THE MECHANICAL POWER OUTPUT AND HYDROMECHANICAL EFFICIENCY OF NORTHERN PIKE (*ESOX LUCIUS*) FAST-STARTS

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Summary

The mechanical power output and hydrodynamic efficiency of northern pike, *Esox lucius*, during acceleration from rest (fast-start) are calculated from hydrodynamic theory for two kinematic patterns, C-starts (used in escape) and S-starts (used in prey capture). The Weihs model is employed and modified to calculate the mechanical power produced by a fish during a fast-start. A term is included for the power required to accelerate body sections laterally. Lateral deceleration of fish body sections and their associated added mass are expressed as an active process requiring energy expenditure or as a passive process requiring no energy expenditure. In addition, two methods of calculating useful power (the power used to accelerate the virtual mass of the fish, i.e. fish body mass + longitudinal added mass, in the direction of motion), one derived from the Weihs model and the second by summing the changes in kinetic energy of the virtual mass of the fish during a fast-start, are compared and found to give similar estimates of useful power (not significantly different; differences average 22 %).

Comparisons of the kinematics and performance of C- and S-starts reveal that C-starts are consistently terminated after two tail flips (stages 1 and 2) whereas S-starts continue for 3–6 tail flips (stages 3–6). In addition, acceleration during C-starts is more rapid and velocities are higher (2.3–$2.8\,\mathrm{m\,s^{-1}}$) than during S-starts (0.8–$1.8\,\mathrm{m\,s^{-1}}$) over the first 100 ms. However, the peak velocities achieved during S-starts and C-starts are similar over the duration of a fast-start. The superior acceleration rates achieved during the initial stages of a C-start can be explained, in part, by the use of greater maximum angles of attack, higher lateral and perpendicular velocities and larger maximum forces by the caudal fin.

Hydrodynamic efficiencies for fast-starts range from 0.16 to 0.39, values that are lower than those observed during either burst-and-coast or steady swimming. Efficiencies are lower for S-starts than for C-starts during the first two tail beats. S-start efficiencies increase with each subsequent tail flip and the maximum efficiencies realised are similar to those achieved during C-starts.

Power output during C- and S-starts (449.0 and 394.9 $\mathrm{W\,kg^{-1}}$ muscle fibre, respectively) approaches the theoretical maximum for vertebrate striated muscle ($500\,\mathrm{W\,kg^{-1}}$). Also, the inferred muscle stress is close to the predicted optimum for maximum power output, at 30 % of the maximum isometric stress recorded for isolated fast muscle fibres. These measurements suggest that fast-start performance is near a physiological limit and is probably constrained by muscle function. The superior acceleration rates achieved by C-starts over S-starts are explained in part by differences in hydrodynamic efficiency, whereas power outputs are similar.

Key words: fast-start, efficiency, power, northern pike, *Esox lucius*.

Introduction

The body form of the northern pike is considered favourable for acceleration performance (Webb, 1978; Harper and Blake, 1990; Frith and Blake, 1991). The long and slender body allows for large-amplitude movements and large angles of attack of the posterior portion of the body, where most thrust is generated (Frith and Blake, 1991). In addition, the posterior placement of the dorsal and anal fins increases the surface area of the caudal region and contributes to thrust production (Webb, 1977; Weihs, 1973). The high percentage of body musculature and large proportion of white, anaerobically fuelled muscle also favour high power output, and thus thrust production, during short bursts of activity (Webb, 1978).

High-powered bursts of acceleration by fish from a resting or near-resting position are termed fast-starts. Two kinematic patterns are commonly observed; C-starts, used in escape from predators, and S-starts, used in prey capture. C-starts are employed by the majority of fish species for escape from attacks by predators. A common assumption about C-start behaviour is that fish swimming performance is maximal

during an escape response and that superior acceleration ability would increase the probability of escape. Fish with 'pike-like' morphological characteristics are therefore predicted to achieve higher maximum acceleration rates during escape than are fish of other morphological designs. Initial studies of C-start performance found acceleration rates to be highly variable within species, obscuring any differences that may occur between species (Webb, 1978). A more recent study clearly demonstrated the superior acceleration rates that can be achieved by northern pike during fast-starts compared with trout, a 'morphological generalist' (Harper and Blake, 1990).

Superior acceleration performance is also expected to improve the probability of prey capture by predatory fish. Northern pike have been observed in the laboratory to stalk fish prey to within one-third to half of their body length and to attack using a fast-start (Harper and Blake, 1990; Webb and Skadsen, 1980). Comparisons of pike or other *Esox* species with fish of a more 'generalist' morphology show that pike capture prey with higher success rates (Savino and Stein, 1989). Other fish with a 'pike-like' body form are often ambush predators, using fast-starts to capture prey (e.g. great barracuda *Sphyraena barracuda*, longnose gar *Lepisosteus osseus*, trumpet fish *Aulostomus maculatus*, Alaska blackfish *Dallia pectoralis*).

The performance and kinematics of the S-starts used for prey capture are different from those of the C-starts employed in escapes. The C-start involves the formation of a C body shape during the preparatory stage of the fast-start, typically followed by a return tail flip during the propulsive phase, although the angelfish *Pterophyllum eimekei* may coast during this phase (Domenici and Blake, 1991). The turning angle realised during a C-start ranges from 0 to 180° (Eaton and Emberley, 1991; Domenici and Blake, 1993). In contrast, the body forms an S shape during an S-start and the direction of motion is maintained. In addition, the average and maximum acceleration rates achieved by northern pike during C-starts are significantly greater than during S-starts (Harper and Blake, 1991).

Hydrodynamic theory predicts that pike-like fish with large caudal surface areas, high-amplitude tail movements and a caudal propulsor at a sharp angle of attack will produce high thrust and realise superior performance (Weihs, 1973). However, this prediction is based on the assumption that power output is maximal. Whilst achieving maximum performance would favour escape ability and prey capture success, other performance criteria (e.g. direction control during prey capture or eliciting large turning angles during escape) may be important, but may not be achievable, at maximum levels of performance. In order to test hypotheses on performance differences between species or between kinematic patterns within species, the assumption that power output is maximal must be tested. For example, the lower acceleration rates observed in S-starts during prey capture by northern pike in comparison with C-starts in response to a startle stimulus could be explained by motivational differences and consequent differences in total power output. Alternatively, power output

could be maximal for both behaviours, but hydrodynamic efficiency lower for S-starts. In order to test these alternatives, hydrodynamic efficiency and power output during fast-starts must be assessed. The high hydrodynamic efficiencies realised during steady swimming are not expected for fast-starts (Webb, 1977). The hydrodynamic efficiencies achieved during push-and-coast swimming are lower than those for steady swimming (McCutcheon, 1977), suggesting that unsteady swimming involves lower hydrodynamic efficiencies than steady swimming.

