enhancement. This is reflected in large recoil movements of the centre of mass. In *Esox* the path of the centre of mass was commonly S-shaped showing a double recoil in each fast-start stage. The path of the centre of mass of most fish is a smooth centripetal spiral reducing the effect of any recoil movements (Webb, 1975a).

#### *Functional design compromises*

Good fast-start performance is an important component of normal behaviour in fish. It is involved in reaching high speeds important in traversing areas of high water flow, avoiding obstacles, etc.; it determines the success of predator strikes and the success of prey escape. Fast-start performance is sufficiently important that the common caudal-fin form of non-scombroid fish has apparently evolved primarily to improve that performance (Webb, 1977). The large bulk of fast white muscle, which must be energetically expensive to maintain, has clearly evolved for such high level activity. In view of these considerations, the performance of several species appears low and could be improved by seemingly small changes in body form. This is, of course, because locomotor and behaviour patterns other than those relating to fast-start performance will also be adaptive. Therefore, each body form represents a compromise between competing demands. In view of the importance of fast-start performance in fish, the nature of such demands and their effects on body form must be considered in order to interpret and understand the evolution of diverse body forms.

The simplest compromise is the structural one seen in the inverse relationship between lateral body profile and percent muscle mass. In *Cottus* and *Etheostoma* the extensive median fins require skeletal support. The low percentage muscle mass ca

Therefore be attributed to the density of these skeletal elements and displacement of muscle by the space occupied. *Cottus* also has a large head further reducing percent muscle mass. A large muscle mass occurs with deeper bodies (e.g. *Lepomis*) and with rounder bodies (e.g. *Perca*). These shapes would be disadvantageous for benthic fish (except Pleuronectiforms) and those found in fast, often rocky, riffles such as *Cottus* and *Etheostoma* (Scott & Crossman, 1973). *Notropis* also illustrates the inverse relationship between lateral body profile and muscle mass, but in this case there is no obvious reason why the muscle mass is not higher. However, it should be noted that protecting acceleration performance by increasing body area with median fins would be energetically more economical than increasing muscle mass.

In terms of compromises in functional design relating to distribution in longitudinal body depth, *Lepomis* has a body and fin form adapted for slow swimming in the tetraodontiform mode (Breder, 1926; Webb, 1975*b*), protection given by the spiny first dorsal fin (Mauck & Coble, 1971) and for manoeuvre (Alexander, 1967) (see Keast & D. Webb, 1966). In the latter case, a short body length is advantageous compared to elongate bodies, because the short length reduces the resistance to motion of caudal and rostral portions during manoeuvre in the yawing and pitching planes. In addition, steady cruising performance of the similar *L. gibbosus* (Brett & Sutherland, 1965) is comparable with that of other fish as is the fast-start performance measured here. Therefore the *Lepomis*-type body and fin shape is a particularly versatile one that does not appear to compromise function in the various locomotor modes.

The body and fin form of *Perca* is also involved in slow swimming, manoeuvre and defence (Keast & D. Webb, 1966). However, behavioural traits may reduce the need for good fast-start performance in this species. Vulnerability of young perch is often reduced by schooling, frequently with other species lacking spiny fins (Mauck & Coble, 1966). Chassin *et al.* (1976) have suggested that poor locomotor performance can be offset by social hunting, which is observed in adult perch (Nursall, 1973).

Behavioural factors may also be important in the body form of *Esox*. Dill (1973) has shown that prey fish respond to an attack when the rate of change of solid angle subtended between the attacker and the prey exceeds threshold values. Small body depth and width, as seen in *Esox*, could reduce the magnitude of the solid angle delaying the prey's response to attack. An anterior fin could decrease this advantage.

Structural and behavioural factors of other species not studied here would be expected to reduce the need for good fast-start performance. These would include spines in Ictalurids, burrowing habits in eel-like forms and toxins. Eaton *et al.* (1977) were unable to elicit fast-starts from the spiny eel. Fast-starts also cannot be elicited from the brightly coloured poisonous lion fish (R. C. Eaton, personal communication).

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