

ACCELERATION PERFORMANCE OF RAINBOW TROUT *SALMO GAIRDNERI* AND GREEN SUNFISH *LEPOMIS CYANELLUS*

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SUMMARY

High unsteady (acceleration) performance of rainbow trout ($L = 14.3$ cm) and green sunfish ($L = 8.0$ cm) was studied in response to electric shock stimulus. Acceleration movements were divisible into a preparatory stage 1 and a main propulsive stage 2. Locomotory behaviour varied between fast-starts and turning manoeuvres.

Taking the centre of mass for the stretched straight body as the reference point, distance covered with time was described by the equation;

$$\text{distance covered} = a \cdot (\text{time})^b.$$

The mean value of b was 1.60 for trout and 1.71 for sunfish. The overall mean distance covered and time to the end of stage 2 was 5.36 cm in 0.078 sec for trout and 2.85 cm in 0.079 sec for sunfish. Velocity increased curvilinearly with time. Maximum values of 20 L/sec were observed, but overall mean values at the end of stage 2 were 8.5 L/sec for trout and 8.3 L/sec for sunfish. Acceleration rate was not uniform but decreased with time. Mean maximum values were calculated of 42 m/s² for trout and 16 m/s² for sunfish, but overall mean values for an acceleration movement were 13 m/s² and 8 m/s² for the two species respectively.

The observed acceleration behaviour is more advantageous than uniform acceleration because a greater distance is covered and greater velocities acquired in a shorter time, while the increased energetic cost is only 2-3% of the total energy expended.

INTRODUCTION

High levels of unsteady (acceleration) propulsion activity are vital components of a fish's locomotory repertoire. Acceleration activities such as high speed manoeuvres, fast-starts from rest or speed changes from one steady speed to another are integral parts of normal activity. The former two propulsive patterns involve high rates of acceleration and are major components of predator-prey interactions, avoidance behaviour in response to a variety of stimuli including fishing nets, and the successful negotiation of such objects as waterfalls and fish ladders.

Very few studies of high levels of unsteady acceleration activity have been made. Kinematics have been qualitatively described by Gray (1933), Hertel (1966) and

Weihs (1972, 1973). Weihs (1972, 1973) has also set out a hydromechanical model which was found to give good agreement with observed performance for single sequences of turning goldfish and rudd and a single sequence of a fast-start for trout. Webb (1975) has developed a simplified theoretical model to describe the possible interactions among acceleration parameters and the work done at several levels of uniform acceleration.

Gero (1952), Gray (1953), Hertel (1966), Fierstine & Walters (1968) and Weihs (1973) report what are considered to be maximum acceleration rates of 40–50 m/sec² for perch, trout, pike and tuna. Experimental methods are not given in detail in most cases. Somewhat lower acceleration rates (maximum 24.5 m/sec², mean 20.6 m/sec²) were reported in a detailed study by Weihs (1973) for a single sequence for a 33 cm trout.

Most studies give no information on the magnitude of *overall* acceleration activity. Data for such parameters as duration of acceleration, mean value, distance covered, and mean and final velocities are required to evaluate acceleration performance properly. Only Weihs (1973) gives sufficient information for a single fast-start from rest for trout. Without more comprehensive information the high acceleration rates reported in the literature have little meaning.

The present experiments were therefore designed as a broad spectrum study to evaluate acceleration performance. Objectives included (1) obtaining more comprehensive information on acceleration behaviour which may or may not fall into relatively narrowly defined fast-turning manoeuvres and fast-start stereotypes; (2) seeking relations between acceleration and basic kinematic parameters as for steady swimming, (3) determining ranges and relationships for acceleration and velocity with time and distance covered. Experiments were performed on two species of fish from different habitats and with different body forms.

MATERIALS AND METHODS

Fish

Rainbow trout *Salmo gairdneri* (Richardson) were used from a laboratory stock. Ten fish of similar length were selected from 40 fish that had been held in a 1000 l tank for 5 months over winter. The tank was supplied with filtered recirculated water which was replaced regularly to prevent the build up of metabolic wastes. Temperature was maintained at 10 ± 1 °C. Dissolved oxygen was maintained close to 100% air saturation by vigorous aeration. Photoperiod was maintained at 16 h daylight. Fish were fed once every 3 days on Purina Trout Chow.

Green sunfish *Lepomis cyanellus* (Rafinesque) were seined from local ponds and held under similar conditions for 4 weeks. Experiments were performed on ten fish of similar size.

All fish were acclimated to 15 °C. Water temperature was increased from 10 to 15 °C over 7 days and controlled at 15 ± 0.2 °C for a further 2 weeks before commencing experiments. Oxygen levels were maintained close to air saturation. Fish were fed to excess once a day during acclimation but each fish was starved for 48 h prior to an experiment.

Apparatus

Observations on acceleration activity were made in an observation chamber 90 cm square and 10 cm deep. The bottom of the chamber was a white $\frac{1}{2}$ in thick polyethylene sheet, diameter 125 cm supported 10 cm below the top of a circular 1000 l tank. Two solid walls delineated an oval chamber 90 cm wide and 125 cm maximum length. Fish were further restricted within this oval chamber by walls of $\frac{1}{2}$ in plastic grid at each end, forming a chamber 90 cm square. The top of the 1000 l tank was lined with a rubber gasket and completely covered by a $\frac{1}{4}$ in thick clear plexiglass lid, which abolished surface effects on propulsion and recordings. The lid was clamped in place during an experiment to ensure a water-tight seal.