In the present study, mechanical power output and hydrodynamic efficiency are estimated for northern pike fast-starts during prey capture and escape behaviours. Estimates are derived from high-speed film records of swimming kinematics and a modified version of the Weihs (1973) hydrodynamic model for fish fast-starts. Hydrodynamic efficiency and power output estimates for C- and S-starts are used to explain swimming performance differences between these kinematic modes. In addition, power output estimates are compared with literature values from isolated muscle preparations, and the question of whether power output is maximal during fast-starts is addressed. Hydrodynamic efficiency estimates for pike fast-starts are compared with those from other steady and unsteady swimming modes.

Materials and methods

Northern pike, *Esox lucius* (Linnaeus), were collected by beach seine in Babtiste Lake, Alberta, and transported to Vancouver by air. Fish were held in 10001 circular tanks supplied with filtered, dechlorinated water at a rate of $5–101\,\text{min}^{-1}$ in an outdoor, covered holding facility at the University of British Columbia. Water temperature was maintained at 8–12 °C. Following a 2 week acclimation period, all pike fed actively on goldfish and appeared healthy. Each pike was fed 4–8 g of goldfish, twice weekly. Fish were maintained in the holding facility prior to laboratory testing. Six pike were used for filming, ranging in mass from 0.397 to 0.430 kg and in fork length from 0.396 to 0.412 m.

Experimental procedure

Six northern pike were tested and approximately ten fast-starts were recorded for each fish. Individual pike were brought into the laboratory and placed in a $1.22\,\text{m} \times 2.45\,\text{m} \times 0.47\,\text{m}$ experimental arena supplied with dechlorinated, filtered tapwater at a rate of $2–31\,\text{min}^{-1}$. Water temperature in the laboratory was within 1 °C of that of the holding tank. A 2 cm square reference grid was placed on the bottom of the tank and was used to calibrate distance measurements on film records. The arena was equipped with an overhead mirror running the length of the tank and angled at 45 °. The mirror position allowed an overhead view of the entire tank through the eyes of an observer or the lens of a camera.

Fast-starts were filmed at 200 or 250 Hz with a 16 mm high-speed cine camera (LOCAM model 51-0002) using Kodak 7250 film. The tank was illuminated with two Berkey 800 W

beams placed 0.5 m from the tank and directed to reflect light through the mirror. Pike were induced to C-start by the rapid introduction of a metre stick within 0.3 m of the fish's head. S-starts were induced by introducing a goldfish prey after 72 h without food. The lights and camera were switched on 1–2 s before the fast-start event to allow time for fish to adjust to the lighting conditions and for the film rate to stabilise.

Film records were analysed on an electronic digitizer (Photographic Analysis Limited Projection Analysis Unit, ZAE 76). The positions of ten reference points located along the dorsal mid-line of the body were recorded for each frame
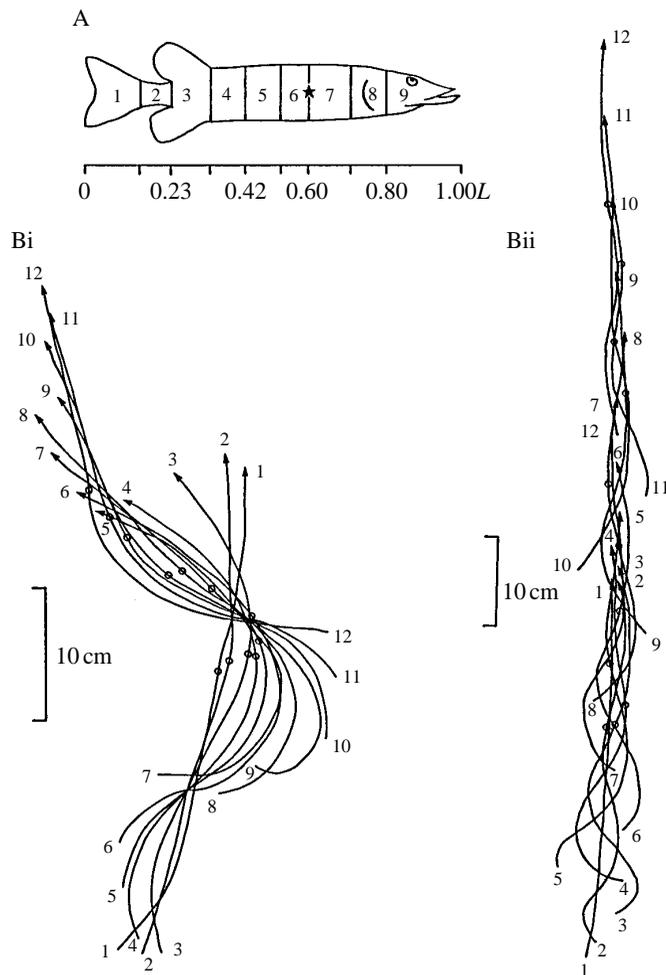

Fig. 1. (A) The positioning of nine divisions along the body of each fish, at similar intervals, used for displacement measurements. *L* refers to body length. The star marks the centre of mass of the fish. (B) Kinematics of fast-starts. Each line defines the backbone of the fish on which the head (identified by the arrowheads) and the centre of mass of the stretched-straight fish (circles) are marked. (Bi) C-start where numbers identify the position of the fish at 0.012 s intervals. There are two stages shown in this C-start; stage 1 occurs from positions 1 to 7 and stage 2 from positions 7 to 12. (Bii) S-start kinematics at 0.015 s intervals. There are six stages displayed during this S-start; stage 1 occurs from positions 1 to 3, stage 2 from positions 3 to 5, stage 3 from positions 5 to 6, stage 4 from positions 6 to 8, stage 5 from positions 8 to 9, and stage 6 from positions 9 to 10. No acceleration occurs after position 10.

of a fast-start event (Fig. 1A). The coordinates of each body position for each film frame were recorded on an IBM AT computer in LOTUS 123. The *x*- and *y*-axes were initially defined by the orientation of the reference grid on each film sequence. The axes were later rotated such that the *x*-axis defined the direction of motion of the centre of mass of the fish. Digitizing error was minimised by ensuring that the fish length represented approximately one-third of the film frame diagonal and by maximizing the size of the image on the digitizer screen (Harper and Blake, 1989*a*).

