REVIEW

THE KINEMATICS AND PERFORMANCE OF FISH FAST-START SWIMMING

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Summary

Fast-starts are brief, sudden accelerations used by fish during predator–prey encounters. The kinematics and performance of fish during fast-start manoeuvres have received a lot of attention since they may determine the outcome of predator–prey interactions in terms of feeding success or survival. We will discuss recent progress on (1) the kinematics of escape responses and feeding strikes, (2) the fast-start performance of species with different body morphologies and from different habitats, and (3) the functional significance of fast-start kinematics and performance within the context of predator–prey interactions.

Key words: kinematics, locomotion, fish, swimming, fast-start, predator–prey interactions, escape response, feeding strike.

Introduction

A fast-start is a high-energy swimming burst starting either from rest or imposed upon periods of steady swimming (Jayne and Lauder, 1993; Domenici and Batty, 1994). Fast-starts are important for most fish when escaping predators and for some fish in achieving prey capture. Under certain circumstances, in some species, fast-start movements can also be associated with social communication (Fernald, 1975). Beamish (1978) defines three major categories of swimming activity: sustained (>200 min), prolonged (20 s to 200 min) and burst (<20 s). In this context, fast-starts may be viewed as a form of burst swimming, lasting for less than approximately 1 s. From a mechanical perspective, fast-starts are unsteady (transient) motions, while sustained and prolonged swimming are steady (periodic) movements (Webb, 1984*a*), except for the case of species performing burst-and-coast swimming for extended periods.

The present paper reviews the kinematics and performance of fast-starts in adult fish, covering kinematic types, distance–time performance characteristics, scaling and temperature effects, technical measurement errors, turning angles and radii, and the relevance of fast-start performance in predator–prey interactions.

Fast-start kinematics

Two main types of fast-starts are recognized, C-starts and S-starts (Figs 1 and 2, respectively), in which the fish is bent into a 'C' or 'S' shape at the end of the first contraction of the lateral musculature. The former are used by predators when attacking prey, whereas the latter are mainly employed by escaping prey. C-starts are usually mediated by the Mauthner neurones and associated networks (Eaton *et al.* 1991). Nothing is known about the mechanisms controlling S-starts, although Mauthner neurones can be active during the terminal phase of prey capture in goldfish (Canfield and Rose, 1993).

C-starts

The first detailed kinematic description of a C-type fast-start is by Weihs (1973), who described the escape response of a trout as L-shaped. The term 'L-start' was utilized by early authors (Weihs, 1973; Webb, 1976) and is synonymous with 'C-start'. Weihs (1973) divides fast-starts into three kinematic stages: stage 1 (the preparatory stroke), stage 2 (the propulsive stroke) and stage 3 (a variable stage, involving continuous swimming or coasting). Earlier studies (e.g. Webb, 1978*a*) describe stage 1 as the formation of the C shape and stage 2 as the return flip of the tail associated with a forward acceleration. Recently, different criteria have been employed to define the onset of stage 2 (corresponding to the end of stage 1). Domenici and Blake (1991, 1993*b*) and Kasapi *et al.* (1993) define it as the change in the turning direction of the anterior body midline (Fig. 3), Foreman and Eaton (1993) define it as the onset of forward propulsion, and Jayne and Lauder (1993) define it as corresponding to the onset of the contralateral electromyographic (EMG) signal. Although these definitions seem synonymous, Foreman and Eaton (1993) showed that the onset of forward propulsion does not correspond to the change in turning direction of the
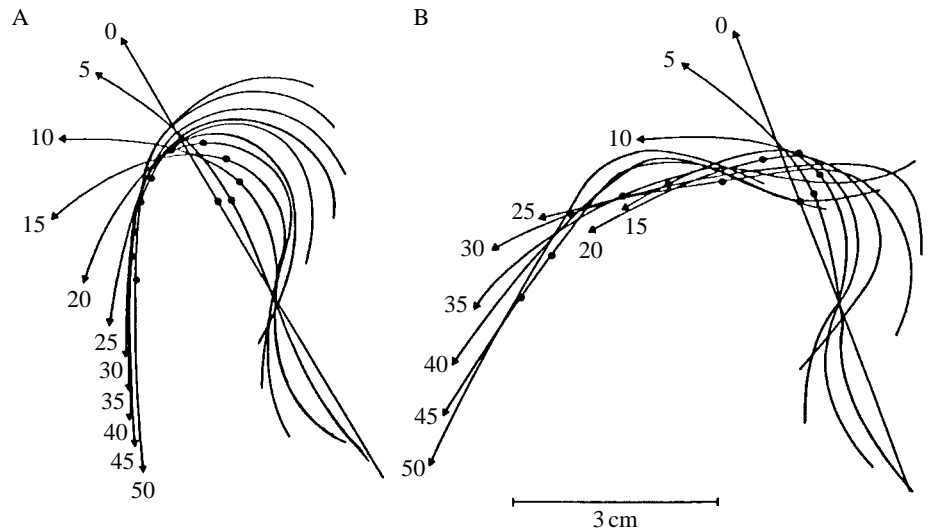
Fig. 1. Single-bend (A) and double-bend (B) C-starts in angelfish *Pterophyllum eimekei*. Times between tracings are in milliseconds from the first detectable movement. The midline and centre of mass (filled circles) of the fish when stretched straight are shown. The head is indicated by the arrowhead. Reproduced from Domenici and Blake (1991) with permission.

anterior body midline, although the latter is temporally correlated to the contralateral EMG signal, which occurs a few milliseconds earlier (7.3 ms in Fig. 7 of Foreman and Eaton, 1993).

Jayne and Lauder (1993) have found that, although the onset of ipsilateral EMG activity is synchronous at different longitudinal locations, its offset is delayed posteriorly. As a result, ipsilateral EMG duration increased posteriorly from 11 to 15 ms. The times of both onset and offset of contralateral EMG activity were found to be asynchronous at different longitudinal locations, with the EMG signal occurring earlier at anterior locations (Jayne and Lauder, 1993).

