

## PREY CAPTURE AND THE FAST-START PERFORMANCE OF NORTHERN PIKE *ESOX LUCIUS*

BY DAVID G. HARPER AND ROBERT W. BLAKE

*Department of Zoology, University of British Columbia, Vancouver, V6T 2A9,  
Canada*

*Accepted 11 July 1990*

### Summary

Fast-start performance of northern pike *Esox lucius* (mean length, 0.38 m) during prey capture was measured with subcutaneously implanted accelerometers. Acceleration–time plots and simultaneous high-speed ciné films reveal four behaviours with characteristic kinematics and mechanics. The fast-start types are identified by the number of large peaks that appear in the acceleration–time and velocity–time data.

Comparisons of mean performance were made between each type of feeding fast-start. Type I fast-starts were of significantly shorter duration (0.084 s) and displacement (0.132 m) than type III (0.148 s and 0.235 m) and type IV (0.189 s and 0.306 m) behaviours, and higher mean and maximum acceleration (38.6 and 130.3  $\text{m s}^{-2}$ , respectively) than type II (26.6 and 95.8  $\text{m s}^{-2}$ ), type III (22.0 and 91.2  $\text{m s}^{-2}$ ) and type IV (18.0 and 66.6  $\text{m s}^{-2}$ ) behaviours. The type II behaviours were of shorter duration (0.115 s) and displacement (0.173 m) and of higher mean acceleration than type IV fast-starts, and were also of significantly shorter duration than type III behaviours.

Prey-capture performance was compared to escapes by the same individuals. When data are combined, regardless of mechanical type, mean acceleration (37.6 vs 25.5  $\text{m s}^{-2}$ ), maximum acceleration (120.2 vs 95.9  $\text{m s}^{-2}$ ), mean velocity (1.90 vs 1.57  $\text{m s}^{-1}$ ) and maximum velocity (3.97 vs 3.09  $\text{m s}^{-1}$ ) were found to be larger and duration shorter (0.108 vs 0.133 s) during escapes than during prey capture. No differences were found through independent comparisons of the performance of feeding and escape types II and III, but type I escapes had significantly higher mean velocity (2.27 vs 1.58  $\text{m s}^{-1}$ ), maximum velocity (4.70 vs 3.12  $\text{m s}^{-1}$ ) and mean acceleration (54.7 vs 38.6  $\text{m s}^{-2}$ ) than type II feeding behaviours.

Prey-capture performance was also related to prey size, apparent prey size (defined as the angular size of the prey on the pike's retina) and strike distance (the distance from the pike to the prey at the onset of the fast-start). Mean and maximum acceleration increased with apparent size and decreased with strike distance, while the duration of the event increased with strike distance and decreased with apparent size. No relationship was found between the actual prey size and any performance parameter.

Strike distance ranged from 0.087 to 0.439 m and decreased as the apparent size

increased from 2.6 to 9.9° ( $r^2=0.75$ ). The type I behaviour was usually employed when the strike distance was small and the prey appeared large. As strike distance increased and apparent size decreased, there was a progressive selection of type II, then III and then IV behaviours.

### Introduction

Much attention has been focused on piscivorous predator-prey interactions. Studies have investigated the behavioural (e.g. Crossman, 1959; Ware, 1971; Nursall, 1973), kinematic (e.g. Webb, 1976; Webb and Skadsen, 1980; Vinyard, 1982) and energetic (e.g. Isaacs and Wick, 1973; Ware, 1975; Kerr, 1982; Harper and Blake, 1988) characteristics of these events. Others have focused on more specific feeding characteristics. Optimal prey size (Wankowski, 1979; Schmitt and Holbrook, 1984; Harper and Blake, 1988), its relationship to optimal foraging (Werner and Hall, 1974) and handling time (Werner, 1974), underlying sensory mechanisms (Ware, 1973; Vinyard and O'Brien, 1976; O'Brien *et al.* 1976; Morgan and Ritz, 1983) and prey response characteristics (Dill, 1973, 1974a,b; Webb, 1984) have all received considerable attention.

Few, however, have focused on the kinematics and mechanics of piscivorous feeding interactions. Studies correlating feeding and general locomotor behaviour (Webb, 1976, 1986; Webb and Skadsen, 1980; Rand and Lauder, 1981) and the specific behaviour, suction feeding (e.g. Lauder, 1979, 1980, 1983), have been conducted employing high-speed film to estimate performance. This is an effective method of analyzing the small-scale movements observed in suction feeding, but comprehensive, whole-body performance estimated from film is subject to considerable error, particularly where acceleration is concerned (Harper and Blake, 1989a,b).

This study combines accelerometry and high-speed ciné film in an investigation of the prey-capture performance of a piscivorous ambush predator, the northern pike *Esox lucius*. It is complementary to a previous study documenting the mechanics and kinematics of escapes of the same individuals (Harper and Blake, 1990).

### Materials and methods

The northern pike *Esox lucius* ( $N=4$ , mass= $0.396\pm 0.058$  kg, fork-length= $0.378\pm 0.019$  m; mean $\pm 2$  s.e.) were seined from Baptiste Lake in northern Alberta. Healthy adults were held for 6–12 months in 1000 l circular outdoor holding tanks (2 m in diameter) which were flushed continuously with fresh water at 15–20°C. Fast-start performance is independent of temperature over this range (Webb, 1978a). They were fed live goldfish thrice weekly until ready for use.

The experimental arena, made of glass and Plexiglas, measured 2.45 m $\times$ 1.22 m $\times$ 0.47 m, and was filled to a depth of approximately 0.30 m. A 0.02 m grid was placed on the bottom of the arena and fresh water, from the same

supply as for the outdoor holding tanks, was slowly circulated, except while filming. Fish were allowed 48 h to acclimate to the aquarium before experimentation and were not fed during that time.

#### *Measurement of acceleration*

Accelerations were measured directly with a Kistler 8616-A1000 low-impedance piezoelectric accelerometer (range  $\pm 1000$  g; frequency response 125 kHz; cylindrical dimensions  $0.0058 \times 0.0051$  m diameter; mass  $< 0.0005$  kg). Acceleration-time data were stored in the mainframe memory of a Nicolet 4094 digital oscilloscope, transferred to floppy disk, and later to a Commodore PC10-II. The accelerometer was calibrated in free-fall using a guillotine-like apparatus (Harper and Blake, 1990). Velocity and distance were derived from acceleration through integration with respect to time.