Analysis

Hydrodynamic efficiency (η) is defined as:

$$\eta = P_u/P_t \tag{1}$$

where P_u is useful power and P_t is total power. The term P_u refers to the power required to accelerate the virtual mass of the fish (body mass + longitudinal added mass) in the direction of motion, and P_t refers to the power required to accelerate the water influenced by a swimming pike plus the power required to accelerate the virtual mass of the fish both in the direction of motion and perpendicular to the direction of motion. Useful power P_u can be calculated as:

$$P_u = F_u U, \tag{2}$$

where F_u is the propulsive force produced by the fins and body in the direction of motion and U is the velocity of the centre of mass of the fish. The Weihs (1973) model is applied to calculate the propulsive forces produced by the fins and body of a fish during a fast-start, where:

$$F_u = \frac{dy}{dt} \int_0^L m_a w \left(\frac{\partial y}{\partial l} \right) dl + \frac{1}{2} \sum_{i=1}^k \rho S_i V_i^2 C_{Li} \phi \cdot \tag{3}$$

The term m_a is the added mass affected by a longitudinal section of the body of length d*l* where motion is perpendicular to the backbone. Added mass is calculated as:

$$m_a = \frac{1}{4} \pi \rho d^2 \beta, \tag{4}$$

where *d* is the depth of section and β is an added mass coefficient and is assumed to be 1 for all pike body sections (Lighthill, 1970). The term *w* in equation 3 is the velocity of each fish section perpendicular to the backbone and $\partial y/\partial l$ is the cosine of the angle between the backbone and the velocity vector of the centre of mass of the fish. The other terms are the length of the fish *L*, the length of a longitudinal section d*l*, the water density ρ, the number of sharp-edged surfaces (i.e. median fins) *k*, the surface area of fin *i* S_i, the velocity of the fin V_i, the coefficient of lift C_{Li}, and the angle of attack of a fin relative to its direction of motion ϕ. Further details of equation 3 can be found in Weihs (1973) and Frith and Blake (1991).

Useful power P_u can also be calculated as the product of the inertial forces F_i and the velocity of the centre of mass of the

fish U. For fish fast-starts, inertial forces are dominated by the acceleration reaction, such that:

$$F_i = (m + m_l)a,\qquad(5)$$

where m is the mass of the fish, m_l is the longitudinal added mass and a is the acceleration of the centre of mass of the fish. The longitudinal added mass refers to the mass of water carried forward by a fish during locomotion. An experimentally derived value of $0.2m$ from Webb (1982) is used for m_l.

Weihs (1973) proposed that total power for fish fast-starts could be described by Lighthill's large-amplitude theory (Lighthill, 1971), given by:

$$P_t = P_u + \frac{1}{2} m_a w^2 U/_{a=0} + \frac{d}{dt} \int_0^L \frac{1}{2} m_a w^2 dl,\qquad(6)$$

where U is the forward velocity of the fish. The other parameters are as described for equation 3. The first term on the right-hand side of equation 6 describes the power required to accelerate the fish (i.e. useful power), the second term describes the kinetic energy lost in the wake and the third term describes the power required to accelerate the added mass of water by all propulsive sections. Equation 6 accounts for the energy required to accelerate the fish in the direction of motion (described by the displacement vector of the centre of mass of the fish), but does not account for the power required to accelerate fish body sections laterally. The latter is defined by:

$$\frac{d}{dt} \int_0^L \frac{1}{2} m_s \frac{\partial y^2}{\partial t} dl,\qquad(7)$$

where m_s is the sectional body mass of the fish of length dl. Equation 7 may be added to equation 6 to obtain:

$$P_t = P_u + \frac{1}{2} m_a w^2 U/_{a=0} + \frac{d}{dt} \int_0^L \frac{1}{2} m_a w^2 dl +$$
$$\frac{d}{dt} \int_0^L \frac{1}{2} m_s \frac{\partial y^2}{\partial t} dl.\qquad(8)$$

The last two terms on the right-hand side of equation 8 give the power required to accelerate the added mass and body mass of propulsive sections. When these terms are positive, the values reflect positive work done by the fish. In order to accomplish work, energy must be expended. Negative values imply a loss of kinetic energy (i.e. deceleration of body and added mass), but may not reflect negative work done by the fish. Negative work or energy gain occurs when energy is stored elastically. Although there is some clear evidence for elastic energy storage in the intervertebral joints of fish backbone during cyclical, low-amplitude motion (Hebrank *et al.* 1990; Long, 1992), studies on isolated muscles in other animals suggest that elastic energy storage is substantially

reduced and most energy is dissipated during the high contraction speeds and high fibre stretch typical of escape manoeuvres (Tidball and Daniel, 1986; Johnston, 1991). Assuming that elastic energy storage is zero for a fast-start, the lateral deceleration of body sections requires either positive work by the fish or no work. The latter is true if we assume that lateral deceleration occurs as a result of passive resistance by the surrounding water and resistive forces within the fish. Positive work is required if energy must be expended to decelerate fish sections. Both active and passive deceleration are considered here, where active deceleration is calculated by taking the absolute value of the third and fourth terms of equation 8 and passive deceleration by summing only the positive values for these terms.

Hydrodynamic efficiency can be calculated from equation 1, where P_u can be calculated as $F_u U$ or as $F_i U$. Note that when F_u is used, the numerator and the first term in the denominator of equation 8 are the same and therefore errors in P_u cancel. The use of F_i to calculate P_u results in errors in the numerator that are independent of the denominator and therefore do not cancel but, owing to the inclusion of only one term requiring displacement measurements for only one position on the fish (centre of mass), error accumulation will be less than for the more complex equation for F_u. A comparison of forces derived from equations for F_i and F_u found estimates to be within 22 % (Frith and Blake, 1991).

Results

Three C-starts and three S-starts, each in a different fish, in which no interference occurred with the tank walls were chosen for analysis [i.e. fish were greater than 1 body length (*BL*) away from tank walls]. Pike consistently responded to a startle stimulus with a C-start and attacked prey with an S-start (Fig. 1B). A typical C-start involves the formation of a C body shape from a stretched straight position in stage 1 (preparatory stage), followed by a rapid tail flip to form a reverse C at the end of stage 2 (propulsive stage). A third stage generally involves braking or coasting (Fig. 1Bi). In contrast, S-starts involve the formation of an S shape at the end of stage 1 (preparatory stage) (Fig. 1Bii). Swimming continues until prey capture and involves 1–4 additional tail flips. Fast-starts have previously been described in three stages, where the third stage involves coasting or continued swimming (Weihs, 1973; Webb and Skadsen, 1980). For most S-starts, pike continue to accelerate beyond stage 2 and thus, for clarity, each subsequent tail flip (half a tail beat) is given a stage number here. Pike never continued swimming beyond the initial position of the prey, which required 1.5–3 tail beats (3–6 tail flips) for the three S-starts analyzed.

Maximum velocities ($2.3–2.8\,\mathrm{m\,s^{-1}}$) and times to maximum velocity ($0.08–0.13\,\mathrm{s}$) were similar for all three C-starts (Table 1). By comparison, S-start performance was more variable; maximum velocities ranged from 1.7 to $3.4\,\mathrm{m\,s^{-1}}$ and times to maximum velocity from 0.08 to 0.19 s. C-starts showed a more rapid initial acceleration rate than S-starts but,

Table 1. *Maximum velocities and time to maximum velocities for three C-starts and three S-starts, each in a different fish, in the northern pike* Esox lucius

	Maximum velocity ($m\,s^{-1}$)	Time to maximum velocity (s)
C-start 1	2.8	0.08
C-start 2	2.3	0.12
C-start 3	2.8	0.13
S-start 1	1.9	0.08
S-start 2	1.7	0.19
S-start 3	3.4	0.16

unlike S-starts, did not continue to accelerate after the end of stage 2 (Fig. 2A). Consequently, one S-start (S-start 3 in Fig. 2B) achieved a higher maximum velocity than all C-starts despite a lower acceleration rate.

