SPEED, ACCELERATION AND MANOEUVRABILITY OF TWO TELEOST FISHES

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SUMMARY

(1) Speed, acceleration rate and turning radius were measured for rainbow trout (*Salmo gairdneri*; length 25·7 cm) and smallmouth bass (*Micropterus dolomieu*; length 23·6 cm) attacking live minnows. The observations sampled a range of values for each kinematic variable up to the limits of maximum performance.

(2) Minimum turning radius was independent of speed and acceleration rate. Expressed as a ratio of total length, L, minimum radii were $0·18 \pm 0·2$ L for trout and $0·11 \pm 0·02$ L for bass ($\bar{X} \pm 2$ s.e.).

(3) Differences in minimum turning radius, R, between trout and bass were attributed to differences in the volume of the body and entrained water, V, and projected lateral surface area of the body and median fins, A. For subcarangiform swimmers, the dimensionless minimum specific turning radius $R/L = 2V/AL$. Since V is numerically equal to the mass of the body, M, and added water mass (approximately $0·2$ M) for neutrally buoyant fish, R/L can be calculated from two easily measured morphological parameters, M and A.

INTRODUCTION

Over the past two decades, major advances have been made in understanding many aspects of aquatic locomotion. These advances have largely followed from the development of techniques to control activity, either at steady swimming speeds (Blazka, Volf & Cepela, 1960; Brett, 1964) or at maximum acceleration rates (Webb, 1975; Eaton, Bombardieri & Meyer, 1977), and from advances in related hydromechanical theory (see Wu, Brokaw & Brennen, 1975; Lighthill, 1975; Pedley, 1977). However, normal fish behaviour involves turns at various speeds and acceleration rates. The performance of fish in making turning manoeuvres has largely been ignored, with the exception of limited observations by Gray (1933), Weihs (1972, 1981), Howland (1974), Webb (1976) and Webb & Keyes (1981). The purpose of the work reported here was to determine turning radius at the limiting condition of its minimum value and the influence of speed and acceleration rate on the minimum turning radius. Since it is not possible to manipulate all these variables in controlled situations, appropriate data were obtained by placing fish in predation situations where a wide range of speeds, acceleration rates and turning radii occur naturally as predators pursue prey.

MATERIALS AND METHODS

Rainbow trout (*Salmo gairdneri* Richardson) and smallmouth bass (*Micropterus dolomieu* Lacépède) were obtained from hatcheries. Fish were held in groups of five in 110 l oval tanks, within which submerged pumps generated a current with a mean speed of about 20 cm s^{-1}. Each tank was continuously flushed with water at a rate of 50 l h^{-1}. Air stones maintained dissolved oxygen levels close to air saturation. The acclimation and experimental temperature was 15 °C. Fish were fed twice a week on live bait minnows.

Experiments were performed on 10 bass (total length, $L = 23·6 \pm 1·1 \text{ cm}$; mass, $M = 158·21 \pm 26·8 \text{ gm}$; total wetted surface area, $A_w = 279 \pm 30 \text{ cm}^2 : \bar{X} \pm 2 \text{ s.e.}$) and 19 trout ($L = 25·7 \pm 1·2 \text{ cm}$; $M = 168·92 \pm 20·02 \text{ gm}$; $A_w = 270 \pm 31 \text{ cm}^2$) as predators on fathead minnow (*Pimephales promelas* Rafinesque) prey. Individual trout or bass were starved for 1 week and then placed in an observation arena, 50 cm wide, 50 cm long and 10 cm deep. The limited depth ensured that observed interactions were essentially two dimensional. The arena was delineated within a larger tank 60 cm long, 30 cm wide, filled with water to a depth of 20 cm. The arena had a glass bottom, and fish were observed via a 45° mirror beneath. After a 24 h acclimation period, individual fathead minnow prey were introduced via one of four side ports.

Locomotor movements of the fish during predation interactions were recorded on video tape. The tape was analysed using a stop-action recorder, giving a framing rate of 60 Hz. Movements of trout and bass were analysed to measure speed and acceleration rate resolved along the path of the fish, and turning radius. These measurements were made for the centre of mass of the stretched-straight fish, approximating the point about which propulsive forces act. Speeds and acceleration rates were evaluated with respect to turning radius. This was because fish are flexing bodies. The propulsive force depends on the tail beat period and amplitude, which must be influenced by the radius of turning. As a result, the force generated by the tail, and hence speeds and acceleration rates, are more likely to be influenced by turning radius than *vice versa*.