In kinematic studies in the absence of EMG recordings, stages 1 and 2 may need to be defined according to their physiological correlates, i.e. ipsi- and contralateral contraction, respectively. The end of stage 1 and the beginning of stage 2 can be considered synchronous since, at any given location, the onset of contralateral EMG activity occurred only 3–6 ms after the offset of ipsilateral EMG activity (Jayne and Lauder, 1993). The onset of stage 2 can be determined by the change in the
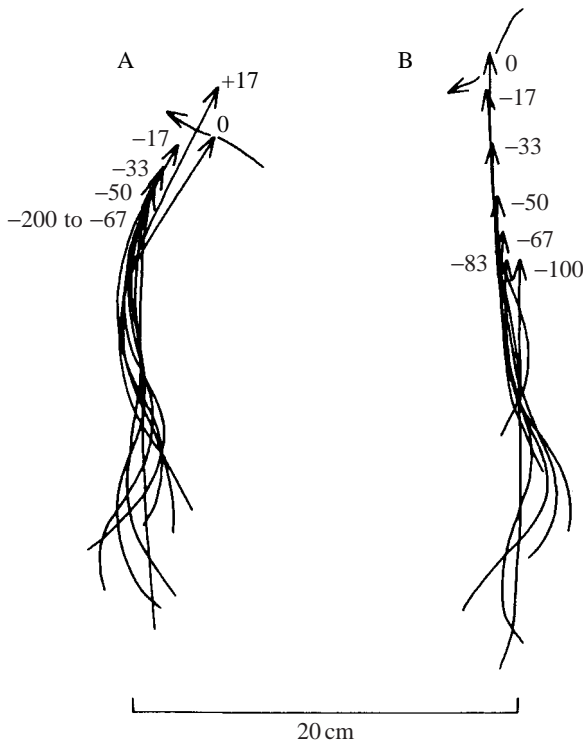

Fig. 2. (A,B) Strike patterns in pike (*Esox* sp.) striking at a fathead minnow (*Pimephales promelas*). Times between tracings are in milliseconds, measured backwards from a reference time of predator–prey contact. The head is indicated by the arrowhead. Reproduced from Webb and Skadsen (1980) with permission.
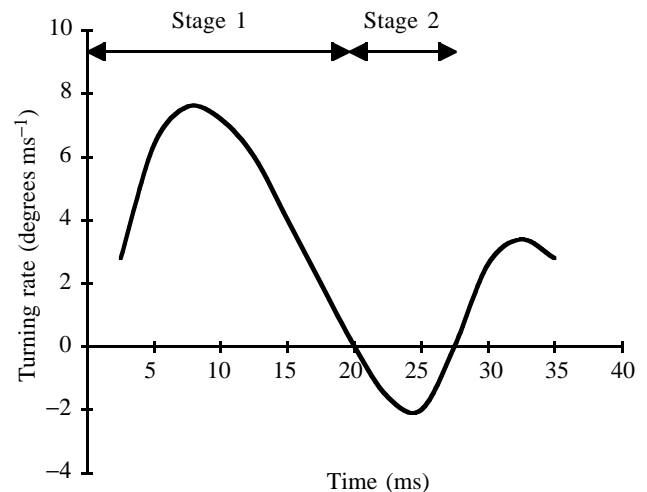

Fig. 3. The turning rate of the midline of the anterior part of the body (snout to centre of mass) during the double-bend escape shown in Fig. 1B. Stage 1 starts at the first detectable movement of the fish and is completed when the turning rate–time curve crosses the *x*-axis at approximately 20 ms, corresponding to a reversal of turning direction. The end of stage 1 coincides with the beginning of stage 2, which is completed when a further reversal of turning direction occurs at approximately 28 ms (from P. Domenici and R. W. Blake, unpublished data).

turning direction of the anterior body midline (Fig. 4 in Kasapi *et al.* 1993; Fig. 3 in the present paper) which, according to Foreman and Eaton (1993), is correlated to the contralateral EMG activity.

Accordingly, escapes responses consist of a stage 1 (ipsilateral EMG activity) which is most often followed by a stage 2 (contralateral EMG activity). Domenici and Blake (1991) and Kasapi *et al.* (1993) observed that the escape responses of angelfish (*Pterophyllum eimekei*) and knifefish (*Xenomystus nigri*) sometimes did not show a contralateral bend and hypothesised that this was due to the absence of a contralateral muscular contraction. Their hypothesis was later confirmed by Foreman and Eaton (1993). Whether the presence of a contralateral bend should be the basis of a further division of C-starts into single-bend and double-bend types (see Fig. 1; Domenici and Blake, 1991; Kasapi *et al.* 1993) or not (Foreman and Eaton, 1993) may depend on the purpose of the study. For example, it would be interesting to estimate the contribution of the passive elastic components in the skin and musculature to the acceleration observed in single-bend escape responses during the passive recoil of the tail (Domenici and Blake, 1991). In this case, only escape responses in which stage 1 is not followed by contralateral EMG activity should be considered. In addition to differential contralateral contraction, C-starts may differ in the relaxation phase of the ipsilateral musculature (Covell *et al.* 1991; Domenici and Blake, 1991).

The kinematics of escape responses along the whole length of bluegill sunfish *Lepomis macrochirus* was carefully studied by Jayne and Lauder (1993). They found that although the onset of the ipsilateral muscular contraction was synchronous (as already observed in the escape responses of carp *Cyprinus carpio* by Kashin *et al.* 1979) there was a posterior propagation of both lateral bending and maximum lateral displacement. The initiation of such posterior propagation cannot be attributed entirely to the posterior increase in EMG duration because a lag in the time of initial lateral flexion was present while the entire side of the fish still had simultaneous stage 1 muscle activity (Jayne and Lauder, 1993). In addition, the rate of propagation of kinematic events was always slower than that of the muscle activity (Jayne and Lauder, 1993).

Median and paired fin movements are associated with C-starts. The median fins are fully erected prior to or soon after acceleration begins (Eaton *et al.* 1977; Webb, 1978*a*). This is consistent with the requirement of a large surface area for high thrust production (Weihs, 1973). Earlier studies found that paired fins are pressed against the body during a fast-start (Webb, 1978*a*), although there are some exceptions (see below).

C-starts usually involve body bends and locomotion in the horizontal plane. However, in some species, movements in three dimensions are associated with changes in pitch and roll. In the escape responses of marble hatchetfish (*Carnegiella strigata*, Eaton *et al.* 1977) and knifefish (*Xenomystus nigri*, Kasapi *et al.* 1993), the pectoral fins are extended during escapes, and their orientation may contribute to displacement in the vertical plane, although a quantitative analysis of fin orientation has not been performed. Pectoral fin extension has been considered as an exception correlated to the unusual three-dimensional escape of these two species (Eaton *et al.* 1977; Kasapi *et al.* 1993). However, pectoral fin extension has recently been observed in various species of pelagic fish (herring *Clupea harengus*; horse mackerel *Trachurus trachurus*; mackerel *Scomber scombrus*, P. Domenici and R. S. Batty, personal observations) that show escape responses primarily in the horizontal plane. Although there must be a drag cost associated with paired fin extension, it may function in reducing the turning radius of pelagic fish. Pectoral fin extension in these species is asymmetrical, with the greater extension on the inside of the turn (P. Domenici and R. S. Batty, personal observation). Therefore, the extended pectoral fin may function as a pivot point to 'anchor' the fish and minimize its turning radius.