The highest maximum lateral velocities ($\partial y/\partial t$) and perpendicular velocities (w) of the caudal fin within a fast-start were greater, on average, for C-starts than for S-starts (by 74 and 77 % respectively; Table 2). Both C- and S-starts showed a consistent increase in lateral and perpendicular velocities from stages 1 to 2, with the exception of lateral velocities for S-start 2. The greatest maximum angle of attack (the angle of a fish section relative to the velocity vector of the centre of mass of the fish) for the caudal fin, within a fast-start, was 126 % greater for C-starts than for S-starts. The largest maximum angles occurred in stage 2 for C-starts and stage 3
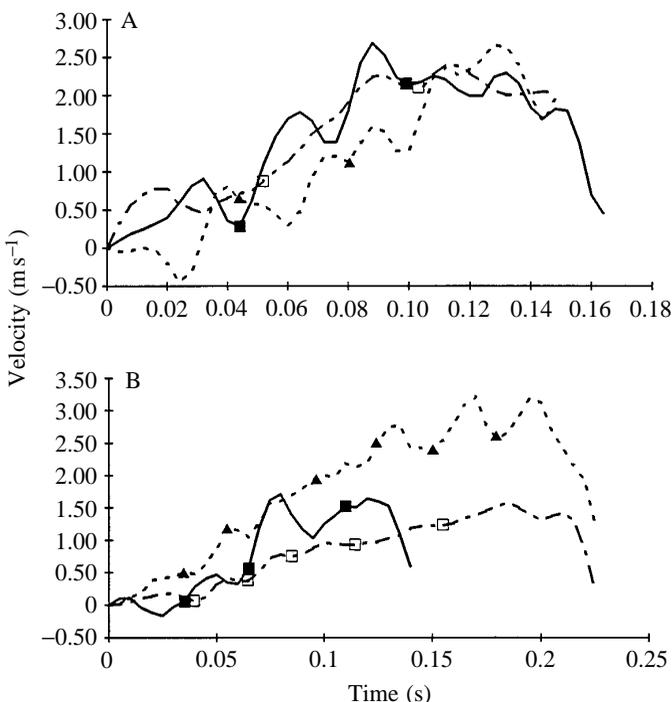

Fig. 2. Velocity profiles of Northern pike for (A) three C-starts (filled squares, C-start 1; open squares, C-start 2; filled triangles, C-start 3 and (B) three S-starts (filled squares, S-start 1; open squares, S-start 2; filled triangles, S-start 3). Symbols mark the end of each subsequent stage.

for S-starts (Table 2). Maximum forces in the direction of motion were 2.8–8.7 times greater in stage 2 than stage 1 for C-starts, averaging 17.6 N in stage 1 and 71.5 N in stage 2. For S-starts, maximum forces in the direction of motion in stage 2 were 0.94–17.1 times the same forces in stage 1, averaging 16.1 N in stage 1 and 45.8 N in stage 2. Forces in the direction of motion between C- and S-starts were not significantly different in stage 1 but were significantly different in stage 2 (averaging 45.8 N for S-starts compared with 71.5 N for C-starts; $P<0.01$, *t*-test). However, the greatest maximum force for an S-start (112.8 N in stage 3 of S-start 3) exceeded that for a C-start (88.6 N in stage 2 of C-start 3) by 27 %.

A comparison of useful power estimates (i.e. power used to accelerate the fish), where useful force is calculated from either equation 3 or equation 5 (Table 3), showed no significant difference (paired *t*-test, $P>0.05$). However, differences between these two useful power estimates, where percentage difference was calculated as $100\% \times absolute\ value\ (X_2-X_1)/0.5(X_2+X_1)$ and where X_1 is propulsive power and X_2 is required power, ranged from 14 to 31 % for the six fast-starts analyzed (Table 3).

Absolute power output values (assuming that deceleration during lateral body movements required positive work by the fish) were 33–57 % (mean 42 %) greater than positive power values, where the process was assumed to be passive and required no work (Table 4). This increase in total power decreased hydrodynamic efficiency, the ratio of useful power to total power (equation 1), by 19–26 % (mean 22 %; Table 5). Because the amount of positive work required for deceleration is unknown, the more conservative power and efficiency estimates, based on the assumption that deceleration is passive, are used below for comparison.

Total power output P_t for a fast-start ranged from 12.6 to 92.3 W and total hydrodynamic efficiency varied from 0.16 to 0.39 (Table 6). A comparison of C- and S-starts showed no consistent difference in total power or efficiency. However, total hydrodynamic efficiency and total power output were less variable for C-starts than for S-starts; total hydrodynamic efficiency ranged from 0.34 to 0.39 for C-starts and from 0.16 to 0.37 for S-starts, while total power output ranged from 45.6 to 81.2 W for C-starts *versus* 12.6 to 92.3 W for S-starts (Table 6). Therefore, both efficiency and total power output can be much lower for S-starts than for C-starts. There was also an increase in power output from stage 1 to stage 2 for all fast-starts except S-start 2 (Table 6). For S-starts, power output remained at a similar level after stage 2.

The greater variation in hydrodynamic efficiency found for S-starts was related to the number of tail beats. Fig. 3 shows that efficiency increased with the number of stages. S-starts had lower efficiencies (0.02–0.19) than C-starts (0.24–0.44) during stages 1 and 2 (Table 6). Efficiencies for S-starts in stages 3–6 ranged from 0.24 to 0.66 and were greater than in the first two stages. However, some of this variation can be explained by differences between S-starts. For example, the hydrodynamic efficiency for S-start 2 is larger than that for S-start 3 during stages 3–5, where the differences averaged 56 %.