One source of error inherent with linearly directional accelerometers is that curved trajectories introduce tangential accelerations that are detected by the instrument. If significant, this artefact must be accounted for by subtraction from the accelerometer data. For a review of artefacts arising from accelerometry and a method for determining tangential acceleration, see Harper and Blake (1990).

Fish were quickly anaesthetized in  $0.002 \text{ kg l}^{-1}$  MS222 buffered with  $0.004 \text{ kg l}^{-1}$  sodium bicarbonate. Once anaesthetized, fish were transferred to a 'wet' table where a recirculating pump continuously flushed one-third strength anaesthetic over the gills. For a description of the anaesthetizing procedure, see Richardson (1985).

The accelerometer was implanted subcutaneously above the centre of mass, parallel to the centre-line of the fish, just lateral to the vertebral column. Centre of mass was assumed to be  $0.41 \times$  fork-length (measured from the nose to the middle of the caudal fin trailing edge, Webb, 1978*b*). The small mass of the accelerometer ( $< 0.2\%$  of fish mass for the smallest specimen) eliminated the need to reconsider the location of the centre of mass after implantation. The incision was never longer or deeper than about 1 cm, involved no tissue removal and no significant loss of blood. Once the accelerometer had been implanted, the incision was tightly closed using Ethicon V-5 tapercut cardiovascular sutures. The shape of the incision and the tight closure prevented the accelerometer from altering its orientation in the fish during experiments (Harper and Blake, 1990). The length and mass of individuals were recorded prior to their recovery from the anaesthetic.

Fish were then placed in a recovery tank where fresh water was flushed over the gills until normal opercular activity resumed. At this point the fish was re-introduced to the experimental arena and allowed to recover for 24 h. No deaths could be attributed to the incision or anaesthetization.

#### *Prey capture events*

Preliminary trials involved introducing one, then several, goldfish into the experimental arena. This method was rejected, primarily because the goldfish tended to huddle in the corners of the tank, which greatly limited the performance

of the pike. It was also evident that performance was not inhibited by the lights, but pike were sensitive to the presence of the investigators.

A blind was erected about 3 m in front of the tank and a system of pulleys and remote controls allowed manipulation of the camera and oscilloscope. The goldfish were maintained in the centre of the tank by a fine thread attached to their lower lip, which was affixed to an overhead lever. Ample slack in the thread allowed normal swimming behaviour near the centre of the tank. The tank was of sufficient size for the walls not to interfere with the event. The goldfish ranged in size (fork-length) from 0.024 to 0.053 m.

Early observations also indicated that pike initiate strikes following sudden movements of their prey. A gentle tug on the overhead lever (from behind the blind) elicited an escape response from the goldfish which, in turn, initiated the attack, thereby affording some control over the approximate start-time of the event.

### *Cinematography*

Forty-one feeding events were filmed with a 16 mm high-speed ciné camera (Locam model 51-0002) on Kodak 7250 400 ISO ciné film at 250 Hz. Fish were filmed as if from above by mounting a 2.45 m × 1.22 m mirror at 45° over the tank. Illumination was provided by two Berkey Beam 800 spot/flood lights mounted in front of the arena and shone into the mirror. Processed films were analyzed on an image analyzer (Photographic Analysis Limited Projection Analysis Unit, ZAE 76). The system includes a variable-speed projector, a ground-glass viewing/digitizing tablet and a digitizing computer. Images of the accelerating fish were directed onto the tablet and frame-by-frame tracings of the fish were made. The distance from the pike to its prey was determined from these tracings. Films were synchronized with accelerometer records by a light beacon, triggered by the oscilloscope, placed in front of the camera.

The field of view provided by the camera allowed only half of the tank to be filmed when maximizing the image size of the pike. Since the camera was in front of the blind, it was necessary to predetermine the view from a given orientation of the camera. This allowed the camera to be aligned to film the entire feeding event.

## **Results**

### *Predator-prey behaviour*

Pike remained stationary in the arena while the prey was secured to the overhead lever arm. The goldfish were distressed upon introduction to the tank, but this subsided after a few seconds. The distress attracted the attention of the pike, which would orient head-on towards the prey. Goldfish movements consisted of small darting motions; pike tracked the prey axially, powered by median and paired fins.

Feeding events usually followed cessation of prey activity. Pike often moved slowly towards the goldfish, maintaining a straight-stretched posture. Occasion-

ally, sudden erections of the median fins were observed independently from accelerative movements. Because median fins are erected prior to acceleration as part of the fast-start routine (Eaton *et al.* 1977; Webb, 1977), these actions may be strikes aborted at a very early stage. Goldfish did attempt escape in most cases. This consisted of C-starts similar to those observed by Weihs (1973), but was rarely successful; prey were usually engulfed before executing the propulsive stage of their escape.

#### *Kinematics and mechanics*

Films of feeding events show that *E. lucius* employs the preparatory, propulsive and variable stages described by Weihs (1973). Kinematics were similar to the S-shaped patterns described by Webb and Skadsen (1980) for the tiger musky, *Esox* sp.

Figs 1–4 show acceleration, velocity and distance travelled over the duration of the behaviour for types I–IV feeding fast-starts. Velocity and distance are obtained by numerical integration of the acceleration data (Harper and Blake, 1990). To compare with escape performance (Harper and Blake, 1990), it is assumed that the event terminates when the fish reaches its maximum velocity. For all but one of the behaviours, pike reach maximum velocity at or beyond the position of the prey. Insets are traces from simultaneous film records. Although these traces are to scale, they have been realigned on the 'grid', and as such they represent the orientation of the body of the fish with respect to its original position, not the actual distance travelled. These figures indicate that, as observed for escapes, there is a functional relationship between the mechanics of feeding fast-starts (strikes), revealed by the accelerometer, and the kinematics of these events, shown by film.

The strikes of *E. lucius* can be categorized into four different mechanical types, based on the number of large peaks apparent in the acceleration–time and velocity–time data. During type I strikes (Fig. 1), the fish bends into an S-shape and makes a change in directional orientation. Maximum acceleration occurs after the head is oriented in the direction of the prey. The acceleration–time plot for this behaviour is unimodal, rising to one significant peak, then declining. This behaviour was only exhibited when the prey was particularly close to the pike and positioned at an angle relative to its longitudinal axis.