Are C-starts and escape responses synonymous?

The early descriptions of escape responses as C- or S-starts are based on the fish shape at the end of stage 1 (Webb, 1976, 1978*a*; Eaton *et al.* 1977). According to this definition, C-starts imply large angles of turn, and S-starts show displacement in line with the original body axis. Webb (1976) observed that the frequency of S-start escape responses increases with body length. Recently, Domenici and Blake (1993*a*) and Foreman and Eaton (1993) showed that the turning angles of C-starts include values from $0°$ to approximately $180°$ on either side of the fish. These authors did not observe S-starts among the escape responses. Are S-starts only displayed by larger fish during escape responses? And how do these S-starts differ from C-starts? It is possible that fish performing an escape response at a small angle will bend their body in an apparent S-shape, as the tail may simply not be stiff enough to follow the C-shape of the body without delay. Jayne and Lauder (1993) suggested that the posterior lateral flexion of the vertebral column in the direction opposite to that of the ipsilateral contraction indicates that most of the posterior muscular activity is counteracting the resistive forces imposed by the fluid rather than performing positive work. The large fish utilized by Webb (1976) may have shown a higher proportion of escape responses with small turning angles, and these S-shaped escape responses do not necessarily correspond physiologically to the S-shaped predatory attacks. C-starts in trout (*Oncorhynchus mykiss*; Webb, 1976) show that the midline of the fish is bent into an S shape in the early portion of stage 1.

In addition, while the large trout utilized by Webb (1976) escaped mainly at small angles of turn (S-starts in Webb, 1976), Domenici and Blake (1991, 1993*a,b*) and Eaton and Emberley (1991) have shown that escape responses utilize a wide range of angles of turn. This discrepancy may arise from the different stimulus type used. Domenici and Blake (1991, 1993*a,b*) and Eaton and Emberley (1991) utilized an acoustic stimulus presented to the fish at different orientations. Since fish tend to have fixed escape trajectories relative to the startling stimulus (Fig. 4; Domenici and Blake 1993*a*;
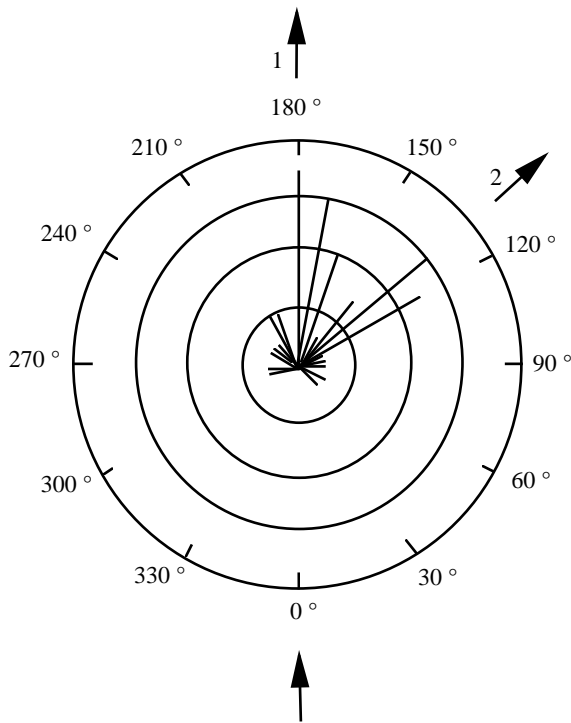
Fig. 4. Circular frequency distribution of escape trajectories (away responses) of angelfish *Pterophyllum eimekei* defined as the swimming direction of the fish at the end of stage 2 with respect to the stimulus orientation at rest (indicated by the arrow at the bottom of the graph). Responses to stimuli from the left or right are plotted as if the stimulus were always on the right side of the fish. The frequency interval is 10°. Each concentric circle represents a frequency of 2. The circular distribution differs significantly from a normal (von Mises) distribution (χ^2 test, $P<0.05$; see Domenici and Blake, 1993*a*). Two main modes, separated by 50°, are present at 180° (arrow 1) and 130° (arrow 2). Reproduced from Domenici and Blake (1993*a*) with permission. A similar circular distribution was found for escape trajectories of solitary herring *Clupea harengus* (Domenici and Batty, 1997).
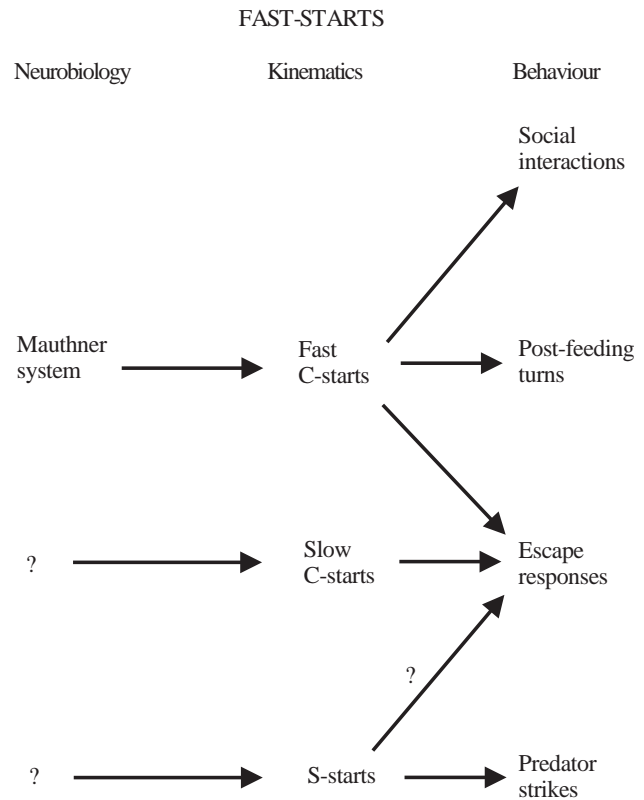

Fig. 5. Diagram illustrating the various types of fast-start neurobiology, kinematics and behaviour. Question marks indicate that the neural commands driving slow C-starts (as in Domenici and Batty, 1994) and S-starts are unknown and that it is not known whether S-starts with distinct neural commands from those for C-starts can occur during escape responses (see text for details).