Table 2. *Maximum velocities, maximum angles and maximum forces for the dominant propulsive element, the caudal fin*

	Stage	Maximum velocity (m s^{-1})		Maximum angle of attack (degrees)	Maximum force (N)
		$\partial y/\partial t$	w		
C-start 1	1	3.44	1.77	116.3	18.7
	2	3.89*	2.87*	142.8*	59.7*
C-start 2	1	3.84	2.38	116.1	24.0
	2	5.92*	4.66*	166.7*	66.2*
C-start 3	1	3.38	1.24	117.9	10.2
	2	6.25*	4.41*	165.8*	88.6*
C-start	Mean 1	3.55	1.80	116.8	17.6
	Mean 2	5.35	3.98	158.4	71.5
	Mean HMV	5.35	3.98	158.4	71.5
S-start 1	1	1.15	0.75	24.6	2.9
	2	3.56*	1.60	37.1	49.5*
	3	2.73	2.12*	52.6*	44.0
S-start 2	1	1.48	1.00	22.4	31.1
	2	1.37	1.47*	34.5	29.1
	3	1.77*	1.19	83.9*	53.8*
	4	1.36	1.07	40.4	22.9
	5	1.76	1.00	59.2	21.1
S-start 3	1	2.14	1.86	36.9	14.3
	2	2.76	3.17*	32.0	58.9
	3	3.38	2.59	73.7*	112.8*
	4	3.14	2.26	36.6	39.9
	5	3.89*	2.49	43.2	56.5
	6	2.73	1.69	30.5	27.2
S-start	Mean 1	1.59	1.20	28.0	16.1
	Mean 2	2.56	2.08	34.5	45.8
	Mean HMV	3.07	2.25	70.1	72.0

The lateral velocity, $\partial y/\partial t$, refers to the velocity of the caudal fin lateral to the direction of motion of the fish and perpendicular velocity w refers to the velocity of the caudal fin perpendicular to the long axis of the fin.

* indicates the highest value for that fast-start.

HMV refers to highest maximum value.

Total power can be broken down into component parts as described in equation 8 (Fig. 4). The power required to accelerate the fish (useful power) averaged over all fast-starts was 30 % of total power, which was similar to the power required to accelerate the added mass of the propulsors (39 %; Fig. 4). Acceleration of body mass contributed a smaller, but consistent, amount to total power (16 %), whereas the loss of kinetic energy in the wake was more variable (15 %, ranging from 2 to 39 %). Greater variability in the percentage contribution of power terms occurred among S-starts than among C-starts. The greatest difference was the 39 % loss of kinetic energy in S-start 1 compared with a 2 % loss in S-start 2.

Discussion

Analysis of model predictions

A comparison of useful power estimates in this study, in which the forces for acceleration were determined from the propulsive model of Weihs (1973) and compared with estimates from equation 5 for the forces required to accelerate the virtual mass of the fish, show no consistent difference and are within 14–31 % for C- and S-starts. Similar differences were found between model estimates and direct measurements for average and maximum acceleration rates for a single trout C-start (Weihs, 1973). Differences between the two methods are expected, given the greater number of terms in equation 3 compared with equation 5 and the resulting potential for error

Table 3. *A comparison of useful power estimates in W for C- and S-starts*

| | Useful power | | |
	Propulsive power* (W)	Required power† (W)	Difference %
C-start 1	16.9	20.1	17
C-start 2	17.9	13.4	28
C-start 3	32.0	40.1	23
S-start 1	2.0	2.3	14
S-start 2	5.6	4.1	31
S-start 3	24.8	20.5	19

*Propulsive power = $F_u \times U$ (equation 3).
†Required power = $F_i \times U$ (equation 5).

Table 5. *A comparison of hydrodynamic efficiency estimates where total power is positive power only or the absolute value of power (see Table 4)*

	Hydrodynamic efficiency using positive power	Hydrodynamic efficiency using absolute power	Difference (%)
C-start 1	0.37	0.29	22
C-start 2	0.34	0.25	26
C-start 3	0.39	0.31	21
S-start 1	0.16	0.13	19
S-start 2	0.37	0.30	19
S-start 3	0.27	0.21	22

Useful power is calculated using propulsive force estimates from the Weihs model (equations 2 and 3).

accumulation. The lack of a consistent difference between the two methods of calculating useful power for three C-starts or three S-starts suggests that the use of the Weihs (1973) model with the summation of terms over nine propulsive elements plus a double integration does not result in additional error accumulation at a filming speed of 200 or 250 Hz, compared with the simpler model, and adequately describes the forces required to propel a fish during a fast-start. The observed differences may, in part, be explained by unrealistic assumptions of the propulsive model. For example, the model used here assumes that propulsive elements are rigid during fast-starts when, in fact, they are flexible.

Errors in film analysis are also important. According to Harper and Blake (1989a,b), the conditions in our experimental system at 200 and 250 Hz would result in a 30 % underestimation of maximum acceleration rates. We argue in Frith and Blake (1991) that analytical errors influence propulsive and inertial forces differently and thus contribute to discrepancies in estimates of force, work and power output. As

efficiency estimates are based on a ratio, where the numerator and denominator are derived from the same theory, errors would cancel for common terms and the effect of analytical error on the resultant estimates would be reduced. Total power estimates, however, are directly affected by analytical error and would therefore be underestimated.

Table 6. *Total power (P_t) in W and hydrodynamic efficiency for each stage and the total for three C- and three S-starts*

	Stage	Efficiency, P_U/P_t	Power, P_t (W)
C-start 1	1	0.24	32.0
	2	0.44	60.1
	Total	0.37	45.6
C-start 2	1	0.32	62.3
	2	0.36	84.5
	Total	0.34	73.1
C-start 3	1	0.25	39.8
	2	0.44	118.0
	Total	0.39	81.2
S-start 1	1	0.09	3.9
	2	0.19	11.0
	3	0.26	21.1
	Total	0.16	12.6
S-start 2	1	0.10	13.1
	2	0.02	12.9
	3	0.58	13.5
	4	0.48	11.8
	5	0.66	14.1
	Total	0.37	15.2
S-start 3	1	0.06	36.6
	2	0.12	112.0
	3	0.36	97.7
	4	0.24	106.7
	5	0.28	95.2
	6	0.41	74.4
	Total	0.27	92.3

Table 4. *A comparison of total power output estimates in W based on positive power only or absolute power*

	Positive power (W)	Absolute power (W)	Difference (%)
C-start 1	45.6	66.5	46
C-start 2	73.1	115.0	57
C-start 3	81.2	114.9	42
S-start 1	12.6	16.8	33
S-start 2	15.2	21.0	38
S-start 3	92.3	127.1	38

Positive power refers to the summation of total power where only positive values are included for the two integral terms in equation 8.

To calculate the absolute power, the absolute value of the two integral terms in equation 8 are taken.
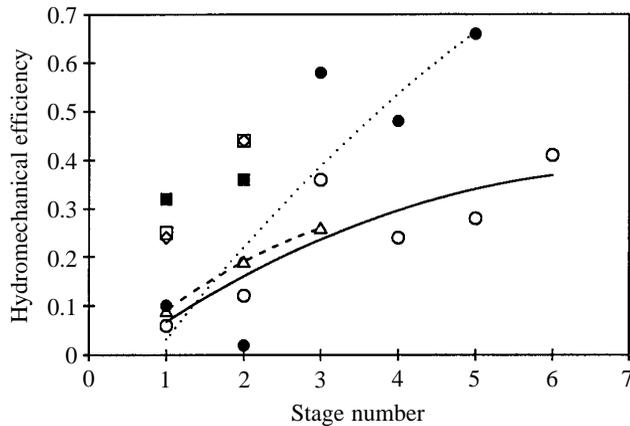
Fig. 3. The relationship between hydromechanical efficiency and fast-start kinematics for pike C-starts (open diamonds, C-start 1; filled squares, C-start 2; open squares, C-start 3) and S-starts (open triangles, S-start 1; filled circles, S-start 2; open circles, S-start 3). The stage numbers refer to the end of each stage as shown in Fig. 1B.