Analysis of video tape provided a cloud of datum points which was assumed to sample the full range of speeds, acceleration rates and turning radii. Such a data cloud must be bounded by the limits of performance. This boundary was examined for the 20 % smallest turning radii. The cut off at 20 % of the smallest radii was arbitrarily selected, and would probably err on the conservative side. There are no recognized methods for defining statistically a single boundary of an irregular cloud of observations.

RESULTS

Kinematics

The swimming behaviour of trout and bass attacking minnow prey was made up of several kinematic components, each of which has been described previously under controlled conditions. Thus periodic tail beats, characteristic of swimming at steady speeds (see Bainbridge, 1958, 1963; Weihs & Webb, 1983) were used during rectilinear progression at uniform speeds and low linear acceleration rates. Turns were

ways associated with asymmetrical body and tail movements that were basically transient rather than periodic (see Weihs & Webb, 1983), as described by Weihs (1972, 1973). The smallest turning radii were observed in fast-start turns (Fig. 1A) which were comprised, as usual, of three stages. In fast-start stage-1 (0–0·067 s in Fig. 1A) the body was bent into a U-shape, which travelled backwards over the body in fast-start stage-2 (0·067–0·133 s in Fig. 1A) as the fish accelerated and turned. The body straightened in fast-start stage-3, usually with the adoption of periodic swimming movements.
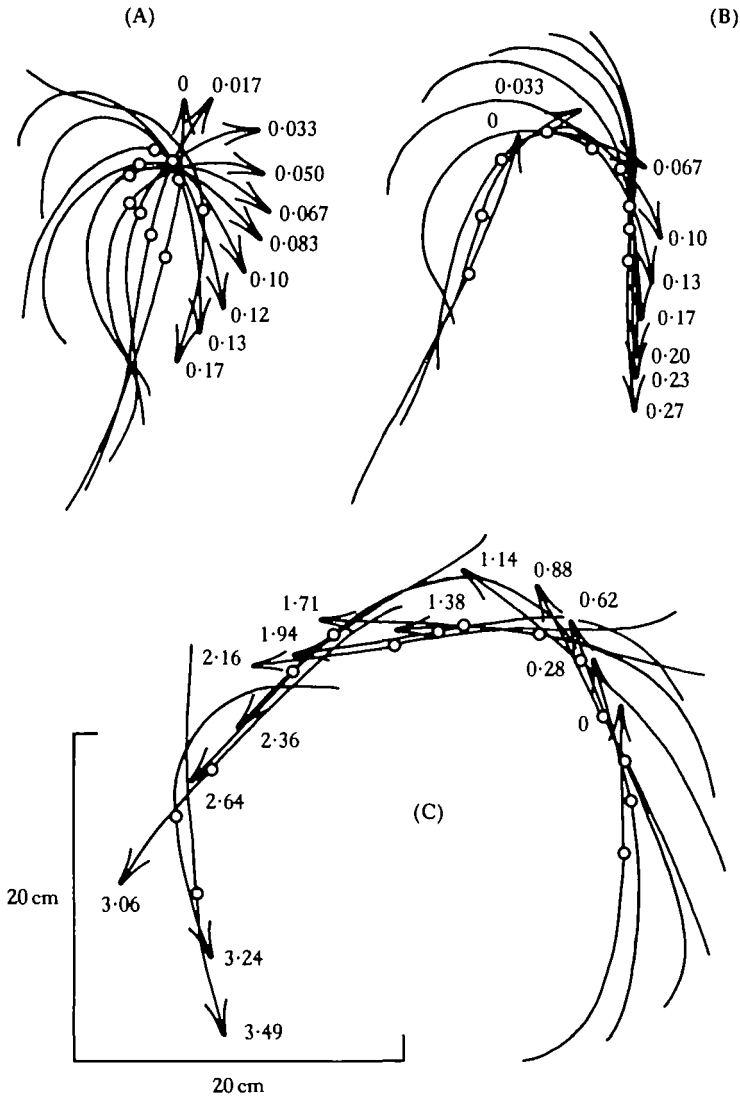

Fig. 1. Tracings of the centre lines of rainbow trout during turning manoeuvres. (A) A fast-start turn through a small radius at high acceleration rates. (B) A swimming turn through larger radius. (C) A large radius turn requiring several tail beats. Times are shown in seconds. Periods between tracings are irregular in (C) as only certain positions in a series of irregular tail beats are shown for clarity. Open circles show the stretched-straight centre of mass.