Domenici and Batty, 1997), the resulting turning angles relative to the body axis of the fish before the escape varied greatly. Webb (1976) employed electrical stimulation, which may not provide the fish with any directional cues, and this may have allowed large fish to escape using one main type of response at a fairly fixed (small) turning angle. The time of completion for an escape response is size-dependent (Domenici and Blake, 1993*b*) and linearly related to turning angle (Domenici and Blake, 1991; Domenici and Batty, 1994). However, no relationship was found between escape latency (measured as the time between the stimulus onset and the first detectable movement of the fish) and fish size (Webb, 1980). For large fish, large turning angles would mean that the largest part of the overall time for escape (escape latency plus stages 1 and 2) would be the turning component during stage 1, while for small fish stage 1 duration would be similar to escape latency even at large turning angles. Although a large range of turning angles in small fish does not greatly affect the overall

time for escape, the same cannot be said for large fish. Therefore, it is possible that, in the absence of directional cues, large fish may show short-duration fast-starts at small angles of turn as a time-minimization strategy.

There is no evidence to suggest that escape responses at a small angle of turn observed in large fish differ physiologically from the Mauthner-mediated C-starts of smaller fish. A detailed kinematic study on fish of different sizes, linked with intracellular recording of Mauthner cell activity, would be necessary to investigate their neurophysiological basis. If S-start escape responses are Mauthner-mediated, they should be considered as C-starts with a small turning angle. Predatory S-starts, first observed by Hoogland *et al.* (1956), are described below. Mauthner-mediated C-starts are also utilized in post-feeding turns (Canfield and Rose, 1993) and possibly in social interactions (Fernald, 1975). Therefore, C-starts and escape responses are not synonymous. While all escape responses are C-starts, not all C-starts are escape responses (Fig. 5). In addition, not all escape responses are Mauthner-mediated C-starts; they can be mediated by other as yet unidentified reticulospinal neurones which trigger escape responses with longer latency than Mauthner-mediated escapes (Eaton *et al.* 1984). Domenici and Batty (1994) show that there are two

types of escape responses in schooling herring (fast and slow C-starts, Fig. 5), associated with different turning rates and escape latencies (30 ms and approximately 100 ms, measured as the time between the stimulus onset and the first detectable movement of the fish). It may be that these two responses are triggered by different neural commands. The more rapid escapes may involve the Mauthner cells, as suggested by the short escape latencies (30 ms, comparable to latency values typical of responses mediated by Mauthner cells; Eaton and Hackett, 1984).

Domenici and Batty (1997) showed that slow C-starts are present in solitary herring as well, but they occur less frequently than in schooling herring. They suggested that schooling may raise the sensory threshold for fast C-starts, giving longer latencies and slower responses (slow C-starts), which are more appropriate in directionality and reduce the possibility of collisions with neighbouring fish.

S-starts

The kinematics of S-starts were described for pike (*Esox lucius*) attacking sticklebacks (*Gasterosteus aculeatus*) by Hoogland *et al.* (1956). The pike body is curved into an S form prior to the strike and this posture corresponds to the S shape displayed by fish during carangiform swimming, with the frontal part of the body less sharply curved than the caudal part (Hoogland *et al.* 1956). Subsequently, the tail is brought to a position almost perpendicular to the spinal axis of the fish, and finally the pike strikes. These events are usually very rapid, lasting 100–200 ms (Webb and Skadsen, 1980). However, if the pike's movements are hampered by water weeds, it may stand in the S posture for a few seconds (Hoogland *et al.* 1956). It would be interesting to investigate whether and to what extent environmental conditions affect the nature and timing of strikes in piscivorous fish.

Webb and Skadsen (1980) and Rand and Lauder (1981) describe the strike patterns of pike (*Esox* sp.) attacking fathead minnows (*Pimephales promelas*). They found that pike showed two different strike patterns. Pattern A strikes (Fig. 2A) start from a straight body posture and involve an initial phase (S shape, stage 1 in Webb and Skadsen, 1980), an intermediate phase (opposite S shape, stage 2 in Webb and Skadsen, 1980) and final phase (continuous swimming, stage 3 in Webb and Skadsen, 1980). In pattern B strikes (Fig. 2B), the acceleration starts from an S posture, formed 0.15–3 s before the strike, similar to that found by Hoogland *et al.* (1956). The subsequent acceleration corresponds to the intermediate phase of pattern A strikes; therefore, the initial phase is absent. The S posture preceding a strike is described for a variety of species of adult (Neill and Cullen, 1974; Hobson, 1974) and larval (Rosenthal, 1969; Hunter, 1972) fish.

Harper and Blake (1991) further divide S-starts into four types on the basis of acceleration peaks, associated with different numbers of half-cycles of the periodic tail motion. As in the study of Webb and Skadsen (1980), the different strike types are utilized for different prey distances. It has not yet been determined whether these strike patterns correspond to

differential neural controls. Although the neural commands triggering S-starts are unknown, various authors have suggested that the Mauthner cells may be involved in predator attacks (Canfield and Rose, 1993; Zottoli *et al.* 1992). If so, there would be no neurophysiological division between S- and C-starts; predatory S-starts may simply correspond to C-starts at 0° with respect to the body axis of the fish prior to the strike. However, S-starts in which the fish keeps the S posture for some seconds (pattern B in Webb and Skadsen, 1980) are too different kinematically from C-starts to imply the same neural control. In addition, these S-starts are unlikely to be Mauthner-mediated because they would require repetitive firing of the circuit and the output synapses that drive the motoneurones would have to be repetitively active. This is unlikely because the Mauthner output connections all fatigue rapidly (R. C. Eaton, personal communication).

Fast-start performance
Distance–time performance

The propulsive performance in a fast-start may be evaluated by quantifying various distance–time parameters (for example, distance travelled within a given time, mean and maximum forward velocity, and mean and maximum linear acceleration during a fast-start; e.g. Weihs, 1973; Webb, 1976, 1978*a*; Harper and Blake, 1990, 1991; Domenici and Blake, 1991, 1993*b*; Frith and Blake, 1991; Kasapi *et al.* 1993; Gamperl *et al.* 1991; Beddow *et al.* 1995). We will refer to forward velocity and linear acceleration as simply velocity (or speed) and acceleration, respectively. In most studies, the analysis of distance-related parameters is based on the centre of mass of the fish when stretched straight. This approximates the instantaneous centre of mass, the point about which propulsive forces act (Webb, 1978*a*).