Types II, III and IV strikes (Figs 2–4, respectively) involve no change in directional orientation; pike had manoeuvred head-on towards the prey. These three behaviours also differ from type I strikes in that the acceleration data tend to be more consistent and less 'noisy'. This is probably due to the directional stability. Types II–IV vary in the number of peaks apparent in the acceleration–time and velocity–time plots, which are the basis for the categories (i.e. type II, two peaks; type III, three peaks; type IV, four peaks). Kinematically, an S-shape is formed at the start of each behaviour. Differences arise from the number of half-cycles of the periodic tail motion. The frequency of this motion is relatively constant, ranging from about 11 to 12.5 Hz (durations of 0.08–0.09 s). The maximum acceleration is

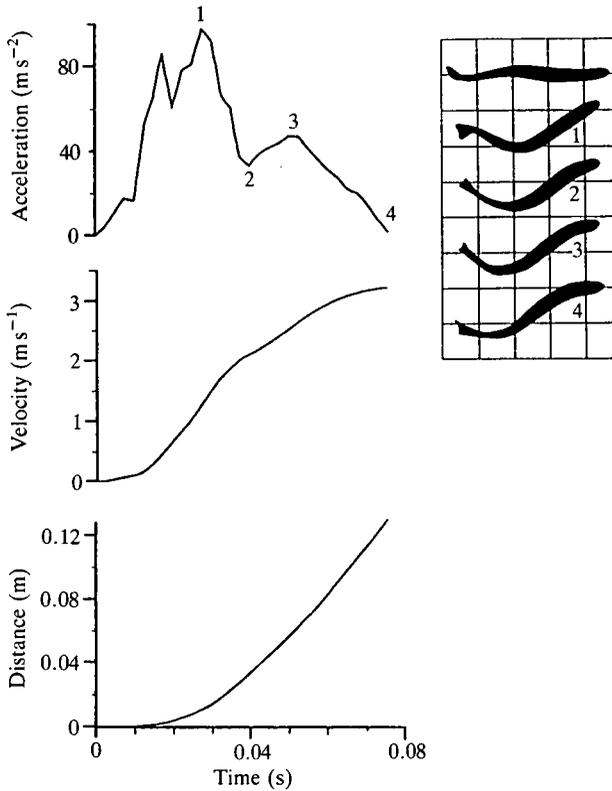


Fig. 1. Kinematic and mechanical data for a representative type I feeding fast-start of *Esox lucius* (mass=0.372 kg, fork-length=0.363 m), corrected for tangential acceleration (as are Figs 2–4). Acceleration, velocity and distance data are shown. Numbers on the tracings correspond to those on the acceleration plot: the grid scale is 10 cm.

characteristically found at the first peak of the type III behaviour, and at the last peak for both types II and IV.

Forty-one predator-prey interactions were analyzed. All fish exhibited all four behaviours (except for one pike which did not exhibit a type I behaviour) and the behaviours are considered characteristic of *E. lucius*. Type III behaviours were most common, occurring in 46 % of the events. Type II behaviours were exhibited in 29 % of the events. Types I and IV strikes were less common, occurring in 15 % and 10 % of the events, respectively.

The locomotor performance of *E. lucius* during feeding, measured by accelerometry, is presented in Table 1. Mean values for duration and displacement, and mean and maximum velocity and acceleration are given. Performance for each mechanical type is included, as well as a total, combining fast-start types. Data from fast-start escapes (Harper and Blake, 1990), exhibited by the same individuals, are also presented for comparison.

The duration of the events increased from 0.084 s for type I, to 0.115 s for type

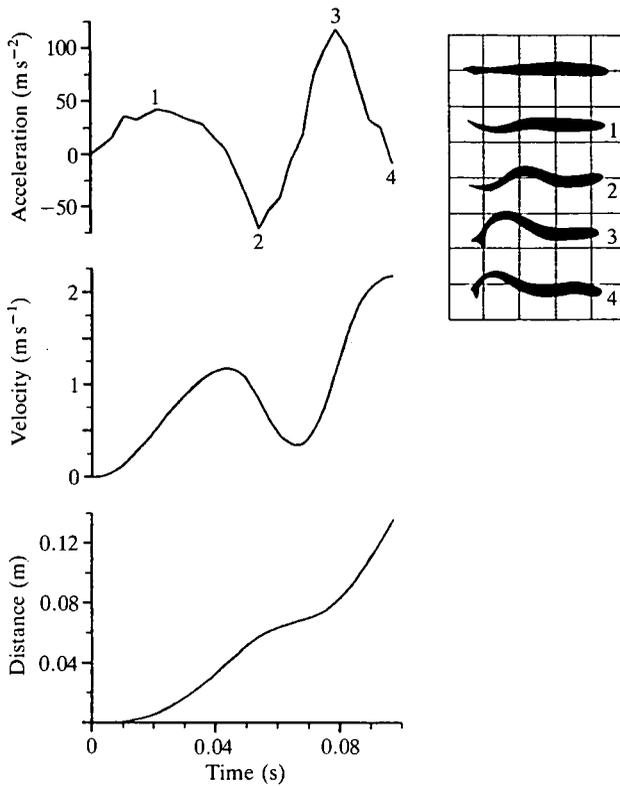


Fig. 2. Kinematic and mechanical data for a representative type II feeding fast-start of *Esox lucius* (mass=0.377 kg, fork-length=0.376 m).

II, 0.148 s for type III and 0.189 s for type IV. Displacement is greatest for type IV (0.306 m), and least for type I (0.132 m) strikes. Mean velocity varied only slightly, ranging from  $1.50 \text{ m s}^{-1}$  for type II to  $1.63 \text{ m s}^{-1}$  for type IV strikes. The type IV strikes also exhibited the highest values for mean maximum velocity ( $3.24 \text{ m s}^{-1}$ ) and lowest values for mean ( $18.0 \text{ m s}^{-2}$ ) and maximum ( $66.6 \text{ m s}^{-2}$ ) acceleration. The latter two variables are highest for the type I strikes ( $38.6$  and  $130.3 \text{ m s}^{-2}$ , respectively). The type II strike had the lowest mean maximum velocity ( $3.01 \text{ m s}^{-2}$ ).