Larger radius turns were also made up of three stages but these differ from the three stages of a fast-start (Weihs, 1972, 1973). The three stages of a turn have been described by Weihs (1972), but were found to overlap in turns through large arcs (Fig. 1B). Thus in turning stage-1 (0–0·10 s in Fig. 1B) the head and tail were rotated in opposite directions so that the body assumed a curved position. The head rotated into the turns towards its final direction for the manoeuvre. In turning stage-2, the angular velocity of the centre of the body increased as it followed the head (0·067–0·17 s in Fig. 1B). The tail also started to move in the opposite direction to the head, powering the turn. In turning stage-3, the body straightened (0·17–0·27 s in Fig. 1B), the movement of the tail continuing to power the turn. Turning stage-3 was usually followed by rectilinear propulsion with periodic body movements.

The fish used several asymmetrical tail beats to make turns of large radius (Fig. 1C). Each tail beat was similar to the single-beat turns described by Weihs (1972), except that lateral body movements were of relatively small amplitude compared to those observed in small radius turns. In large radius turns, the body movements, being of small amplitude and frequently repeated, tended to be more similar to the periodic body movements of rectilinear swimming than to the transient body movements associated with high angular and linear acceleration rates.

Performance

Speed and acceleration rate varied during turns as previously described by Weihs. Thus, speed increased continuously through a fast-start turn as originally shown by Weihs (1973). Acceleration rates varied during each stage but generally declined throughout a fast-start turn. In a swimming turn, speed decreased in turning stage-1 as the head rotated into the turn, and usually increased in later stages. Initial decelerations were therefore found in turning stage-1 and large accelerations could occur in turning stages-2 and -3 (Weihs, 1972). Deceleration rates were large in later stages of a swimming turn when a turn was passively sustained or when additional braking was applied by the fins.

Observations on turning radius, speed and acceleration rates generated a cloud of data, an example of which is shown in Fig. 2A for maximum speeds attained during turns by bass. In the example, the 20 % smallest turning radii ranged from 1·5–3·5 cm and included speeds from 16 cm s^{-1} to a maximum of 250 cm s^{-1}. Speed could not be shown to be a significant function of turning radius, or *vice versa*. The 20 % minimum turning radii and maximum speeds are also shown for trout in Fig. 2A. These selected 20 % datum points only are shown for trout and bass for mean speeds and acceleration rates in Figs 2B and 2C, respectively. In all instances, radius was not related to speed or acceleration rate in a turn.

Mean values of minimum turning radii were 4·6 ± 0·4 cm (0·18 ± 0·02 L) for trout and 2·6 ± 0·5 cm (0·11 ± 0·02 L) for bass ($\bar{X}$ ± 2 s.E.). These results are comparable to minimum turning radii of 0·17 L for rainbow trout in forced maximum fast-starts (Webb, 1976) and of 0·13 L for feeding dolphins, *Coryphaena hippurus* (Webb & Keyes, 1981).