The relevance of fast-start performance has to be considered in the context of the 'attack–escape sequence' phase of the predator–prey interaction. A fish that can achieve high speed will not necessarily be able to capture a prey or escape from a predator unless that high speed is achieved within a relatively short time. Unsteady swimming performance must be evaluated together with the timing of the responses; therefore, distance, speed attained within a given time and acceleration are the relevant parameters to consider.

Most studies of fast-start performance are based on fish starting from rest. The fish accelerates from rest during the two stages of a fast-start, with further increases in speed after the end of stage 2 if the fish continues swimming. The shape of the velocity–time curve is related to the timing of the two kinematic stages (Domenici and Blake, 1991). Speed increases throughout the fast-start, but the rate of increase drops around the end of stage 1 and the beginning of stage 2. Therefore, the acceleration profile shows two peaks, one per stage. The timing of the propulsive power is related to the kinematics of the tailbeats. When a full return-flip of the tail is not present (single bend, Fig. 1), velocity does not increase beyond stage 1, and the high acceleration peak in stage 1 is followed by a much

lower peak. Since there is evidence that in such escape responses a contralateral contraction during stage 2 is absent (Foreman and Eaton, 1993), the acceleration produced after stage 1 in single-bend responses suggests that thrust production may be due to passive elastic elements (such as skin, collagen fibres and elasticity in the muscle itself), as suggested by Kasapi *et al.* (1993). The use of single-bend escapes increases with size in angelfish (*Pterophyllum eimekei*) (Domenici and Blake, 1993*b*). Domenici and Blake (1993*b*) suggest that single-bend responses allow large fish to achieve large turning angles through a coasting phase, despite their limited flexibility around the centre of mass.

Velocity and acceleration profiles of S-starts are more complex. Harper and Blake (1991) showed that S-starts can have 1–4 peaks of acceleration, where the number of acceleration peaks is related to fast-start duration. The type of fast-start depends on the strike pattern of the predator, which in turn is determined by the apparent size of the prey (Harper and Blake, 1991). Performance during feeding fast-starts appears to maximize and maintain velocity to the point of contact with the prey (Harper and Blake, 1991).

Scaling of distance–time performance

Wardle (1975) showed that the burst swimming speed of fish is related to the minimum muscle contraction time, which in turn is related to fish size. The total distance covered and the final speed attained in a fast-start are also size-dependent, because larger fish perform longer fast-starts (Webb, 1976). The relationship between maximum speed and fish size is not linear (Wardle, 1975); small fish attain higher specific speed (body lengths s^{-1}) than larger fish (see Table 1). In contrast, fast-start acceleration is size-independent (Webb, 1976; Domenici and Blake, 1993*b*). Theoretically, acceleration should vary as length^{-1} (Daniel and Webb, 1987). However, Webb and Johnsrude (1988) suggest that this may not be so, because of summation of muscle twitches.

Since maximum acceleration is size-independent and fast-start duration increases with size, speed should be measured within a given time interval (Webb, 1976). Both Webb (1976) and Domenici and Blake (1993*b*) found that speed within a given time is size-independent. Domenici and Blake (1993*b*) found that the occurrence of low-performance fast-starts with large turning angles increased with size. They suggested that larger fish may not be able to employ high-performance fast-starts with large turning angles, because of morphological constraints such as limited flexibility at the centre of mass.

Temperature effects on distance–time performance

Temperature can have an effect on fast-start performance (Webb, 1978*b*; Johnson *et al.* 1993; Beddow *et al.* 1995). Webb (1978*b*) showed that the time to completion of a fast-start in trout (*Oncorhynchus mykiss*) decreased with increasing temperature. This result is consistent with Wardle's (1975) findings on the effect of temperature on minimum muscle contraction time, although Webb's values for the duration of each propulsive stroke are slightly higher than those predicted by Wardle's model. This discrepancy may be explained by the fact that Webb's experiments were conducted on whole animals while Wardle's experiments were conducted on isolated muscle blocks. Webb (1978*b*) showed that, in acclimated fish, speed and acceleration are affected by temperature within the range 5–15 °C, but are temperature-independent at higher temperatures (15–25 °C). Johnson *et al.* (1993) investigated the effect of temperature on fast-starts of goldfish (*Carassius auratus*). They concluded that the thermal dependence of speed at the observed temperatures (5 and 20 °C) was due to changes in physiological processes rather than to physical changes (e.g. changes in water viscosity) in the environment.

Beddow *et al.* (1995) studied the effect of temperature acclimation in fast-starts of short-horned sculpin (*Myoxocephalus scorpio*). They showed that fast-start performance in terms of speed and acceleration is higher in fish acclimated and observed at 15 °C than in fish acclimated at 5 °C and transferred to 15 °C for the experiment. There is evidence that the contractile properties of white muscle fibres in sculpin vary with acclimation temperature (Beddow and Johnston, 1995). These authors suggested that a mechanism for the adaptation in maximum muscular contraction speed may be a change in myosin gene expression in fast muscle fibres, as found in common carp (*Cyprinus carpio*) (Johnston *et al.* 1990).

Johnson and Bennett (1995) showed that the thermal acclimatory responses of fast muscles at the molecular, biochemical and cellular levels of organization are reflected in alterations in escape performance. They showed that goldfish acclimated to 35 °C can swim at a speed of 1 m s^{-1} at 35 °C, but only at a speed of 0.2 m s^{-1} at 10 °C. However, following a period of acclimation to 10 °C for 4 weeks, goldfish swim at speeds up to 0.9 m s^{-1}, demonstrating almost perfect temperature compensation (Johnson and Bennett, 1995).

Webb and Zhang (1994) investigated the effect of heat shock on the escape response performance of goldfish (*Carassius auratus*) attacked by rainbow trout (*Oncorhyncus mykiss*). Goldfish acclimated at 15 °C were exposed to a temperature of 34–39 °C for 2 min prior to the experiment. This treatment did not affect escape speed but did decrease the reaction distance of the prey to an attacking predator (Webb and Zhang, 1994). This reduced responsiveness results in increased vulnerability. Temperature is known to have an effect on escape response latencies (Webb, 1978*b*). Therefore, the influence of temperature changes on predator–prey interactions found by various authors (e.g. Yocom and Edsall, 1974; Webb and Zhang, 1994) may be due to timing factors rather than to distance–time performance (e.g. velocity, acceleration).