Water was pumped into the acceleration chamber from a 450 l reservoir tank at approximately 150 l/h. The flow rate was sufficient to maintain the oxygen tension in the water of the chamber between 95 and 100% air saturation. The water left the observation chamber by a central drain into the bulk of the 100 l tank. This tank was connected to a constant-head tank through which excess water overflowed to the reservoir. The constant-head tank maintained a pressure of about 5 cm of water in the observation chamber. This guarded against air entering and obscuring observation in the event of any small leak in the lid seal.

The water in the observation chamber slowly rotated because water was pumped in at either end of the oval chamber outside the grids of the observation section. Water entered the chamber through large openings, streamlined upstream, so that the maximum water velocity at the edges of the chamber was approximately 2 cm/sec, decreasing with distance towards the drain. The velocity field was determined by filming neutrally buoyant particles.

The temperature in the observation chamber was maintained at 15 ± 0.2 °C by adjusting the temperature of the incoming water.

An aluminium grid lined each end of the oval chamber outside the grids delineating the observation section. The aluminium grids were connected to a stimulator operated by a hand key. The output voltage could be altered by means of a variable transformer and was rectified and smoothed.

Electric shock was used as a stimulus in spite of possible effects on the muscle system that might affect the acceleration response. Other stimulus methods were difficult to apply in the required enclosed chamber and could not be controlled, and the fish usually habituated rapidly. Preliminary observations suggested that electric shock of short duration (approximately 10 msec) produced responses similar to those from other stimuli, except that electric shock tended to produce higher maximum responses (Fisher & Elson, 1950).

Fish movements were recorded via a 45 degree mirror on 16 mm ciné-film taken at approximately 64 frames per second. The record included an electrically driven clock accurate to 0.01 sec and a neon indicator light separately connected to the stimulator.

Experimental procedure

Experiments were performed during the spring. Single fish were left in the chamber overnight or for at least 16 h and under continuous illumination. During this period

Table 1. *Characteristics of rainbow trout and green sunfish used in experiments*(Values shown as mean \pm 2 S.E.)

	Rainbow trout	Green sunfish
Length, L (cm)	14.3 ± 0.7	8.0 ± 0.8
Weight, M (g)	27.32 ± 2.7 $M = 0.009L^3$	8.18 ± 0.9 $M = 0.016L^3$
Wetted surface area, S (cm ²)	69.7 ± 3.1 $S = 0.34L^2$	29.0 ± 1.5 $S = 0.45L^2$
Axial muscle weight, M_a (g)	13.39 ± 1.2 $M_a = 0.49M$	2.78 ± 0.21 $M_a = 0.34M$
Position of centre of mass along body from nose	$0.35 \pm 0.02L$	$0.34 \pm 0.02L$

floodlights were switched on several times. Fish initially reacted to these but habituated rapidly.

The following day, movements were recorded after stimulation at a series of voltages. A given voltage was applied two or three times. Fish were then left undisturbed for 60 min after which a second voltage was applied in the same way. The procedure was repeated for voltages of 20, 40, 60, 80, 100 and 120 V. Voltages were applied in a random sequence. Floodlights were switched on 1 min before stimulating the fish to avoid the development of learned responses to the lights.

At the end of an experiment fish were weighed to the nearest 0.01 g and their total length measured to the nearest 0.1 cm. The centre of gravity (centre of mass) for the body in the stretched straight position was measured by suspending fish from three different points against a plumbline. The centre of mass was assumed to be centrally located at the point where the plumbines intersected. Total wetted surface area and axial muscle weight were measured as described elsewhere (Webb, 1971, 1973). Characteristics of the fish used are given in Table 1.

Film records of acceleration movements were analysed frame by frame. It was found that the first two strokes (stages 1 and 2 discussed below) were most important in acquiring significant momentum when starting from rest; analysis therefore concentrated on these. Tracings of successive body positions were superimposed to observe kinematics, and positions of the centre of mass for the stretched-straight body about which propulsive forces act. Distance covered by this centre of mass was plotted against time for all acceleration sequences. It was found that distance covered usually increased continuously with time through stages 1 and 2 but thereafter the slope of the relationship changed as a result of various behaviour patterns.

Least squares linear regression equations were calculated for a power equation relating distance covered and the time for stages 1 and 2 and excluding data following a break in the curve resulting from variable behaviour patterns in stage 3 (discussed below). Then;

$$s = a \cdot t^b, \quad (1)$$

where s = distance covered, t = time, a, b = fitted constants.

All regressions were highly significant usually at $P \leq 0.01$ and always at $P < 0.05$.

Velocity and acceleration were then calculated by successive differentiation of the

Empirical equation relating s and t . This was considered more accurate than successive numerical differentiation which is subject to large error of uncertain magnitude (Gero, 1952; Weihs, 1972, 1973). Most additional calculations, for example of mean velocity and work done, were derived on the basis of equation (1).