Statistical analyses (Table 2) first employed the Student's *t*-test to identify differences between escape and feeding performance when fast-start types are totalled, regardless of mechanical type. This indicated that the escapes incorporated significantly higher mean velocity ( $1.90$  vs  $1.57 \text{ m s}^{-1}$ ;  $P < 0.001$ ), maximum velocity ( $3.97$  vs  $3.09 \text{ m s}^{-1}$ ;  $P < 0.001$ ), mean acceleration ( $37.6$  vs  $25.5 \text{ m s}^{-2}$ ;  $P < 0.001$ ) and maximum acceleration ( $120.2$  vs  $95.9 \text{ m s}^{-2}$ ;  $P < 0.01$ ) over a shorter duration ( $0.108$  vs  $0.133 \text{ s}$ ;  $P < 0.05$ ). One-way analysis of variance (ANOVA) of individual types of feeding and escape behaviours showed that the type I escapes were of significantly higher mean velocity ( $2.27$  vs  $1.58 \text{ m s}^{-1}$ ;  $P < 0.005$ ), maximum

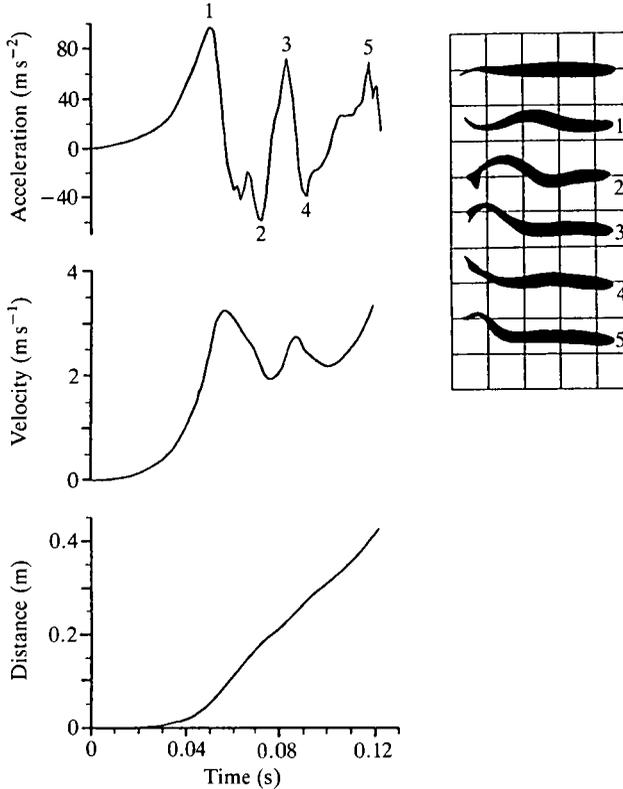


Fig. 3. Kinematic and mechanical data for a representative type III feeding fast-start of *Esox lucius* (mass=0.377 kg, fork-length=0.376 m).

velocity ( $4.70$  vs  $3.12$   $\text{m s}^{-1}$ ;  $P < 0.005$ ) and mean acceleration ( $54.7$  vs  $38.6$   $\text{m s}^{-2}$ ;  $P < 0.005$ ) than the type I feeding behaviours.

A second ANOVA was conducted on the feeding behaviours, indicating strong significant differences between means for duration, displacement and mean and maximum acceleration (Table 2). Tukey's test was then used to indicate where robust differences between means could be found, considering all possible comparisons.

Table 2 shows that the type I behaviour is of significantly higher mean ( $38.6$  vs  $26.6$   $\text{m s}^{-2}$ ;  $P < 0.001$ ) and maximum acceleration ( $130.3$  vs  $95.8$   $\text{m s}^{-2}$ ;  $P < 0.01$ ) than the type II behaviour, and of significantly higher mean and maximum acceleration and shorter duration and displacement than the type III and IV behaviours ( $P < 0.001$  for all comparisons; see Table 1 for values). The type II behaviour is of shorter duration than the type III ( $0.115$  vs  $0.148$  s;  $P < 0.025$ ), and has higher mean acceleration ( $26.6$  vs  $18.0$   $\text{m s}^{-2}$ ;  $P < 0.005$ ) and shorter duration ( $0.115$  vs  $0.189$  s;  $P < 0.005$ ) and displacement ( $0.173$  vs  $0.306$  m;  $P < 0.01$ ) than the type IV behaviour. There was no significant difference in mean or maximum velocity for any comparison.

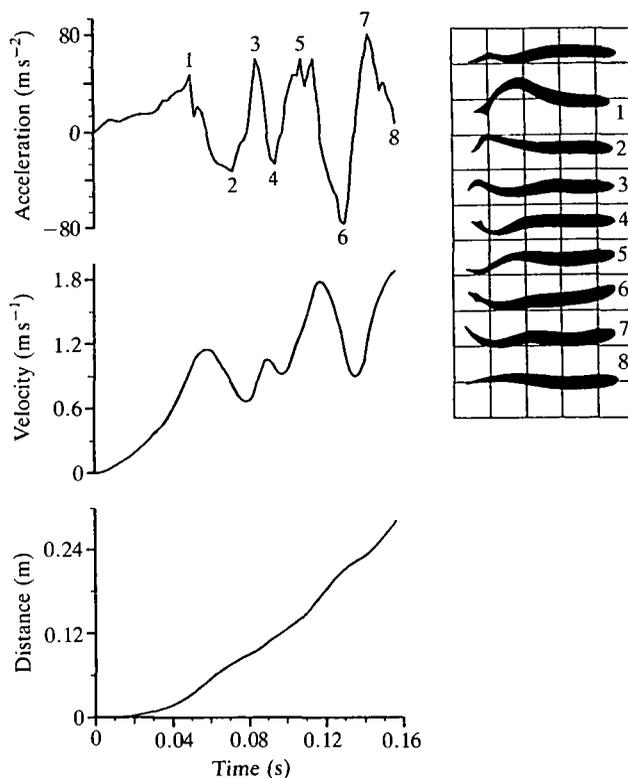


Fig. 4. Kinematic and mechanical data for a representative type IV feeding fast-start of *Esox lucius* (mass=0.372 kg, fork-length=0.363 m).

#### *Effect of prey size and strike distance on performance*

Measurements of prey size and the distance from predator to prey at the start of the feeding behaviour (strike distance) were related to mechanical types and performance. Prey size was a linear measurement (fork-length); strike distance was determined from film by measuring from the centre of a straight line bisecting the eyes of the pike to the centre of mass of the goldfish (assumed to be about one-third of the length measured from the nose, Weihs, 1972). The relationship between the two is presented in Fig. 5. The poor correlation ( $r^2=0.06$ ) indicates that these two variables act independently in the interaction. However, strike distance does seem to be related to the type of fast-start employed. Fig. 6 supports this; generally, as strike distance increases, pike progressively select type I, II, III and IV behaviour to travel this distance.

Fig. 7 demonstrates a relationship between feeding behaviour and performance. As prey distance increases, the mean and maximum accelerations decrease, and duration increases. Velocity is not related to prey distance. Similar relationships to performance are found as the behaviour changes from type I, to II, to III and then to IV.