The power required to accelerate the body mass of fish sections laterally, during pike fast-starts, averages 16 % of the total power. Exclusion of this component from the calculation of total power would result in overestimation of hydrodynamic efficiency by 4 % for an average efficiency of 32 %. For higher efficiencies, the overestimation would be greater. The third term in equation 8, for this component of total power, is clearly significant and should not be excluded.

The loss of power (negative power) occurs when kinetic energy is lost as a result of the deceleration of propulsive elements. The energy cost to the fish depends on whether this deceleration is an active process, requiring energy expenditure, or is passive, requiring no energy. Including the power loss term either as a positive cost or as zero results in total power output values that differ by 33–57 % and hydrodynamic efficiency values that differ by 19–26 %. Unfortunately, insufficient information exists to quantify the relative

importance of active forces (i.e. muscle contraction) to the deceleration of lateral body movements. There is some evidence to suggest that both passive and active forces contribute. The backbone of a fish passively resists bending, requiring no energy expenditure (Hebrank *et al.* 1990; Long, 1992). Other internal structures, such as connective tissue and skin, are also expected to resist bending passively. In contrast, the stretching of active muscle provides resistance and requires energy expenditure (Goldspink, 1977; Johnston, 1991). For consistency, deceleration is assumed to be a passive process and to incur zero energy expenditure.

Hydrodynamic efficiency

Hydromechanical efficiencies for fast-starts by pike (0.16–0.39) are lower on average than values for other swimming modes involving body and caudal fin undulations. The highest efficiencies reported are for continuous swimming at 4–8 $BL\,s^{-1}$, where $BL\,s^{-1}$ is the velocity of the fish U normalized to the fish's length L (U/L), ranging from 0.7 to 0.9 (e.g. Webb, 1975, 1988; Videler and Hess, 1984). McCutcheon (1977) found hydromechanical efficiency for push-and-coast swimming to be intermediate, ranging from 0.18 to 0.7. There is, however, significant overlap in efficiencies between swimming modes (Fig. 5). Efficiencies of continuous swimming at a low speed (1 $BL\,s^{-1}$) are 0.3 for pike and 0.46 for trout and increase with speed (Webb, 1988). A similar positive relationship occurs for push-and-coast swimming. Hydromechanical efficiencies for fast-starts show a similar trend. The lowest efficiencies occur in stages 1 and 2 of S-starts, where the velocities attained are less than 2 $BL\,s^{-1}$. Although velocity is variable for all swimming modes shown, the decrease in efficiency from continuous to fast-start swimming is consistent at all velocities. These results show that the more unsteady the propulsive mechanism, the lower is the efficiency.
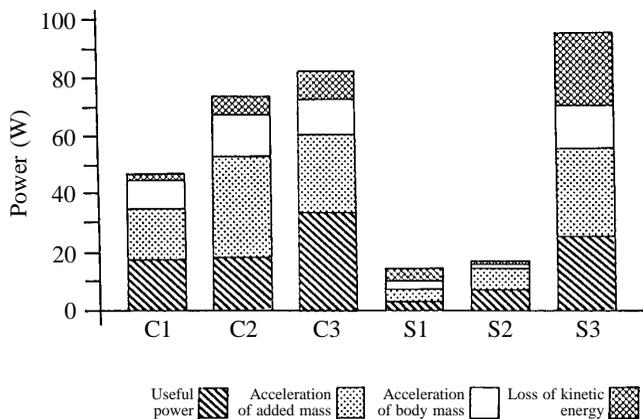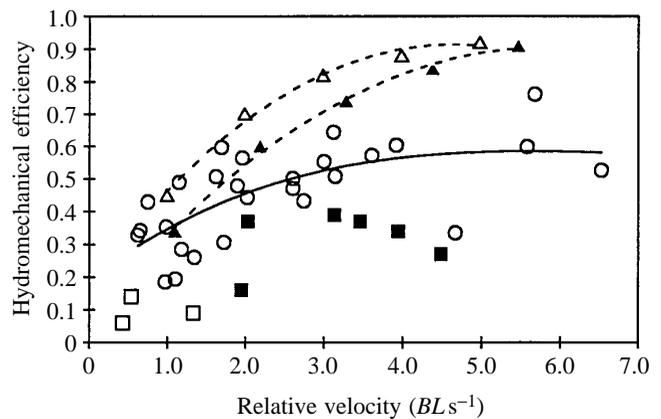

Fig. 4. A comparison of power output for C- and S-starts. The subdivisions represent the four terms on the right-hand side of equation 8 (see text).

Fig. 5. The relationship between hydrodynamic efficiency and relative speed ($BL\,s^{-1}$). Data for continuous swimming (open triangles, trout; filled triangles, pike) are from Webb (1988), data for push-and-coast swimming (open circles, zebra danio) are from McCutcheon (1977) and data for fast-starts (open squares, stage 1 of pike fast-starts; filled squares, stages 1+2 of pike fast-starts) are from the present study.

Table 7. *Total power expressed per kilogram muscle tissue (= 55.3 % body mass) and per kilogram muscle fibre (= 91 % muscle mass) for six northern pike*

Fish	Total power	
	(W kg^{-1} muscle)	(W kg^{-1} muscle fibre)
C-start 1	229.4	252.1
C-start 2	265.6	291.9
C-start 3	408.6	449.0
Mean	301.2	331.0
S-start 1	69.8	76.7
S-start 2	157.8	173.4
S-start 3	359.4	394.9
Mean	195.7	215.0

Why are fast-starts so expensive? The energy required to accelerate the added mass is a major component of total power, contributing 39 % on average. For continuous swimming, the time average of this component is zero, if deceleration of the added mass is assumed to represent an energy gain by the fish (Lighthill, 1975). The approach taken here, where deceleration of added mass is assumed to incur either a zero cost or a positive cost, has not previously been used in energetic analyses of fish continuous swimming using body undulations for propulsion. However, this approach has been employed in the analysis of other swimming modes (Blake, 1979, 1986). The resultant cost to the fish of decelerating propulsive elements, whether they be fins or sections of the body, is positive in all swimming modes. But, owing to lower tail-beat amplitudes and frequencies during continuous swimming, the cost is probably lower for this swimming mode than for fast-starts.

The mass of water influenced by propulsive sections is a determinant of hydrodynamic efficiency (Alexander, 1983) where the greater the mass of water acted on by a fish, the greater the proportion of total energy expended that will be used for propelling the fish. McCutcheon (1977) found, from flow visualization studies of the zebra danio (*Brachydanio rerio*) in burst-and-coast swimming, that the average water mass in the trailing edge vortex was large at 2.64 times body mass for stage 1 and 4.38 times body mass for stage 2. The large-amplitude movements of the pike tail and the large surface area in the tail region suggest that the mass of water affected by a pike during fast-starts is probably greater than for most fish.