Film sequences of fish close to the observation chamber walls were rejected because of possible edge effects. A few sequences where fish used paired fins to brake or change direction before the completion of acceleration were also rejected, the additional drag obscuring acceleration effects. In most sequences, discontinuities in acceleration were not observed as fish continued swimming through several thrust-generating propulsive movement cycles which did not affect initial acceleration rates. The majority of the acceleration movements analysed were for fish at some distance from the observation chamber walls. As a result, movements of the centre of mass with rotation of the water were negligible in comparison with acceleration movements. Correction for water rotation was not made when these movements were less than 1% of an acceleration movement.

The method of determining velocity and acceleration by successive differentiation of the distance/time empirical relationship smooths any possible higher frequency variations of velocity and acceleration. Such variation in velocity and acceleration will occur to some extent because the relationship between distance and time was slightly S-shaped when plotted on logarithmic co-ordinates. The relationship could not be distinguished mathematically from the simple fitted power equation with the number of data points available. In observing over 200 acceleration sequences, major deviations that would markedly affect calculation of velocity and acceleration were not observed. The only exceptions occurred as a result of changed behaviour in later stages of acceleration activity, and these were not included in calculating the empirical relationship between distance and time for stages 1 and 2. Therefore, instantaneous values for velocity and acceleration, as reported for example in Figs. 2 and 3, will be subject to some error, but the magnitude of that error is likely to be small. Possible error from oversmoothing will also be small in determining mean values for velocity, acceleration and work done. In general, possible oversmoothing of time relations of distance covered, velocity and acceleration will not change the conclusions from the present work.

RESULTS AND DISCUSSION

General observation

Acceleration activity of both rainbow trout and green sunfish usually consisted of the three stages described by Weihs (1973). In the preparatory stage 1 (frames 1 to 3 in Fig. 1A), the tail and anterior of the body rotated in opposite directions about the centre of mass. This was associated with a recoil lateral displacement of the centre of mass which was of small magnitude in comparison with the movements of the nose and trailing edge of the body. The preparatory stage was occasionally omitted when fish were resting with the body curved prior to stimulation.

In the main propulsive stage 2 (frames 4-6 in Fig. 1A), the anterior part of the body was propelled forward as the tail moved laterally, usually almost normal to the path of the centre of mass and at a small angle of attack. During this stage the body gave the appearance of unwinding as a wave of curvature passed backwards along

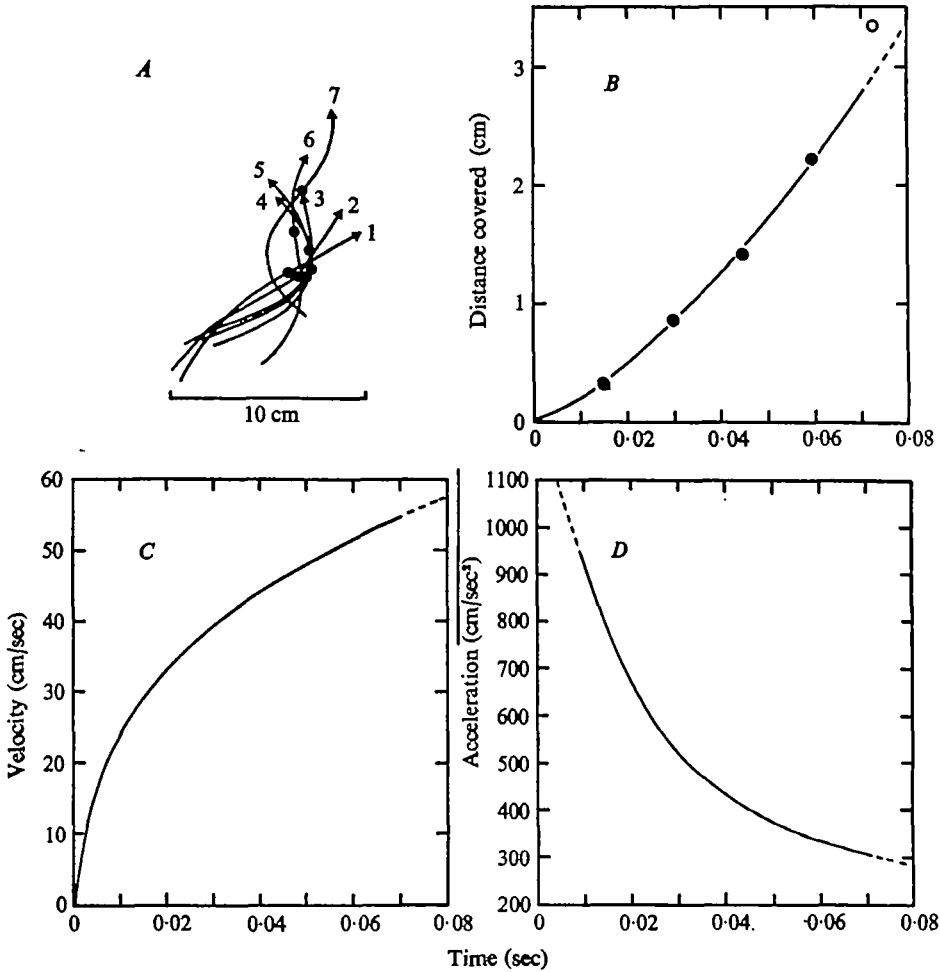


Fig. 1. (A) Successive positions of the body centre-line shown at 0.015 sec intervals for rainbow trout accelerating from rest. The centre of mass is shown by the closed circles. Remaining panels show the time relationships of distance covered (B), velocity (C) and acceleration rate (D) for the centre of mass for the stretched-straight body for the fish shown in (A). Solid circles in (B) are observed points, used to calculate the curve shown. The open circle deviates from this curve as a result of increased acceleration behaviour in stage 3 overlapping stage 2.

one side of the body (Fig. 1A), analogous to the passage of a single half wavelength along the body of a steadily swimming fish.