Table 1. *Feeding performance of Esox lucius determined by accelerometry*

	N	Total time (s)	Distance (m)	Mean velocity (m s <sup>-1</sup> )	Mean maximum velocity (m s <sup>-1</sup> )	Mean acceleration rate (m s <sup>-2</sup> )	Mean maximum acceleration (m s <sup>-2</sup> )
Feeding							
Type I	6	0.084 (±0.016)	0.132 (±0.028)	1.58 (±0.31)	3.12 (±0.13)	38.6 (±6.5)	130.3 (±21.7)
Type II	12	0.115 (±0.017)	0.173 (±0.028)	1.50 (±0.12)	3.01 (±0.37)	26.6 (±1.9)	95.8 (±7.9)
Type III	19	0.148 (±0.021)	0.235 (±0.064)	1.60 (±0.09)	3.11 (±0.32)	22.0 (±2.3)	91.2 (±9.7)
Type IV	4	0.189 (±0.042)	0.306 (±0.100)	1.63 (±0.44)	3.24 (±1.05)	18.0 (±8.3)	66.6 (±6.2)
Total	41	0.133 (±0.010)	0.209 (±0.022)	1.57 (±0.11)	3.09 (0.29)	25.5 (±1.9)	95.9 (±7.8)
Escape							
Type I	7	0.085 (±0.005)	0.194 (±0.044)	2.27 (±0.28)	4.70 (±0.52)	54.7 (±7.0)	157.8 (±37.3)
Type II	11	0.110 (±0.013)	0.192 (±0.032)	1.76 (±0.18)	3.69 (±0.46)	33.2 (±5.0)	107.9 (±16.4)
Type III	7	0.132 (±0.013)	0.223 (±0.027)	1.72 (±0.31)	3.61 (±0.68)	25.1 (±6.6)	91.4 (±22.8)
Total	25	0.108 (±0.010)	0.201 (±0.020)	1.90 (±0.17)	3.97 (±0.36)	37.6 (±6.1)	120.2 (±20.0)

Values in brackets indicate error as ±2 s.e.

Totals combine data, regardless of mechanical type, for both feeding and escape (from Harper and Blake, 1990).

Total time is the elapsed time to  $V_{\max}$ .

Table 2. Statistics and feeding performance, and a comparison of feeding fast-starts with escapes, for *Esox lucius*

Comparison	Time (s)	Distance (m)	Mean velocity (ms <sup>-1</sup> )	Mean maximum velocity (ms <sup>-1</sup> )	Mean acceleration rate (ms <sup>-2</sup> )	Mean maximum acceleration (ms <sup>-2</sup> )	Distance to prey (m)	Apparent size of prey (degrees)
<b>Feeding</b>								
Type I vs II	NS	NS	NS	NS	$P < 0.001$	$P < 0.01$	NS	NS
Type I vs III	$P < 0.001$	$P < 0.001$	NS	NS	$P < 0.001$	$P < 0.001$	$P < 0.05$	$P < 0.025$
Type I vs IV	$P < 0.001$	$P < 0.001$	NS	NS	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.005$
Type II vs III	$P < 0.025$	NS	NS	NS	NS	NS	NS	NS
Type II vs IV	$P < 0.005$	$P < 0.01$	NS	NS	$P < 0.05$	NS	$P < 0.005$	$P < 0.01$
Type III vs IV	NS	NS	NS	NS	NS	NS	$P < 0.05$	NS
<b>Feeding vs escapes</b>								
Type I	NS	NS	$P < 0.005$	$P < 0.005$	$P < 0.005$	NS		
Type II	NS	NS	NS	NS	NS	NS		
Type III	NS	NS	NS	NS	NS	NS		
Total	$P < 0.05$	NS	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.01$		

Probabilities are indicated (NS denotes no significant difference); i.e.  $P > 0.05$ .

Where a difference is indicated, Table 1 identifies the larger value.

Total combines data, regardless of mechanical type.

Tukey's test is used except for total, where the Student's *t*-test was employed.

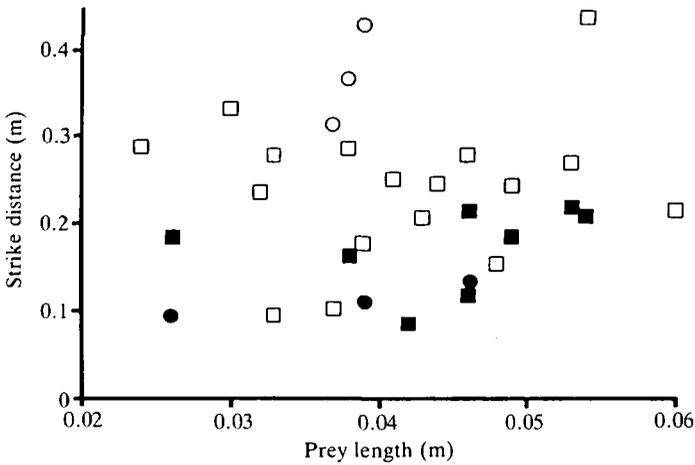


Fig. 5. Prey distance (m) upon initiation of the feeding fast-start (strike distance) related to prey length (m). No correlation was found ( $r^2=0.06$ ). Fast-start type is indicated for each event (type I, ●; type II, ■; type III, □; type IV, ○).

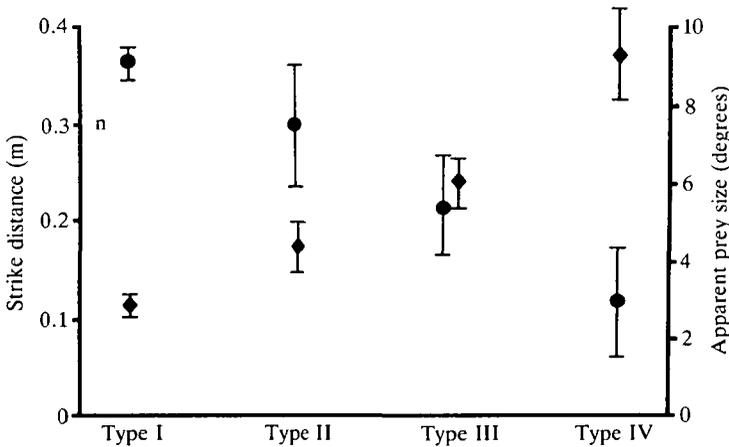


Fig. 6. Mean strike distance (◆) and apparent size (●) for the four feeding types. Errors are indicated as  $\pm 1$  s.e. ( $N=41$ ).