Energy can be lost during swimming by accelerating water laterally to the direction of motion. McCutcheon (1977) found this to be a major cause of the lower hydromechanical efficiency of zebra danio in push-and-coast swimming. For pike during C-starts, the angles maintained by the caudal region are larger than for S-starts and favour higher thrust efficiencies (Frith and Blake, 1991). The lower caudal fin angles for S-starts suggest that the lower efficiencies in this swimming mode are, in part, due to water being pushed laterally instead of in the useful direction. Although C-starts

are more efficient than S-starts, the large-amplitude movements and lateral orientation of propulsive elements during fast-starts undoubtedly result in a greater amount of energy loss than during continuous swimming.

The increase in efficiency with each subsequent stage of a fast-start parallels a declining acceleration rate. The preparatory stage involves very low efficiencies, in part due to more water being pushed laterally and to smaller propulsive forces in the direction of motion. With each stage, the angle of attack and the lateral velocities increase and contribute to higher efficiencies. The majority of prey captures by pike, however, occur within 2–3 stages (Rand and Lauder, 1981; Harper and Blake, 1990). Lower hydromechanical efficiencies are implied, averaging 0.22 for the first three stages of all three S-starts, and 0.11 for the first two stages. A comparison of S- and C-starts by stages shows that C-starts are more efficient, on average, than S-starts, by 225 % in stage 1 and 275 % in stage 2. However, tail-beat frequency for S-starts is approximately twice that for C-starts and therefore the end of stage 2 for C-starts occurs at the same time as the end of stage 4 for S-starts (i.e. 0.13 s). An analysis of efficiency over this time interval shows that C-starts are only 50 % more efficient than S-starts.

Maximum performance

Maximum power output for northern pike, expressed per kilogram of muscle (muscle mass = 0.553 body mass; Webb, 1978), ranges from 229.4 to 408.6 W kg^{-1} for escape behaviour and from 69.8 to 359.4 W kg^{-1} for prey capture (Table 7). Values are only slightly higher when expressed per kilogram of muscle fibre (76.7–449.0 W kg^{-1}) because of the high concentration (91 %) of muscle fibres in fish white muscle (Johnston, 1983). The largest maximum power output values for a C-start and an S-start are 449.0 and 394.9 W kg^{-1} muscle fibre respectively (Table 7). Average power output estimates for C-starts in this study are 331.0 W kg^{-1} and for S-starts are 215.0 W kg^{-1} muscle fibre (Table 7). The maximum predicted power output for vertebrate anaerobic muscle is only slightly higher at 500 W kg^{-1} (Weis-Fogh and Alexander, 1977). Given that smoothing of velocity and acceleration values derived from digitized film records gives underestimates of actual performance, estimates of power output using this method are also apt to be underestimates. Alternatively, more recent analyses of fish muscle fibres employ a sinusoidal model for calculating power output, which is considered to be more realistic than the linear model adopted by Weis-Fogh and Alexander (1977); estimates of power output from the sinusoidal model are 10–20 % lower than those resulting from the linear model (Josephson, 1989). The sinusoidal model would therefore estimate maximum power output for vertebrate anaerobic muscle to be 400–450 W kg^{-1} muscle fibre. By comparison, power output of isolated white muscle fibres during cyclic oscillations is less than the theoretical maximum and rarely exceeds 300 W kg^{-1} (Johnston and Wokoma, 1986). Although precision is lacking, the general implication is that the power output of fish white

muscle during fast-starts in pike approaches the maximum power output limit of fish white muscle and, therefore, fast-start performance is probably constrained by available power from muscles.

Maximum isometric stress of muscles has also been suggested to constrain animal locomotory performance (Daniel and Webb, 1987; Daniel and Meyhofer, 1989). In order to assess isometric stress as a constraint mechanism, maximum stress in muscle fibres for pike fast-starts (maximum force/cross-sectional area) can be calculated and compared with literature values for isolated white muscle preparations of fish. Alexander (1969) reported that some muscle fibres in fish were oriented at angles approaching 30–35 ° to the longitudinal axis. This implies that the cross-sectional area of the body of a fish is a conservative estimate of muscle fibre cross-sectional area. The maximum force produced by pike, divided by cross-sectional area at the dorsal–anal fin placement point, gives values of 32.1–$73.2 \, \mathrm{kN \, m^{-2}}$. Maximum muscle isometric stresses for isolated muscle fibres (145–$315 \, \mathrm{kN \, m^{-2}}$) are at least twice these values (Johnston and Salamonski, 1984; Johnston and Wokoma, 1986; Altringham and Johnston, 1988; Curtin and Woledge, 1988; Langfeld et al. 1989). However, during cyclic contractions, maximum power output of muscle fibres is known to occur at about 0.3 maximum isometric stress (Hill, 1950). Using the range of literature values for maximum isometric stresses of isolated fish muscle fibres, the predicted stress at maximum power output (0.3 maximum isometric stress) is therefore 43.5–$94.5 \, \mathrm{kN \, m^{-2}}$ and overlaps the measured range of maximum stress for pike muscle fibres during a fast-start. Force measurements for fast abdominal myotomes isolated from the shorthorn sculpin (*Myoxocephalus scorpius*) during cyclic contractions are less than half of isometric measurements (110 and $130 \, \mathrm{kN \, m^{-2}}$ for cyclic contractions, from Johnson and Johnston, 1991, and $281 \, \mathrm{kN \, m^{-2}}$ for isometric measurements, from Altringham and Johnston, 1988; both taken from Table 2 in Luiker and Stevens, 1992) and confirm this pattern. This implies that muscle fibres in pike during fast-starts are operating near an optimum for maximum power output and well below maximum isometric stress measurements for fish white muscle fibres.

References

Alexander, R. McN. (1969). The orientation of muscle fibres in the myomeres of fishes. *J. mar. biol. Ass. U.K.* **49**, 263–290.

Alexander, R. McN. (1983). *Animal Mechanics.* London: Blackwell.

Altringham, J. D. and Johnston, I. A. (1988). The mechanical properties of polyneurally innervated, myotomal muscle fibres isolated from a teleost fish (*Myoxocephalus scorpius*). *Pflügers Arch.* **412**, 524–529.

Blake, R. W. (1979). The mechanics of labriform locomotion. I. Labriform locomotion in the angelfish (*Pterophyllum eimekei*): an analysis of the power stroke. *J. exp. Biol.* **82**, 255–271.

Blake, R. W. (1986). Hydrodynamics of swimming in the water boatman, *Cenocorixa bifida. Can. J. Zool.* **64**, 1606–1613.