The duration of each of these acceleration stages, (approximately 0.04 sec) was similar both between stages and between the two species (Table 2). Weihs (1973) recorded a longer duration of about 0.075 sec for each of the same two stages (total time 0.150 sec) for a 33 cm trout, which suggests the possibility of a size effect. The acceleration times observed for rainbow trout and green sunfish are similar to those suggested in a simple model by Webb (1975) in which least work is done in attaining a variety of different final velocities at acceleration rates above 1000 cm/sec².

Activity was variable in the third stage. The most common behaviour patterns were the adoption of continuous swimming or an unpowered glide. Typical examples

Table 2. Summary of overall mean values for acceleration parameters of rainbow trout and green sunfish

	Rainbow trout	Green sunfish
Duration of stage 1, t_1 sec ($\bar{X} \pm 2$ S.E.)	0.039 \pm 0.006	0.033 \pm 0.006
Duration of stage 2, t_2 sec ($\bar{X} \pm 2$ S.E.)	0.039 \pm 0.006	0.046 \pm 0.005
Duration of stages 1 and 2, t sec ($\bar{X} \pm 2$ S.E.)	0.078 \pm 0.007	0.079 \pm 0.007
Distance covered at t_1 (cm)	1.95	0.85
Distance covered at t (cm)	5.36	2.85
Velocity at t_1 (cm/sec)	69	42
(L/sec)	4.8	5.3
Velocity at t (cm/sec)	121	67
(L/sec ³)	8.5	8.3
Maximum acceleration (cm/sec ³)	4208	1567
(L/sec ³)	294	196
Acceleration at t_1 (cm/sec ³)	1475	983
(L/sec ³)	103	122
Acceleration at t (cm/sec ³)	1205	704
(L/sec ³)	84	88
Work done against frictional drag for observed data (erg)	5.78 \times 10 ⁴	6.18 \times 10 ³
Work done against frictional drag for equivalent uniform acceleration (erg)	5.06 \times 10 ⁴	4.78 \times 10 ³
Kinetic energy at t (erg)	2.64 \times 10 ⁵	5.08 \times 10 ⁴

of these patterns have been given by Hertel (1966) and Weihs (1973). Fig. 1A illustrates a third behaviour pattern, which was less common in the present experiments, in which the fish executed further propulsive acceleration strokes in stage 3. Furthermore, where stage 3 behaviour was continued power locomotion, propulsive movements began in the anterior part of the body before completion of the second propulsive stage. For the sequence shown in Fig. 1A, the second propulsive stage is completed by frame 7 when the wave of muscle contraction has travelled the length of the body. However, further acceleration in stage 3 commences in frame 6 as the anterior part of the body moves rapidly to the right.

The overlap between the main propulsive stage 2 and continued powered propulsion in stage 3 resulted in the centre of mass being deflected from its initial normal path. The magnitude of the deflexion was greatest when fish continued to accelerate during subsequent propulsive strokes. This overlap between stages 2 and 3 presented some problems in analysis. Thus for the sequence shown in Fig. 1B, the solid circles represent movements of the centre of mass during stages 1 and most of stage 2, while the open circle reflects the additional acceleration in stage 3 overlapping stage 2. Such points representing initial and successive positions for a new stage 3 acceleration were not used to calculate distance/time regressions for stages 1 and 2. It was also necessary to base calculations of the duration of various acceleration stages on both kinematics and discontinuities in the distance/time curve because of overlap between stages 2 and 3.

It should be noted that the sequence shown in Fig. 1 was selected to complement

descriptions of more commonly encountered and less problematic acceleration patterns which have been previously described (Hertel, 1966; Weihs, 1973).

Hertel (1966) and Weihs (1973) predict that the angle subtended between the path of the centre of mass during acceleration and the initial body axis will be correlated with acceleration rate. Attempts to relate these were not successful because no simple fast-starts followed by glides were observed during these experiments. Instead, the path of the centre of mass was initially curved and then, towards the end of stage 2, was deflected by the beginning of subsequent propulsive strokes. As a result, no obviously linear acceleration path could be discriminated with confidence.

The locomotory patterns observed for both trout and green sunfish were not simple fast-starts as described by Hertel (1966) and Weihs (1973), but were often more similar to turning manoeuvres (Gray, 1933; Weihs, 1972). However, in both turning manoeuvres and fast-starts, the fish accelerate following a series of movements that bear close kinematic similarities, amenable to analysis by the same mechanical theory (Weihs, 1972, 1973). In practice 'turning manoeuvres' and 'fast-starts' by Weihs appear to be extremes of a common locomotor pattern. The majority of observations made on the present species are intermediate, with characteristics of both of the sets of movements described by Weihs.