A significant relationship ( $r^2=0.75$ ) is found when strike distance is plotted against apparent prey size (Fig. 8). This variable differs from actual prey size in that it represents the angular size of the prey's image on the retina of the predator, in degrees (O'Brien *et al.* 1976). Previous studies indicate that fish are particularly sensitive to apparent prey size (Ware, 1973; Dill, 1974b; O'Brien *et al.* 1976). From Fig. 8 it is evident that mechanical fast-start type is related to apparent size. Fig. 6 demonstrates that, as apparent prey size decreases, pike progressively select type I, II, III and then IV behaviour. Statistical support for this relationship is found in Table 2.

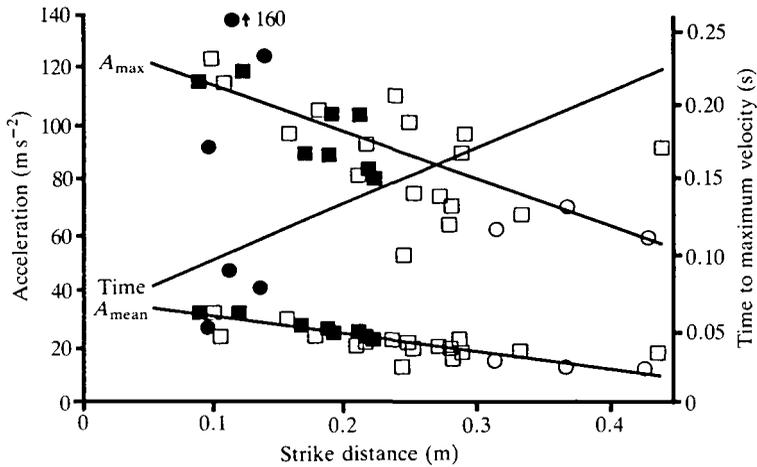


Fig. 7. Relationships of mean ( $A_{\text{mean}}$ ) and maximum ( $A_{\text{max}}$ ) acceleration and event duration (Time) to strike distance.  $r^2$ :  $A_{\text{mean}}=0.59$  ( $y=-64.1x+38.2$ ),  $A_{\text{max}}=0.45$  ( $y=-166x+130$ ) and  $\text{time}=0.50$  ( $y=0.38x+0.06$ ). For clarity, individual data points for event duration are not included. Fast-start type for each event are indicated (type I, ●; type II, ■; type III, □; type IV, ○).

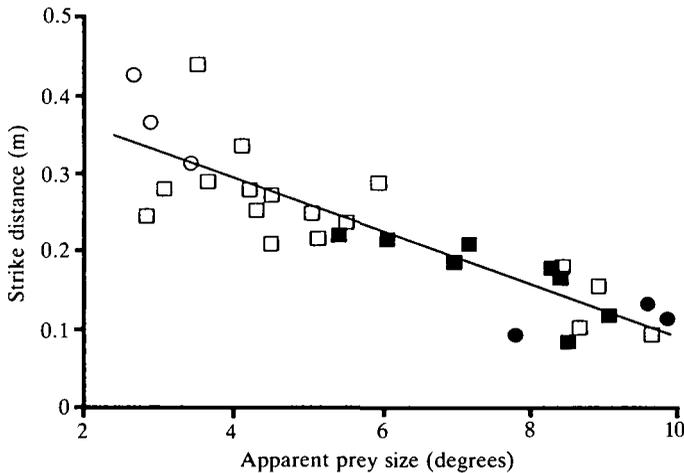


Fig. 8. Relationship of strike distance (m) to the apparent size (degrees) of the prey.  $r^2$  for the regression line is 0.75 ( $y=0.034x+4.30$ ). Fast-start types for each event are indicated (type I, ●; type II, ■; type III, □; type IV, ○).

Fig. 9 shows the relationship between performance, mechanical type and apparent size. As apparent size increases, mean and maximum acceleration increase, and duration decreases. Velocity is not related to apparent prey size. Similar relationships to performance are found as the mechanical type selected changes from IV, to III, to II and then to I.

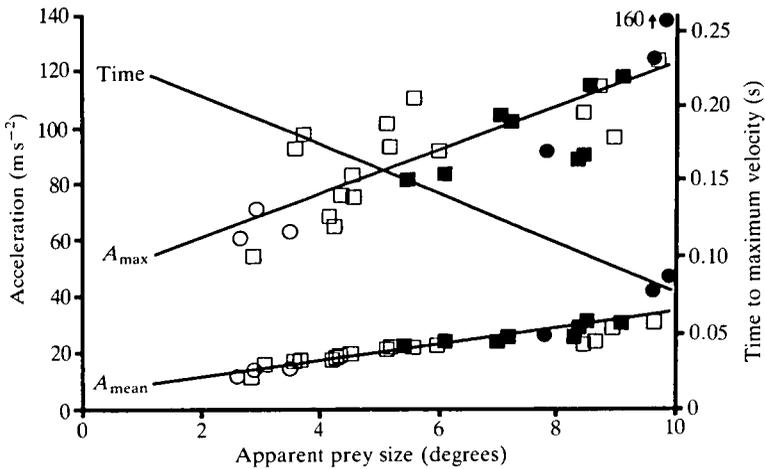


Fig. 9. Relationships of mean ( $A_{\text{mean}}$ ) and maximum ( $A_{\text{max}}$ ) acceleration and event duration (Time) to the apparent size of the prey.  $r^2$ :  $A_{\text{mean}}=0.79$  ( $y=2.92x+6.10$ ),  $A_{\text{max}}=0.65$  ( $y=7.81x+45.0$ ) and time=0.63 ( $y=-0.017x+0.240$ ). For clarity, individual data points for event duration are not included. Fast-start types for each event are indicated (type I, ●; type II, ■; type III, □; type IV, ○).

## Discussion

### *Sources of error*

The most significant source of error inherent in accelerometry is the tangential error arising from curved trajectories (Harper and Blake, 1990). Feeding fast-start types II–IV were not significantly affected by tangential error, owing to their directional stability. However, the type I behaviours did involve tangential accelerations, which significantly affected the predicted displacements. Therefore, corrections to these data were made, and Figs 1–4 were corrected following the procedure described by Harper and Blake (1990). Other possible sources of error, such as transient motion between the body of the fish and the accelerometer, and consideration of the orientation of the instrument relative to the centre of mass, were investigated and found to involve maximum errors of less than 5% (Harper and Blake, 1990).