Curtin, N. A. and Woledge, R. C. (1988). Power output and force–velocity relationship of live fibres from white myotomal muscle of the dogfish, *Scyliorhinus canicula. J. exp. Biol.* **140**, 187–197.

Daniel, T. L. and Meyhofer, E. (1989). Size limits in escape locomotion of carridean shrimp. *J. exp. Biol.* **143**, 245–265.

Daniel, T. L. and Webb, P. W. (1987). Physical determinants of locomotion. In *Comparative Physiology: Life in Water and on Land* (ed. P. Dejours, L. Bolis, C. R. Taylor and E. R. Weibel), pp. 343–369. New York: Liviana Press, Springer-Verlag.

Domenici, P. and Blake, R. W. (1991). The kinematics and performance of the escape response in the angelfish (*Pterophyllum eimikei*). *J. exp. Biol.* **156**, 187–205.

Domenici, P. and Blake, R. W. (1993). Escape trajectories in angelfish (*Pterophyllum eimekei*). *J. exp. Biol.* **177**, 253–272.

Eaton, R. C. and Emberley, D. S. (1991). How stimulus direction determines the trajectory of the Mauthner-initiated escape response in a teleost fish. *J. exp. Biol.* **161**, 469–487.

Frith, H. R. and Blake, R. W. (1991). Mechanics of the startle response in the Northern pike, *Esox lucius. Can. J. Zool.* **69**, 2831–2839.

Goldspink, G. (1977). Muscle energetics. In *Mechanics and Energetics of Animal Locomotion* (ed. R. McN. Alexander and G. Goldspink), chapter 9, pp. 222–248. London: Chapman and Hall.

Harper, D. G. and Blake, R. W. (1989a). On the error involved in high speed film when used to evaluate maximum acceleration rates of fish. *Can. J. Zool.* **67**, 1929–1936.

Harper, D. G. and Blake, R. W. (1989b). 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. (1990). Fast-start performance of rainbow trout *Salmo gairdneri* and northern pike *Esox lucius. J. exp. Biol.* **150**, 321–342.

Harper, D. G. and Blake, R. W. (1991). Prey capture and fast-start performance of northern pike *Esox lucius. J. exp. Biol.* **155**, 175–192.

Hebrank, J. H., Hebrank, M. R., Long, J. H., Jr, Block, B. A. and Wainwright, S. A. (1990). Backbone mechanics of the blue marlin *Makaira nigricans* (Pisces, Istiophoridae). *J. exp. Biol.* **148**, 449–459.

Hill, A. V. (1950). The dimensions of animals and their muscle dynamics. *Scient. Prog.* **38**, 209–230.

Johnson, T. P. and Johnston, I. A. (1991). Power output and fish muscle fibres performing oscillatory work: effects of acute seasonal temperature change. *J. exp. Biol.* **157**, 409–423.

Johnston, I. A. (1983). Dynamic properties of fish muscle. In *Fish Biomechanics* (ed. P. Webb and D. Weihs), pp. 36–67. New York: Praeger.

Johnston, I. A. (1991). Muscle action during locomotion: a comparative perspective. *J. exp. Biol.* **160**, 167–185.

Johnston, I. A. and Salamonski, J. (1984). Power output and force–velocity relationship of red and white muscle fibres from the Pacific blue marlin (*Maikaira nigricans*). *J. exp. Biol.* **111**, 171–177.

JOHNSTON, I. A. AND WOKOMA, A. (1986). Effects of temperature and thermal acclimation of contractile properties and metabolism of skeletal muscle in flounder (*Platichthys flesus*). *J. exp. Biol.* **120**, 119–130.

JOSEPHSON, R. K. (1989). Power output from skeletal muscle during linear and sinusoidal shortening. *J. exp. Biol.* **147**, 533–537.

LANGFIELD, K. S., ALTRINGHAM, J. D. AND JOHNSTON, I. A. (1989). Temperature and the force–velocity relationship of live muscle fibres from the teleost *Myoxocephalus scorpius*. *J. exp. Biol.* **144**, 437–448.

LIGHTHILL, M. J. (1970). Aquatic animal propulsion of high hydrodynamic efficiency. *J. Fluid Mech.* **44**, 265–301.

LIGHTHILL, M. J. (1971). Large-amplitude elongate body theory of fish locomotion. *Proc. R. Soc. Lond.* **179**, 125–138.

LIGHTHILL, M. J. (1975). *Mathematical Biofluiddynamics*. Philadelphia: Soc. Ind. Appl. Math.

LONG, J. H. (1992). Stiffness and damping forces in the intervertebral joints of blue marlin (*Makaira nigricans*). *J. exp. Biol.* **162**, 131–155.

LUIKER, E. A. AND STEVENS, E. D. (1992). Effect of stimulus frequency and duty cycle on force and work in fish muscle. *Can. J. Zool.* **70**, 1135–1139.

McCUTCHEON, C. W. (1977). Froude propulsive efficiency of a small fish measured by wake visualization. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 339–363. London: Academic Press.

RAND, D. M. AND LAUDER, G. V. (1981). Prey capture in the chain pickerel, *Esox niger*: correlations between feeding and locomotion behaviour. *Can. J. Zool.* **59**, 1072–1078.

SAVINO, J. F. AND STEIN, R. A. (1989). Behaviour of fish predators and their prey: habitat choice between open water and dense vegetation. *Env. Biol. Fishes* **24**, 287–293.

TIDBALL, J. G. AND DANIEL, T. L. (1986). Elastic energy storage in rigored skeletal muscle cells under physiological loading conditions. *Am. J. Physiol.* **250**, R56–R64.

VIDELER, J. J. AND HESS, F. (1984). Fast continuous swimming of two pelagic predators saithe (*Pollachius virens*) and mackerel (*Scomber scombrus*): A kinematic analysis. *J. exp. Biol.* **109**, 209–228.

WEBB, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 1–159.

WEBB, P. W. (1977). Effect of median fin amputation on fast-start performance of rainbow trout (*Salmo gairdneri*). *J. exp. Biol.* **68**, 123–135.

WEBB, P. W. (1978). Fast-start performance and body form in seven species of teleost fish. *J. exp. Biol.* **74**, 211–226.

WEBB, P. W. (1982). Fast-start resistance of trout. *J. exp. Biol.* **96**, 93–106.

WEBB, P. W. (1988). 'Steady' swimming kinematics of tiger musky, an esociform accelerator and rainbow trout, a generalist cruiser. *J. exp. Biol.* **138**, 51–69.

WEBB, P. W. AND SKADSEN, J. M. (1980). Strike tactics of *Esox*. *Can. J. Zool.* **58**, 1462–1469.

WEIHS, D. (1973). The mechanism of rapid starting of slender fish. *Biorheology* **10**, 343–350.

WEIS-FOGH, T. AND ALEXANDER, R. McN. (1977). The sustained power output from striated muscle. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 511–525. London: Academic Press.