For example, the behaviour of the centre of mass in a pure turning manoeuvre and in a pure fast-start is different. In the former case it describes a continuous gentle curve (Weihs, 1972). During a fast-start Weihs' (1973) data show that the centre of mass follows a slight S-shaped path that is close to a straight line. Trout and green sunfish typically show the gentle curvature of Weihs' stage 2 turning manoeuvre, together with continuous acceleration during both stages 1 and 2, typical of a fast start. The present observations differ only in that there is a more marked initial curvature from recoil displacement of the centre of mass (Fig. 1A). This displacement was greater for both fish than Weihs observed for trout but was relatively less for deep-bodied sunfish than for trout.

The path of the centre of mass may in fact normally be curved for all manoeuvres and the linearity observed by Weihs could result from the behaviour in stage 3. Fish frequently change their direction of motion as a result of paired-fin use (Weihs, 1972) or as a result of variable behaviour in stage 3. Such changes are an integral part of acceleration behaviour as discussed below but they obscure original details of the motion of the centre of mass.

Kinematics

Attempts to identify key kinematic parameters to which acceleration may be quantitatively related were not successful in this series of experiments. The reason for this stems from an essential mechanical difference between steady swimming and acceleration. In the former case vorticity upstream of the trailing edge makes negligible contributions to thrust. Vortex sheets shed anterior to the trailing edge are absorbed in the flow about the caudal fin while other effects are also small for fish swimming steadily in the sub-carangiform mode (Lighthill, 1970) as do the present species. In contrast all laterally moving portions of the body contribute significantly to thrust during acceleration when lateral movements are of large amplitude (Weihs, 1972, 1973). Therefore evaluation of mechanics requires that all parts of the body be considered.

The possible variation of interacting kinematic factors is extreme for a continuous variation between 'turning manoeuvre' and 'fast-start' behavioural types. As a result, unless activity can be controlled in terms of magnitude and direction, or response patterns are stereotyped, the number of observations required to identify key variables becomes prohibitive. The former could not be controlled while providing sufficient space for unrestricted acceleration. The absence of stereotyped acceleration responses has already been noted.

Advances in understanding the mechanics of steady state propulsion have been largely contingent upon developing water tunnels to control locomotory behaviour and response magnitude. The problems involved in controlling behaviour at high unsteady activity levels may prevent simple practical analysis of acceleration based on key kinematic parameters. An analysis based on such behavioural control might also be of uncertain practical utility.

The magnitude of an acceleration response was also poorly correlated with stimulus voltage, perhaps because the stimulus was non-directional. In addition, the stimulus would not be uniform in the observation chamber at any voltage. It is well known that responses of fish to a direct current depend not only on the current intensity but also on the position of the fish in the voltage field. The latter could not be controlled while providing fish with sufficient space for unrestricted acceleration.

Time relationships of distance, velocity and acceleration

Significant distance is covered and forward velocity acquired by the fish only through acceleration along the path of the centre of mass.

An example of the time relationships between distance covered, velocity and acceleration is shown in Fig. 1 for rainbow trout.

Acceleration stages 1 and 2 are clear, together with continued, higher acceleration in phase 3 beginning before the end of stage 2 (Fig. 1A).

In stages 1 and 2 the distance covered by the fish typically increased continuously with time according to the power function given in equation (1) (Fig. 1B). Therefore, acceleration was usually continuous through both stage 1 and stage 2. Occasionally, acceleration would be discontinuous, jumping from a low value during stage 1 to a high value in the main propulsive stage 2. This would be reflected by a break in the distance-time relation plotted on logarithmic coordinates. The distance-time curve often showed a break at the end of stage 2 usually with a distinct reduction in slope as fish adopted some steady swimming mode in stage 3. Then acceleration reduced towards zero. Alternatively, the pattern of acceleration was continued for several more propulsive cycles with no break in the distance-time curve. Occasionally, increased acceleration was seen during stage 3 as in the sequence shown in Fig. 1.

The exponent, b , of the distance-time curve (equation (1)) was between 1 and 2 for 85% of all sequences observed and between 2 and 3 for the remainder. The overall mean value was 1.60 for trout and 1.71 for sunfish. Therefore, acceleration was not uniform. As a result, velocity increased rapidly early in acceleration to reach high values in a short time, successive increases in velocity progressively decreasing with time (Fig. 1C).

Acceleration was highest early in stage 1 and rapidly decreased with time (Fig. 1D). This agrees with Weihs' (1973) analysis of a single acceleration sequence for a 33 cm

trout, which had a maximum acceleration of 2450 cm/sec^2 in stage 1 but a mean value for stage 2 of 2060 cm/sec^2 .

The shapes of the various curves shown in Fig. 1 are important in terms of the likely requirements of acceleration in fish. It is assumed that the function of acceleration-type movements is to cover the greatest distance in minimum time in such activities as striking prey or avoiding predators. This is achieved when velocity increases as rapidly as possible early in an acceleration movement, as observed in the present experiments. However, continued increases in velocity at the initial rate are not feasible because the kinetic energy of the fish also increases rapidly, together with frictional drag. As a result each successive velocity increment requires more energy. If the initial rate of increase in velocity were maintained throughout an acceleration sequence, thrust generated would have to increase rapidly with time. This cannot occur through increased muscle tension which will decrease with time (see, for example, Alexander, 1968). Increased mechanical efficiency of the 'propeller' system may partially offset decreasing muscle tension similar to the increased efficiency of stage 2 movements compared to stage 1 (Weihs, 1973). However the efficiency increases required would have to be very large to sustain initial rates of acceleration. Therefore acceleration rate would be expected to decrease with time as observed (Fig. 1D).