### *Comparison to previous studies*

The feeding behaviours described here are the first categorizations based on mechanical data. Film-based studies have not presented acceleration–time data, as in Figs 1–4, making comparisons to previous work, based on mechanical criteria, impossible. Previous studies classify fast-starts by kinematic criteria, as C- or S-starts.

Mean maximum accelerations during strikes averaged  $95.9 \pm 7.8 \text{ m s}^{-2}$ , lower than values recorded for escapes ( $120.2 \pm 20.0 \text{ m s}^{-2}$ , Harper and Blake, 1990), but much higher than values previously reported from film-based studies ( $40 \text{ m s}^{-2} \pm 25\%$ , Webb, 1978b). Mean accelerations were of the order of those

found for chain pickerel, *Esox niger*, feeding fast-starts (Rand and Lauder, 1981) and tiger musky, *Esox* sp., escape fast-starts (Webb, 1986), and were significantly less than those for escape fast-starts of the same individuals (Tables 1 and 2). Mean durations were significantly longer than for escapes (Tables 1 and 2), but within the range of previous reports (see Harper and Blake, 1990, for a summary). The mean and maximum velocities were also found to be significantly lower during feeding than during escapes, but higher than values previously reported (Webb, 1978b). The reason for the disparity of mean maximum accelerations between this and other studies is probably the large degree of error inherent in evaluating accelerations from double-differentiated, film-generated distance–time data. Harper and Blake (1989a,b) show that, when determined from film, maximum accelerations incorporate errors of 35–100 %.

Types I and II feeding fast-starts were found to be kinematically different from escape types I and II, respectively. The difference arises from the directional stability inherent in the feeding behaviours. However, type III feeding and escape fast-starts were kinematically and mechanically similar. From Tables 1 and 2, it is evident that pike escapes are of shorter duration and of higher mean and maximum acceleration and velocity than feeding events. This is reasonable, since fish should maximize performance during escapes to avoid capture; failure to capture prey is not catastrophic. However, the overwhelming similarity of the kinematics and mechanics of the type III escapes and feeding strikes (the most common feeding behaviour) implies that the same neural pathways are being employed in both behaviours. For a review of the neural basis of behaviour see DiDomenico and Eaton (1988).

#### Strike performance

Performance during feeding fast-starts appears to maximize and maintain velocity to the point of contact with the prey. Because tail beats involve periodic accelerations and decelerations, mean acceleration declines during longer strikes (Table 1) and, because the distance travelled is related to the number of tail beats, the pike executes a given number of tail beats to attain its prey. This does not appear to be a predetermined behaviour for directionally stable strikes (Figs 2–4). Type I strikes cannot be directly compared in this manner because of the inherent directional change. In general, the pike executes one full-cycle tail beat, then continues to add half-cycle beats until the prey is captured. Therefore, it can be concluded that *E. lucius* maximizes performance, while maintaining directional stability, throughout the feeding fast-start.

Single-event, maximum performance data are reported in Table 3. As for mean performance, maximum performance is higher for pike escapes than for feeding strikes. In particular, the maximum acceleration during escapes ( $244.9 \text{ m s}^{-2}$ ) is considerably higher than during strikes ( $159.6 \text{ m s}^{-2}$ ). Maximum performance data are important because they demonstrate locomotor capability under extreme conditions. This is useful in assessing the energetic cost and efficiency of ambush predation. Harper and Blake (1988) have shown that the strike portion of a

Table 3. *Maximum performance for all types of feeding and escape (from Harper and Blake, 1990) exhibited by Esox lucius*

	Distance (m)	Maximum mean velocity (m s <sup>-1</sup> )	Maximum final velocity (m s <sup>-1</sup> )	Maximum mean acceleration (m s <sup>-2</sup> )	Maximum acceleration rate (m s <sup>-2</sup> )
Feeding					
Type I	0.158	2.17	3.35	47.7	159.6
Type II	0.221	1.96	3.80	31.6	118.6
Type III	0.311	2.13	4.61	31.6	136.0
Type IV	0.429	2.21	4.75	30.4	72.9
Escape					
Type I	0.213	2.50	7.06	80.3	244.9
Type II	0.289	2.26	4.70	47.4	141.2
Type III	0.227	2.14	4.50	35.5	130.5

piscivorous predator-prey interaction accounts for up to 80 % of the total energy expended by the predator.

#### *Effect of prey size and strike distance on behaviour*

Strike distance is not dependent on prey size (Fig. 5), but is related to its apparent size (Fig. 8). This relationship arises because apparent prey size is a function of the actual size of the prey and its distance from the predator (O'Brien *et al.* 1976). *E. lucius* interprets fish of apparently smaller size as being at a greater distance, and initiates strikes from further away. Types III and IV fast-starts are then employed to travel this distance. The opposite is true of apparently larger prey, where types I and II are commonly used (Fig. 6). This contradicts the previous suggestion that fast-start type is not predetermined. Figs 6 and 8 indicate that strike type is determined before the event is initiated, based on the apparent size of the prey. This suggests that pike disregard actual prey size, and use apparent size to determine strike distance and feeding behaviour. This would be appropriate if available prey were of similar size, which may be true in Baptiste Lake. 'Assuming' prey to be one size is an effective strategy for an ambush predator. If the prey turns out to be smaller than expected, it is still practical to capture it to compensate for the energy expended during the fast-start. If the prey is too large to consume, it will be too distant to capture.

Figs 7 and 9 demonstrate that acceleration performance is related to both strike distance and apparent size. Performance is maximal for small strike distance and large apparent size. This is directly related to the selection of feeding behaviour (Table 2), suggesting that, if pike predetermine strike type, they also predetermine acceleration performance.

Feeding performance of the northern pike *Esox lucius*, determined by accelerometry, is shown to be significantly lower than escape performance by the same

individuals when duration and mean and maximum acceleration and velocity are considered. Displacement values, however, are similar. Four mechanical types of feeding strikes are identified; they are predetermined for use, depending on the apparent size of the prey. The relationship between prey-capture performance and the apparent size of the prey could be further investigated by simultaneously offering an individual pike a selection of prey, varying in size and distance. This would complement the findings here, and also further our understanding of prey selection by an ambush predator.

We would like to thank the Natural Science and Engineering Council of Canada for financial support and Mr H. R. Frith for his assistance.