Turning angles

Turning angles concern only C-starts, because S-starts involve striking in line with the fish's body axis at rest. Fish escape responses were initially thought always to involve a turn characterized by a fixed angle (Webb, 1976). More recent studies (Domenici and Blake, 1991; Foreman and Eaton, 1993)

Table 1. *Summary of previous fast-start performance studies*

Author	Species	Common name	Fast-start type	Temperature (°C)	Method†	Maximum acceleration (m s^{-2})	Maximum velocity (L s^{-1})	Duration (ms)	Body length, L (cm)
Weihs (1973)	*Oncorhynchus*	Rainbow trout	ER	?	40	40	–	–	33
Webb (1975)	*mykiss*	,,	ER	15	64	42.1	8.5	78	14.3
Webb (1976)	,,	,,	ER	15	64	33.2	15.9	71	9.6
,,	,,	,,	ER	15	64	32.1	8.1	74	15.0
,,	,,	,,	ER	15	64	32.3	8.2	78	20.4
,,	,,	,,	ER	15	64	31.7	7.1	84	24.5
,,	,,	,,	ER	15	64	36.2	6.1	96	29.6
,,	,,	,,	ER	15	64	34.6	5.3	100	34.6
,,	,,	,,	ER	15	64	40.6	7.4	100	38.7
Webb (1977)	,,	,,	ER	15	250	26.6	8.3	109	17.4
Webb (1978*b*)	,,	,,	ER	5	250	16	7.4	116	13.6
,,	,,	,,	ER	10	250	31	11.0	98	13.6
,,	,,	,,	ER	15	250	41	12.5	79	13.6
,,	,,	,,	ER	20	250	40	12.5	68	13.6
,,	,,	,,	ER	25	250	41	12.5	65	13.6
Webb (1978*a*)	,,	,,	ER	15	250	32.6	8.1	114	19.5
Harper and Blake (1990)	,,	,,	ER	15–20	ACC	59.7	8.7	125	31.8
Gamperl *et al.* (1991)	,,	,,	ER	10	200	19.8*	13.7*	74*	9.5
,,	,,	,,	ER	10	200	18.2§	14.1§	77§	9.5
Weihs (1973)	*Esox* sp.	Pike	ER	?	40	50	–	–	?
Webb (1978*a*)	,,	,,	ER	15	250	39.5	7.2	115	21.7
Harper and Blake (1991)	,,	,,	ER	15–20	ACC	120.2	10.5	108	37.8
Harper and Blake (1991)	,,	,,	FS	15–20	ACC	95.9	8.2	133	37.8
Frith and Blake (1991)	,,	,,	ER	10–14	250	151.3‡	8.7‡	129‡	40
Rand and Lauder (1981)	,,	,,	FS	21	200	–	9.0	92	27.3
Webb (1986*b*)	,,	,,	ER	15	60	–	21.0	–	6.5
Domenici and Blake (1991)	*Pterophyllum.* sp.	Angelfish	ER	24–26	400	79.0	17.8	36	7.3
Domenici and Blake (1993*b*)	,,	,,	ER	24–26	400	93.2	27.3	30	4.9
,,	,,	,,	ER	24–26	400	78.9	18.9	34	7.3
,,	,,	,,	ER	24–26	400	114.7	13.6	36	10.9
,,	,,	,,	ER	24–26	400	109.4	9.3	46	13.5
Kasapi *et al.* (1993)	*Xenomystus nigri*	Knifefish	ER	24–25	400	127.9	12.9	32	11.3
Beddow *et al.* (1995)	*Myoxocephalus*	Short-horned	FS	5 (5)	200	16.2	3.3	183	24
,,	*scorpio*	sculpin	FS	10 (5)	200	17.0	3.5	173	24
,,	,,	,,	FS	15 (5)	200	18.4	4.1	152	24
,,	,,	,,	FS	15 (15)	200	22.0	5.4	96	24
Webb (1975)	*Lepomis cyanellus*	Green sunfish	ER	15	64	15.7	8.4	79	8
Webb (1978*a*)	*Perca flavescens*	Yellow perch	ER	15	250	23.9	7.4	103	15.5
,,	*Notropis cornutus*	Common shiner	ER	15	250	28.7	10.7	78	10.7
,,	*Cottus cognatus*	Slimy sculpin	ER	15	250	22.7	9.4	81	8.2
,,	*Etheostoma caeruleum*	Rainbow darter	ER	15	250	32.3	14.4	56	6.2
Webb (1986*b*)	*Micropterus salmoides*	Largemouth bass	ER	15	60	–	18.8	–	5.1
Webb (1986*b*)	*Pimepales promelas*	Fathead minnow	ER	15	60	–	14.0	–	5.8
Webb (1986*b*)	*Lepomis*	Bluegill sunfish	ER	15	60	–	15.8	–	6.4
Webb (1978*a*)	*macrochirus*	,,	ER	15	250	28.8	8.5	88	15.3
Dubois *et al.* (1976)	*Pomotamus saltatrix*	Bluefish	ER	?	ACC	20.6‡	4.0‡	210	63

Duration corresponds to the sum of stages 1 and 2, over which maximum velocity and maximum acceleration were calculated.

ER, escape response; FS, feeding strike; ?, data not reported; temperatures in parentheses denote acclimation temperature; †filming rate (Hz) or accelerometry (ACC); ‡calculated mean value; §fish were subject to a training protocol; *fish were not subject to a training protocol.

show that the turning angles of escape responses can span approximately 180° on either side of the fish and therefore include swimming trajectories in line with the body axis at rest. As escape responses are often divided into two stages, various authors have studied stage 1 angle (defined as the angle between the midlines of the anterior part of the body at rest and the end of stage 1) and stage 2 angle (defined as the angle between the midlines of the anterior part of the body at the end of stage 1 and the end of stage 2) (Eaton and Emberley, 1991; Foreman and Eaton, 1993; Kasapi *et al.* 1993; Domenici and Blake 1991, 1993*a*,*b*). Stage 1 is the main turning component of an escape response, with larger turning angles on average than during stage 2 (Eaton *et al.* 1988; Domenici and Blake, 1991). Stage 1 angles were found to be correlated to EMG duration (Eaton *et al.* 1988) and to stage 1 duration (Domenici and Blake, 1991).

Nissanov *et al.* (1990) showed that sensory-evoked responses had a higher mean turning rate than responses triggered by invasive electrical stimulation of the Mauthner cells. Domenici and Batty (1994) showed that schooling herring (*Clupea harengus*) responded to a startle stimulus with two distinct latencies, each one associated with a different relationship between stage 1 duration and turning angle. This relationship gives an indication of mean turning rate. However, the turning rate–time curve of an escaping fish has a sinusoidal shape (Fig. 3; Kasapi *et al.* 1993), so differences in mean turning rates could be due to differences in maximum turning rates or to different shapes of the turning rate–time curve.