Maximum acceleration rates were 80 m s^{-2} for trout and 110 m s^{-2} for bass. Mean values of 40 m s^{-2}, with 95 % confidence limits of ±25 % of the mean are reported for teleosts (Webb, 1978). The maximum values obtained in the present experiments are
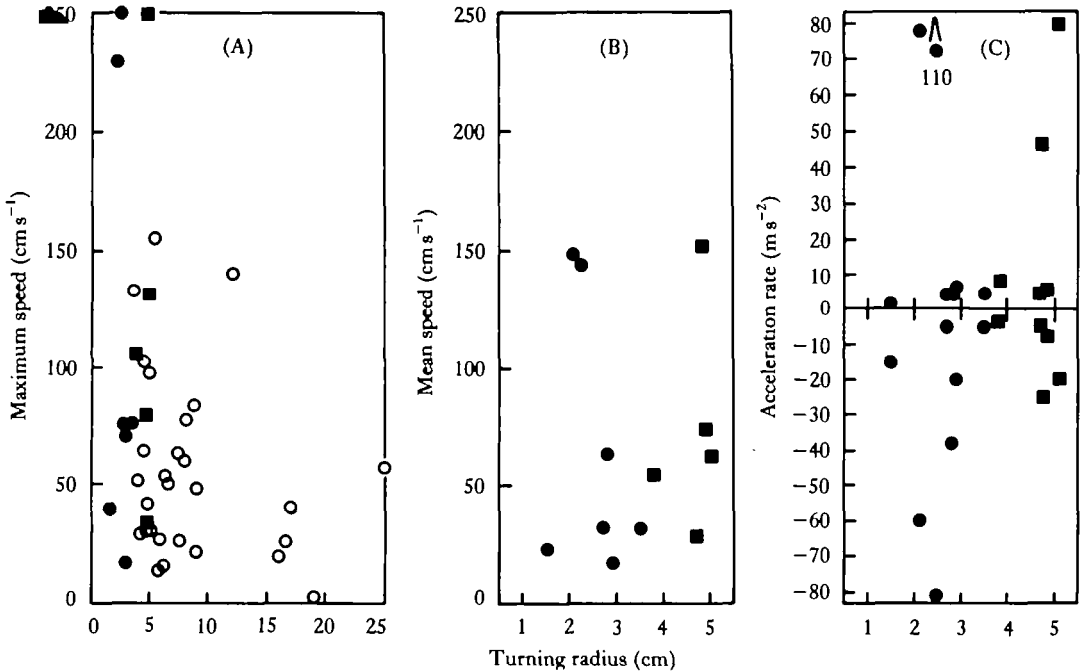
Fig. 2. Relationships between speed and acceleration rate with turning radius. (A) shows a data cloud of various maximum speeds and turning radii for bass (circles) attacking minnows. The closed circles show the 20 % of observations used to evaluate interactions between minimum turning radius and maximum speed. Solid squares are the 20 % minimum turning radius data used for trout. (B) and (C) show the 20 % minimum turning radius data for trout (squares) and bass (circles) used to evaluate relationships with mean speed (B) and acceleration rates (C).

range limits, and are expected to be higher. Range limits up to $100 \, \mathrm{m \, s^{-2}}$ have been obtained for other teleosts (P. W. Webb, unpublished data).

Maximum deceleration rates in predation interactions were $-35 \, \mathrm{m \, s^{-2}}$ for trout and $-80 \, \mathrm{m \, s^{-2}}$ for bass. The higher value for bass reflects the use of the paired fins for brakes. There are no other reported deceleration rates for comparison.

Maximum speeds in turns were $250 \, \mathrm{cm \, s^{-1}}$ for both bass and trout. These values are, of course, lower than maximum rectilinear speeds because the additional centripetal force in a turn must reduce that for sustaining speed (Weihs, 1981). However, the maximum speeds observed were comparable to maximum speeds in fast-start turns of $210{-}250 \, \mathrm{cm \, s^{-1}}$ (Webb, 1976, 1978).

DISCUSSION

It is extremely difficult, perhaps impossible, to force fish to manoeuvre under precisely controlled and repeatable conditions of speed, acceleration rate and turning radius. The experiments described here attempted instead to utilize natural variability in behaviour where there was a good likelihood of sampling the full ranges for these three factors. The similarity of performance limits, measured during the predation interactions and limits found in other experiments on mechanically similar activities, indicates that the approach was adequate, and the results reliable.

The general conclusions from these experiments are that turning radius is indepen-
dent of speed and acceleration rate, and that some differences occur between the two
species. The independence of turning radius with speed may be explained because
both the centrifugal force and available turning force vary similarly with speed (How-
land, 1974). Thus the available turning force (T) is given by:

$$T = \tfrac{1}{2}\varrho A U^2 C_T \tag{1}$$

where ϱ = density of water
        A = projected lateral area
        U = speed
        C_T = thrust coefficient
The centrifugal force (C) is given by:

$$C = (\varrho_b V_b + \varrho v_w)\, U^2/R \tag{2}$$

where ϱ_b = density of the body
        V_b = volume of the body
        v_w = volume of 'entrained water', about $0.2\,V_b$ (Webb, 1982)
and ϱv_w is the added mass of water.

For neutrally buoyant fish ϱ_b and ϱ are equal. Then, writing V for the sum of V_b
and v_w, equation (2) becomes:

$$C = \varrho V U^2/R. \tag{3}$$

In a turn; C and T must be equal;

$$\tfrac{1}{2}\varrho A U^2 C_T = \varrho V U^2/R \tag{4}$$

where U^2 cancels, so that R is independent of U as observed.