### References

- CROSSMAN, E. J. (1959). A predator-prey interaction in freshwater fish. *J. Fish. Res. Bd Can.* **16**, 269-281.
- DiDOMENICO, R. AND EATON, R. C. (1988). Seven principles for command and the neural causation of behaviour. *Brain Behav. Evol.* **31**, 125-140.
- DILL, L. M. (1973). An avoidance learning submodel for a general predation model. *Oecologia* **13**, 291-312.
- DILL, L. M. (1974a). The escape response of the zebra danio (*Brachydanio rerio*). I. The stimulus for escape. *Anim. Behav.* **22**, 711-722.
- DILL, L. M. (1974b). The escape response of the zebra danio (*Brachydanio rerio*). II. The effect of experience. *Anim. Behav.* **22**, 723-730.
- EATON, R. C., BOMBARDIERI, R. A. AND MEYER, D. L. (1977). The Mauthner-initiated startle response in teleost fish. *J. exp. Biol.* **66**, 65-81.
- HARPER, D. G. AND BLAKE, R. W. (1988). Energetics of piscivorous predator-prey interactions. *J. theor. Biol.* **134**, 59-76.
- HARPER, D. G. AND BLAKE, R. W. (1989a). A critical analysis of the use of high-speed film to determine maximum accelerations of fish. *J. exp. Biol.* **142**, 465-471.
- HARPER, D. G. AND BLAKE, R. W. (1989b). On the error involved in high-speed film when used to evaluate maximum accelerations of fish. *Can. J. Zool.* **67**, 1929-1936.
- HARPER, D. G. AND BLAKE, R. W. (1990). Fast-start performance of the rainbow trout *Salmo gairdneri* and northern pike *Esox lucius*. *J. exp. Biol.* **150**, 321-342.
- ISAACS, J. D. AND WICK, G. L. (1973). Optimized tactics for open-water marine predators. In *Marine Biological Association of India Special Publication dedicated to Dr N. K. Panikar*. Cochin, India: S. T. Reddiar and Sons. pp. 192-199.
- KERR, S. J. (1982). Estimating the energy budgets for actively predatory fishes. *Can. J. Fish. aquat. Sci.* **39**, 371-379.
- LAUDER, G. V. (1979). Feeding mechanics in primitive teleosts and in the halecomorph fish *Amia calva*. *J. Zool., Lond.* **187**, 543-578.
- LAUDER, G. V. (1980). Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. *J. Morph.* **163**, 283-317.
- LAUDER, G. V. (1983). Prey capture hydrodynamics in fishes: experimental tests of two models. *J. exp. Biol.* **104**, 1-13.
- MORGAN, W. L. AND RITZ, D. A. (1983). Sensory cues and mechanisms involved in the capture of euphausiids by the Australian salmon, *Arripis trutta*. *J. Fish Biol.* **23**, 489-493.
- NURSALL, J. R. (1973). Some behavioural interactions of spottail shiners (*Notropis hudsonius*), yellow perch (*Perca flavescens*), and northern pike (*Esox lucius*). *J. Fish. Res. Bd Can.* **30**, 1161-1178.
- O'BRIEN, W. J., SLADE, N. A. AND VINYARD, G. L. (1976). Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). *Ecology* **57**, 1304-1310.
- RAND, D. M. AND LAUDER, G. V. (1981). Prey capture in the chain pickerel, *Esox niger*: correlations between feeding and locomotor behaviour. *Can. J. Zool.* **59**, 1072-1078.

- RICHARDSON, S. C. (1985). Effects of sampling on blood parameters in the rainbow trout. *J. Fish Biol.* **26**, 725–732.
- SCHMITT, R. J. AND HOLBROOK, S. J. (1984). Gape-limitation, foraging tactics and prey selectivity of two microcarnivorous species of fish. *Oecologia* **63**, 6–12.
- VINYARD, G. L. (1982). Variable kinematics of Sacramento perch (*Archoplites interruptus*) capturing evasive and nonevasive prey. *Can. J. Fish. aquat. Sci.* **39**, 208–211.
- VINYARD, G. L. AND O'BRIEN, W. J. (1976). Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *J. Fish. Res. Bd Can.* **33**, 2845–2849.
- WANKOWSKI, J. W. J. (1979). Morphological limitations, prey size selectivity, and growth response of juvenile Atlantic salmon, *Salmo salar*. *J. Fish Biol.* **14**, 89–100.
- WARE, D. M. (1971). Predation by rainbow trout (*Salmo gairdneri*): the effect of experience. *J. Fish. Res. Bd Can.* **28**, 1847–1852.
- WARE, D. M. (1973). Risk of epibenthic prey to predation by rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Bd Can.* **30**, 787–797.
- WARE, D. M. (1975). Growth, metabolism, and optimal swimming speed of a pelagic fish. *J. Fish. Res. Bd Can.* **32**, 33–41.
- WEBB, P. W. (1976). The effect of size on the fast-start performance of rainbow trout *S. gairdneri*, and a consideration of piscivorous predator–prey interactions. *J. exp. Biol.* **65**, 157–177.
- WEBB, P. W. (1977). Effects of median-fin amputation on fast-start performance of rainbow trout (*S. gairdneri*). *J. exp. Biol.* **68**, 123–135.
- WEBB, P. W. (1978a). Temperature effects on acceleration of rainbow trout *S. gairdneri*. *J. Fish. Res. Bd Can.* **35**, 1417–1422.
- WEBB, P. W. (1978b). Fast-start performance and body form in seven species of teleost fish. *J. exp. Biol.* **74**, 211–226.
- WEBB, P. W. (1984). Chase response latencies of some teleostean piscivores. *Comp. Biochem. Physiol.* **A 97**, 45–48.
- WEBB, P. W. (1986). Effect of body form and response threshold on the vulnerability of four species of teleost prey attacked by largemouth bass (*Micropterus salmoides*). *Can. J. Fish. aquat. Sci.* **43**, 763–771.
- WEBB, P. W. AND SKADSEN, J. M. (1980). Strike tactics of *Esox*. *Can. J. Zool.* **58**, 1462–1469.
- WEIHS, D. (1972). A hydromechanical analysis of fish turning manoeuvres. *Proc. R. Soc. B* **182**, 59–72.
- WEIHS, D. (1973). The mechanism of rapid starting of slender fish. *Biorheology* **10**, 343–350.
- WERNER, E. E. (1974). The fish size, prey size, handling time relation in several sunfishes and some implications. *J. Fish. Res. Bd Can.* **31**, 1531–1536.
- WERNER, E. E. AND HALL, D. J. (1974). Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* **55**, 1042–1052.