If stage 2 is defined as the directional change relative to stage 1, then the stage 2 angle always bears a negative sign, as it is in the opposite direction to the stage 1 angle. Both Eaton *et al.* (1988) and Domenici and Blake (1991) found a weak relationship between stage 1 and stage 2 angles, such that large stage 1 turns are associated with small stage 2 opposite turns, and *vice versa*. Eaton *et al.* (1988) pointed out that because stage 1 and stage 2 angles are correlated, the neural commands for the escape trajectory could be organized by the end of stage 1.

Escape angles (defined as the angle between the body axis of the fish at rest and its orientation at the end of stage 2) are linearly related to the angle at which the stimulus is presented (Eaton and Emberley, 1991; Domenici and Blake, 1993*a*). Most escape responses show a C-bend in the direction opposite to the stimulus (i.e. 'away responses'; Blaxter *et al.* 1981; Domenici and Blake, 1993*a*; Domenici and Batty, 1994, 1997). Domenici and Blake (1993*a*) found that the distribution of the escape trajectories of away responses in angelfish *Pterophyllum eimekei* (measured as angles relative to the stimulus direction) showed a bimodal pattern with trajectories at 130° and 180° (Fig. 4). Such a bimodal pattern is also found in away responses of herring when separated from the rest of the school (Domenici and Batty, 1997), but it is not present in schooling herring (which show a unimodal pattern of trajectory distribution with a peak around 150°), possibly as a result of interactions between neighbouring fish (Domenici and Batty, 1994).

A relevant parameter for the interspecific comparison of turning performance would be the range of escape angles performed by a given species. Mean values would be irrelevant because they would depend on stimulus angle (Eaton and Emberley, 1991; Domenici and Blake, 1993*a*). If the stimulus is presented randomly, the mean escape angle is likely to be around 90°, as that would be the mean value of a uniform distribution between 0° and 180°. While escape angles of goldfish and angelfish were found to cover the entire 180° range on either side of the fish (Eaton and Emberley, 1991; Domenici and Blake, 1993*a*), it is not known whether other species show a limited range of angles. In angelfish, the range of escape angles of double-bend escapes (i.e. escape responses with directional change, Fig. 1) is limited and its upper limit is inversely proportional to body length, possibly because of a decrease in flexibility around the centre of mass in larger fish (Domenici and Blake, 1993*b*). Double-bend escapes show on average higher speed and acceleration but smaller escape angles than single-bend escapes (i.e. escape responses without directional change, Fig. 1; Domenici and Blake, 1991, 1993*b*). It would be worthwhile investigating such a trade-off between linear performance and turning in other fish species of different size, as well as the range of escape angles for both single- and double-bend responses.

Turning radius

Turning radius is a relevant variable in predator–prey interactions (e.g. Howland, 1974; Webb, 1976; Weihs and Webb, 1984). The turning radius of the approximately circular path of the centre of mass during an escape has been calculated for various species (Webb, 1976, 1983; Webb and Keyes, 1981; Domenici and Blake, 1991; Blake *et al.* 1995). Turning radius is independent of velocity but proportional to body length (Howland, 1974; Webb, 1976; Domenici and Blake, 1991). Therefore, the relative turning radius of an escaping fish is estimated as turning radius/body length. A low relative turning radius can be beneficial in complex environments (e.g. coral reefs and weedy rivers), and species from such environments (e.g. angelfish *Pterophyllum eimekei*, pike *Esox lucius*, knifefish *Xenomystus nigri*) show smaller relative turning radii than pelagic species such as yellowfin tuna (*Thunnus albacares*) and yellowtail (*Seriola dorsalis*) (Table 2). The latter two species are specialized pelagic cruisers, and the stiffness of their body helps to reduce drag during continuous swimming, although it is detrimental for turning radius performance. Consequent impairment of manoeuvrability in these predator species may be mitigated by group foraging behaviour (Webb and de Buffrenil, 1990; Blake *et al.* 1995).

Comparing performance

Technical errors and problems in comparing performance from different studies

When measuring the performance and kinematics of a short and fast event such as an escape response, high-speed

Table 2. *Summary of previous turning radius data*

Species	Common name	Relative turning radius	Author
Xenomystus nigri	Knifefish	0.055	M. A. Kasapi (unpublished)
Pterophyllum eimekei	Angelfish	0.065	Domenici and Blake (1991)
Esox lucius	Pike	0.09	D. G. Harper (unpublished)
Micropterus dolomieu	Smallmouth bass	0.13	Webb (1983)
Coryphaena hippurus	Dolphinfish	0.13	Webb and Keyes (1981)
Oncorhynchus mykiss	Rainbow trout	0.17, 0.18	Webb (1976, 1983)
Seriola dorsalis	Yellowtail	0.23	Webb and Keyes (1981)
Thunnus albacares	Yellowfin tuna	0.47	Blake *et al.* (1995)

Species are listed in order of increasing turning radius.
Relative turning radius is turning radius/body length.

cinematography or video recording is employed in order to resolve peak performance. While the measurement precision of most parameters such as speed, turning angle and turning radius increases with higher filming rates, the same is not necessarily true when a second derivative such as acceleration is considered. Harper and Blake (1989) consider the total error present in maximum acceleration data to be derived from two sources: sampling frequency error (SFE) and measurement error (ME). SFE is the error derived from the fact that filming samples an event periodically and therefore tends to average (or over-smooth) instantaneous acceleration. As the interval between frames lessens, so does the difference between frame-averaged and actual instantaneous accelerations. ME is the error involved in measuring the distance moved from frame to frame. Because ME arises during digitization of each frame of the film, it will also increase with film speed. As film speed increases, the distance moved per frame decreases, so digitizing error becomes a greater proportion of the measured distance. As a result, Harper and Blake (1989) found 300 Hz to be the optimal filming rate for their system. The potential error involved in acceleration measurements and its dependence on filming rate and the accuracy of the digitizing system have led various authors to consider other parameters of unsteady performance, such as velocity within a given time (Webb, 1976). Arguably, acceleration remains a key performance parameter for evaluating fast-start performance, although the implication of different filming rates used in various studies must be taken into account when comparing data for different species.