Equation (4) also shows the important variables relating to morphology that affect
R. Howland (1974) suggested R could be related simply to $1/A$. In practice V must
be considered and C_T may vary due to morphologically related differences in kinemat-
ics. However C_T is expected to be similar for fish swimming in the same mode and
can be evaluated here for trout and bass. First, the projected area, A must be obtained.
The depth distribution along the length of bass and trout was measured and is shown
in Fig. 3. Median fins were maximally extended. Then, A was 91 cm^2 and 139 cm^2 for
the trout and bass used, respectively. V was taken numerically as $1.2 \times$ mass (Webb,
1982). Similar values of C_T were obtained from equation (3) of 0.97 for trout and 1.05
for bass, with an average of 1.0, so that the minimum turning radius is numerically
obtained from two easily measured morphological parameters:

$$R = \frac{2V}{A}, \tag{5A}$$

or numerically:

$$R = \frac{2.4\ \text{mass}}{\text{projected lateral area}}. \tag{5B}$$

Alternatively, R may be expressed as a dimensionless ratio, or specific radius, to
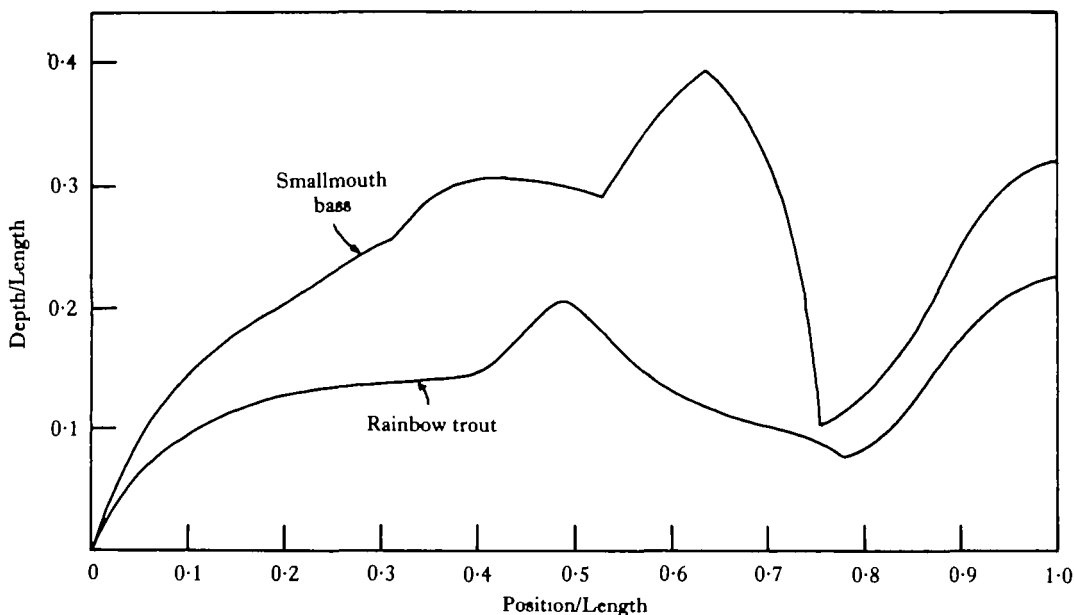facilitate comparisons:

Fig. 3. The distribution of body depth (normalized with respect to total length) along the body of trout and bass.

$$\frac{R}{V} = \frac{2V}{LA}, \tag{6A}$$

or numerically:

$$\frac{R}{L} = \frac{2.4 \times mass}{projected\ area \times length}. \tag{6B}$$

Equations (5) and (6) may apply only to subcarangiform fish because C_T may vary with morphologies and kinematics associated with anguilliform and thunniform modes. Furthermore, the minimum turning radius feasible from the available turning forces may not be achievable with the thick, relatively inflexible bodies of more thunniform species.

Indeed, it might also be considered that the minimum turning radius would be determined by the limit of body flexibility. In practice, unpowered turns should have a larger radius than the smallest body curvature because of sideslip. In contrast, powered turns could achieve smaller radii than that anatomically possible because lateral recoil forces displace the centre of mass towards the turning axis (Weihs, 1972, 1973). This can be seen in Fig. 1A where the path of the centre of mass falls within the curvature of body.

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