The advantages of these time relations of velocity and acceleration can be appreciated from a comparison with uniform acceleration at a mean rate consistent with the observed velocity, distance and time data. The mean acceleration rate was calculated from the mean velocity (obtained by integration) and acceleration time. The mean acceleration rate could not be obtained directly by integration, because, on the basis of equations relating acceleration and time, when time is zero, acceleration is equal to infinity. In practice the relationship between acceleration rate and time must be discontinuous for very small values of time.

For the fish illustrated in Fig. 1, the mean velocity was 41 cm/sec after 0.075 sec during which a distance of 3.1 cm was covered. The final velocity was 57 cm/sec .

The mean acceleration was calculated to be 548 cm/sec^2 . Uniform acceleration at this rate for 0.075 sec would cover a distance of only 1.5 cm . Alternatively, if the mean acceleration was applied over a distance of 3.1 cm , 0.130 sec would be required to obtain the same final observed velocity. Thus, the normal acceleration patterns observed for rainbow trout and green sunfish result in fish traversing the greatest distance in the least time.

It also seems likely that there is a functional difference between the first two acceleration stages and the variable third stage. The first stage ends with the fish having acquired substantial momentum but, because acceleration cannot be achieved without a change in direction, the fish's orientation is changed. Clearly this will not matter in some cases, for example avoiding a predator when there is adequate space for manoeuvre and no particular cover. Indeed, the combination of fast acceleration plus the re-orientation of a fish's direction could be advantageous in avoiding a predator. However, a change in direction of motion as a consequence of acceleration is disadvantageous to most fish which are presumably accelerating towards a specific objective, for example prey or shelter. Then the third stage becomes necessary for direction control. But this stage occurs at a time following acceleration when further

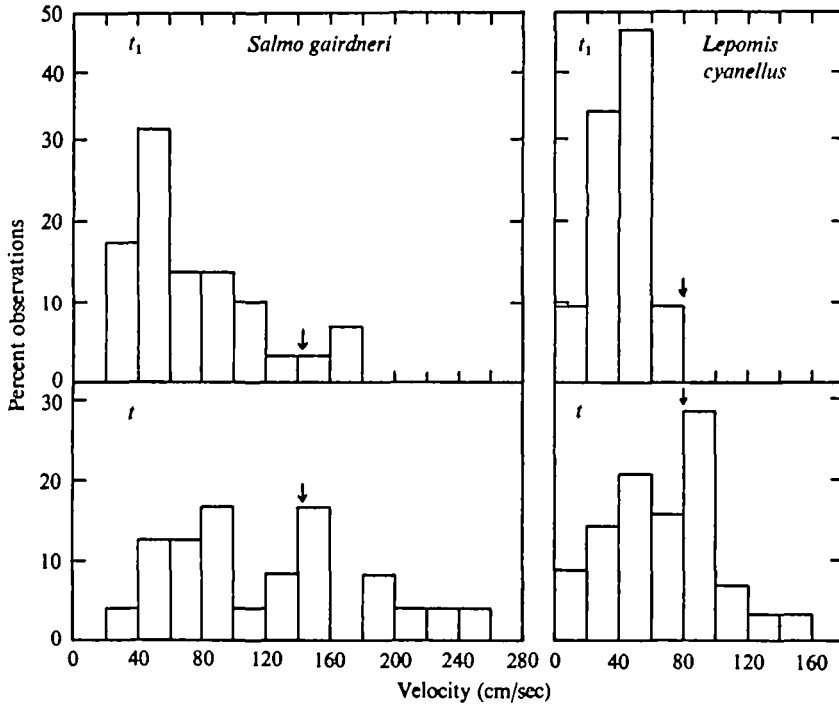


Fig. 2. Frequency distributions for observed velocities attained by rainbow trout and green sunfish at time t_1 at the end of acceleration stage 1 and at time t at the end of acceleration stage 2. The arrows indicate velocities of 10 L/sec .

increase in velocity is small but when relatively large distances can still be covered by virtue of the speed already acquired.

It would be expected that the third stage described by Weihs (1973) should control direction through continued power propulsion rather than by an unpowered glide so that initial gains in velocity are not lost. This was usual for trout, which live in a relatively open and fast-flowing water. Green sunfish commonly showed braking and direction control using pectoral fins after completion of stage 2. These fish tend to live in sluggish, weedy water where such activity would be normal.

In general it appears that overall acceleration activity is divisible into an initial phase, when a high speed is obtained, followed by a second orientation phase. These phases roughly correspond to stages 1 and 2 and to stage 3 respectively, based on kinematics.

Velocity

Velocities attained by rainbow trout and green sunfish are summarized in Fig. 2 for the end of stage 1 (at t_1) and at the end of stage 2 (at t). Maximum and minimum velocities for both the species varied by one order of magnitude, the range increasing to include higher velocities at t as expected. The distribution of velocities was skewed towards lower values.

A maximum specific sprint speed of 10 length/sec (L/sec) is often considered usual for fish (Bainbridge, 1958) and is presumably obtained immediately following an acceleration period. This speed was just reached by some rainbow trout and green

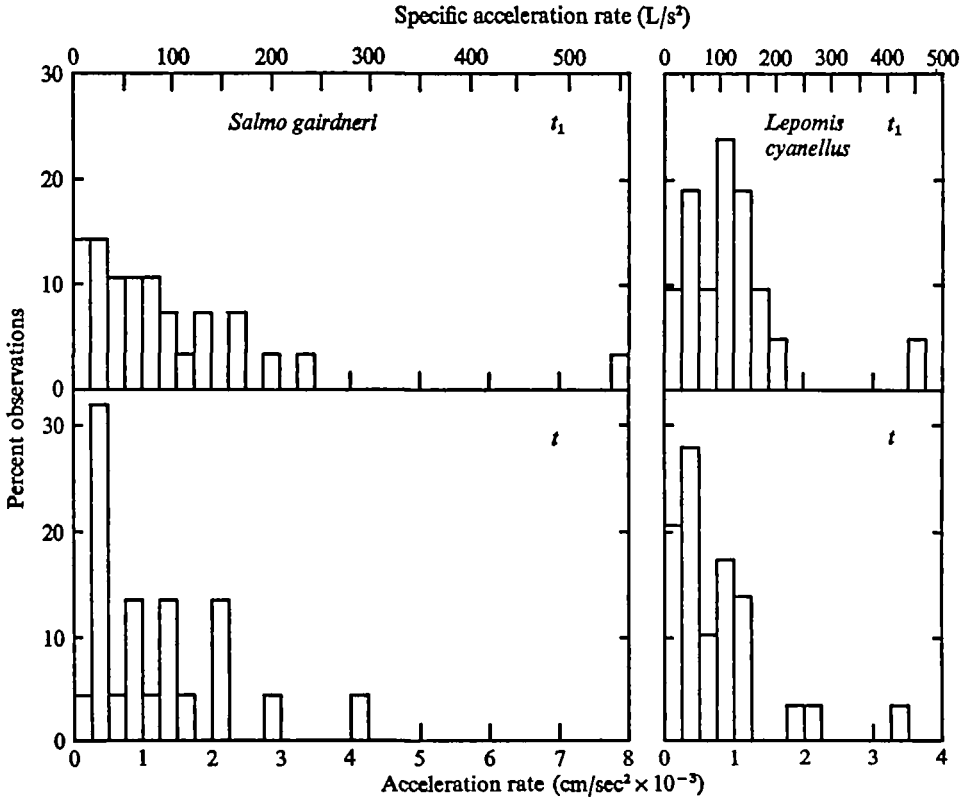


Fig. 3. Frequency distribution for acceleration rates (cm/sec²) and specific acceleration rates (L/sec²) of rainbow trout and green sunfish calculated at t_1 and at t .

sunfish at t_1 but mean speeds at the end of the first stage of acceleration were 4.8 L/sec and 5.3 L/sec (Table 2) respectively. A speed of 10 L/sec was close to the mode in the frequency distribution for velocities at t (Fig. 2) although maximum specific speeds as high as 20 L/sec were found. Webb's (1975) theoretical model for uniformly accelerating fish shows that velocities of this order at t are well within the energetic capacity of the fish. Overall mean velocities at t were very much lower than the maximum values, being 8.5 L/sec for trout and 8.3 L/sec for green sunfish (Table 2).

Acceleration

Frequency distributions for acceleration rates calculated from solutions to equation (1) are shown in Fig. 3. The range of acceleration rates at t_1 and at t was large for both species, most values being somewhat irregularly distributed between 10^3 and 10^4 cm/sec². Some apparent discrepancies occur. For example, for green sunfish, at t , 6.8% of observed acceleration rates fell between 1750 and 2250 cm/sec² and 3.4% between 3250 and 3500 cm/sec² whereas at t_1 only 4.8% of acceleration rates were higher than 1750 cm/sec². This cannot be explained if all acceleration rates decreased with time. Such effects result from the 15% of acceleration rates which increased with time and also from variations in t_1 and t .

Acceleration rates may be expressed as specific acceleration rates in body lengths,

sec^2 (L/sec^2). When acceleration rates are expressed in this way, the relative performance of the smaller green sunfish is better than that of the larger trout (Fig. 3). Thus at t , the peak in the acceleration frequency distribution occurs at approximately $500 \text{ cm}/\text{sec}^2$ for both species, or approximately $35 L/\text{sec}^2$ and $63 L/\text{sec}^2$ for trout and sunfish respectively.

Overall mean values for acceleration rates at t_1 and t are included in Table 2 together with calculated maximum acceleration rates. These were calculated from the mean acceleration rate, derived as discussed above, for stage 1 and the overall acceleration performance to the end of stage 2. The mean acceleration rate was assumed to be the geometric mean of the maximum acceleration rate and that at t_1 and t .

The mean maximum acceleration rate for trout of $4208 \text{ cm}/\text{sec}^2$ was of the same order as maximum reported values for other fish (Gero, 1952; Gray, 1953; Hertel, 1966; Fierstine & Walters, 1968; Weihs, 1973). The performance of green sunfish was initially poorer than that of trout in terms of absolute acceleration rates but specific acceleration rates were higher. Final specific acceleration rates were similar in both species (Table 2).

Maximum acceleration rates of $4000\text{--}5000 \text{ cm}/\text{sec}^2$ (with peaks up to $9500 \text{ cm}/\text{sec}^2$ observed here for trout) are impressive, but because acceleration rate decreases with time they are not representative of overall activity. The mean value of acceleration rate for a given movement is more representative. Overall mean acceleration rates to the end of stage 2 were $1291 \text{ cm}/\text{sec}^2$ ($90 L/\text{sec}^2$ for trout) and $813 \text{ cm}/\text{sec}^2$ ($102 L/\text{sec}^2$) for green sunfish.

Work done

The resultant of all forces acting on the body appears as motions of centre of mass about which various couples act (Weihs, 1972, 1973). In these experiments, the path of the centre of mass was a variety of centrifugal spirals. As a result of the shape of the path of the centre of mass, the resultant forces acting on the body at any instance may be resolved into two components. The first is a force tangential to the path of the centre of mass, which does external work against frictional drag and body inertia. The second is a centrifugal force, which does no external work as it has no component in the direction of motion.

A measure of the net useful work appearing as forward motion can be calculated using a simple model described by Webb (1975). The work done against frictional drag was calculated by integration of instantaneous frictional drag values over the acceleration period using equations obtained for velocity and acceleration rate as functions of time. The method assumed instantaneous drag to be equal to that predicted by standard hydrodynamic equations for steady outer flow and turbulent boundary layer flow. Boundary layer flow is likely to be turbulent for flexing fish (Webb 1975). The assumption that instantaneous drag tends toward that for steady conditions will result in frictional drag being over-estimated for a rigid body and might under-estimate this component for a flexing fish when body movements will affect boundary layer thickness (Lighthill, 1971; Webb, 1973). Nevertheless a good first approximation for work done against frictional drag is expected.

The net inertial work is readily calculated from the kinetic energy at the end of a

particular acceleration stage. The added mass of the body was taken as 20% of the body mass (Gero, 1952; Bainbridge, 1961; Webb, 1971).

The calculation of useful work is analogous to the calculation of thrust or thrust power for steady swimming. In both cases wasted energy which dictates mechanical "propeller" efficiency is not included. In acceleration, these energy losses result from vorticity shed by all medium fins and sharp dorsal and ventral edges of the body as well as from recoil reactions of the centre of mass. The latter includes couples resulting in centrifugal forces acting at the centre of mass. It should be noted that the latter forces are minimized because the radius of the spiral-type movements increases with velocity, being smallest when velocity is also small.

Estimates of the overall mean work done against frictional drag and net inertial work are included in Table 2. The work done against frictional drag was 18% of the total work done for rainbow trout and 11% for green sunfish. The trout value is higher because the percentage of work done against frictional drag increases with acceleration rate for a given time period. This follows because:

$$W_f \propto V^{1.8}s = V^{2.8}t \quad (2)$$

and
$$W_I \propto V^2, \quad (3)$$

when W_f = work done against frictional drag, W_I = work done against inertia, V = velocity, s = distance, t = time.

Table 1 also shows estimates of work done against frictional drag for the overall mean uniform acceleration rates, the net inertial work done being the same for either uniform or non-uniform acceleration. For rainbow trout, work done against frictional drag was 1.14 times greater than that for uniform acceleration. For green sunfish this ratio was 1.29. The work done is higher for the observed non-uniform acceleration pattern than for uniform acceleration because fish achieve higher velocities earlier and hence for a longer period of the acceleration time. The greater value for green sunfish occurs because the wetted surface area is relatively greater than for trout (Table 1).

These calculations show that the advantages of covering a large distance at a rapidly acquired high velocity are made at the cost of increased energy requirements. However, the difference between the frictional energy costs for observed non-uniform and uniform acceleration patterns is small when considered in the context of total work done. The observed acceleration pattern results in an increase in total drag of approximately 2% for rainbow trout and 3% for green sunfish compared with uniform acceleration. These energetic costs are presumably negligible in comparison with the survival advantages of the observed acceleration pattern.

General discussion

The maximum acceleration rate calculated for trout is of the same order (40–50 cm/sec²) as reported maxima for other fish of a wide size range (Gero, 1952; Gray, 1953; Hertel, 1966; Fierstine & Walters, 1968; Weihs, 1973). These observations suggest that maximum acceleration rates may be relatively independent of size.

In contrast the calculated maximum acceleration rate for green sunfish was only 1567 cm/sec². The fish was also the smallest for which acceleration data have been reported. However, the fish also differs in gross morphology from all other species,

studied. Trout, perch, pike, and tuna are roughly similar in body form having fusiform or cylindrical bodies, while the sunfish has a more laterally compressed truncate body. Such body compression reduces the proportion of axial muscles so that the sunfish has a relatively smaller amount compared with trout (Table 1). Differences in axial muscle proportion can be removed in an approximate way by expressing calculated work done as the work done per gram of axial muscle. Assuming half of the axial muscle works at any instant, values are 4.81×10^4 erg/g muscle for trout and 4.10×10^4 erg/g muscle for green sunfish. The different acceleration rates therefore reflect the different amounts of axial muscle associated with different body forms.

The observations on trout and green sunfish provide insight into the typical elongate cylindrical or fusiform body shape of fish where acceleration is a major component of the propulsive repertoire, e.g. lunging for prey by pike. Webb (1975) suggested that such fish would be expected to have body forms that minimize drag, for example the cylindrical body section reducing added mass. It also follows that such a section maximizes the amount of axial muscle possible for a given surface area. Reduction in wetted surface area relative to the amount of muscle will also reduce the total energy required by reducing the frictional drag component.

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