Comparing species performance in fast-starts can be confounded not only by differences in filming speeds but also by differences in temperature, fish size and fast-start type (feeding strikes tend to show lower performance than escape responses; Harper and Blake, 1991; Frith and Blake, 1995). Table 1 shows maximum acceleration and specific speed (body lengths s^{-1}) data for 14 different species. Acceleration data recorded at a filming rate of less than 100 Hz are unreliable, being subject to an underestimating error of more than 60 % (Harper and Blake, 1989), and higher filming rates need to take into account underestimation errors of 30 %

(filming rate 200 Hz) to 8 % (filming rate 400 Hz). Maximum speed during a fast-start is reported in body lengths s^{-1} because speed is size-dependent (Wardle, 1975). The comparison of speeds should be made between fish of similar sizes, because small fish can attain higher length-specific speeds than larger fish (Wardle, 1975). Ideally, speed within a given time should be considered in fast-start studies (Webb, 1976). However, only a few authors have measured this parameter (Webb, 1976; Gamperl *et al.* 1991; Domenici and Blake, 1993*b*).

Comparative performance and functional design

In the following paragraphs, we will refer to velocity, acceleration and turning radius together as fast-start performance, unless specified. The species most often considered for comparisons are those for which all these parameters have been measured. For acceleration values, those derived by accelerometry or the highest filming rates are the most reliable. Turning angles are not considered below because there are only two species for which the range of turning angles has been measured (*Carassius auratus*, Eaton and Emberley, 1991; *Pterophyllum eimekei*, Domenici and Blake, 1991, 1993*a,b*). Both fish can escape at turning angles as large as approximately 180 ° on either side of the body axis.

Webb (1984*a*) attempted to divide fish into three basic categories according to their body shape, swimming style and the performance data available at the time. Webb argued that there are three main swimming specializations, cruising (BCFP, body/caudal fin periodic propulsion), accelerating (BCFT, body/caudal fin transient propulsion) and manoeuvring (MPF, median/pair fin propulsion). Specialist fish which excel in one of these functions sacrifice performance in the others. Alternatively, generalist fish perform moderately well in all functions but have superior performance in none. Harper and Blake (1990) showed that pike, an acceleration specialist, has a higher fast-start performance (velocity and acceleration) than trout, a generalist (Table 1).

Recent data on unsteady swimming of manoeuvring specialists (Domenici and Blake, 1991; Kasapi *et al.* 1993, Table 1) suggest some necessary amendments to Webb's view.

His idea seems to hold for cruising and accelerating, when fish propel themselves utilizing one locomotory system (body/caudal fin locomotion). Adaptations for acceleration clearly contrast with those for cruising. High acceleration performance requires a large tail and a deep body to enhance thrust, body flexibility which allows large-amplitude propulsive movements, and a high percentage of anaerobic musculature to power burst swimming. In contrast, cruising adaptations include a lunate tail to minimize drag, a stiff body to minimize recoil and therefore drag, and a high percentage of red musculature for endurance. Fast-starts imply axial locomotion and manoeuvring implies median/pair fin locomotion. These are decoupled systems, and adaptation for one does not necessarily impair performance in the other (Blake, 1996). Manoeuvre 'specialists', such as angelfish, are propelled at low speed by their pectoral fins. High manoeuvrability is facilitated by the lateral insertion of these fins, by extended anal and dorsal fins, and by a deep laterally flattened body (Webb, 1984*a*). Despite a relatively low percentage of muscle mass, the deep body and high flexibility allow angelfish to perform relatively well in fast-starts (Domenici and Blake, 1991). Their maximum acceleration is similar to that of pike, an acceleration specialist, and superior to that of trout, a generalist (Table 1).

Webb's ideas on form and function are based on locomotory modes employed when feeding. However, fish that are considered to be low-speed cruisers with respect to their foraging behaviour feature a decoupled system that allows them to perform bursts of high acceleration when attacked by predators. Arguably, swimming abilities have not been selected solely as a means of foraging, but also as an anti-predator adaptation. In addition, predicting performance from a given morphology may not be as straightforward as previously thought. This is particularly true for fish with decoupled systems, such as the knifefish, where designs are not the result of simple trade-offs. The knifefish body is tapered posteriorly and lacks a caudal fin. Knifefish swim at low speed, undulating their long anal fin while keeping their body rigid (Blake, 1983*b*; Lighthill and Blake, 1990). When startled, like most fish, knifefish execute an escape response. On the basis of their morphology, one would predict poor fast-start performance, because of their narrow body depth posteriorly and their lack of a tail (Webb, 1984*a*). However, their fast-start performance is relatively good (Kasapi *et al.* 1993; Table 1). Knifefish perform an unusual three-dimensional escape response where the C-bend is restricted to the anterior two-thirds of the body, and rolling and pitching are involved. The peculiarity of the response may account for the surprising performance.

Linking habitat type and performance characteristics

Any given body 'design' characteristic may influence more than just swimming performance (e.g. body form influences the conspicuousness of a predator or a prey and, consequently, its ability to catch prey or to escape from a predator, respectively). This makes it difficult to find a single design factor which may

serve as a true indicator of swimming 'ability'. Similarly, species that show similar performance levels may have different anatomical and physiological characteristics. Therefore, particular design characteristics are not always reliable predictors of swimming performance.

Swimming performance may be related to habitat type. Fish living in complex environments such as coral reefs and weedy rivers tend to have better fast-start performance than fish living in habitats of intermediate complexity or open-water species. Angelfish (*P. eimekei*), knifefish (*X. nigri*) and pike (*E. lucius*) show better unsteady swimming performance (turning radius, velocity, acceleration) than trout (*O. mykiss*), yellowtail (*Seriola dorsalis*) and yellowfin tuna (*Thunnus albacares*) (Domenici and Blake, 1991; Kasapi *et al.* 1993; Harper and Blake, 1990; Webb and Keyes, 1981; Blake *et al.* 1995; Tables 1, 2). While the body forms of pike, angelfish and knifefish are quite different, they are all found in complex habitats. Complex habitats reduce predator–prey interactions to brief encounters, where unsteady swimming ability and manoeuvrability are advantageous to both predators and prey. The endurance requirements in complex habitats are 'decoupled' from the unsteady locomotory system. While the latter is provided by the anaerobic axial musculature, endurance at low speed is powered aerobically by the median/pectoral fins. Pike are predators specialized in median- and paired-fin swimming, which is utilized in hovering and manoeuvring while positioning before striking at prey (Webb and Skadsen, 1980; Harper and Blake, 1988). In addition, speed and acceleration contribute to high capture success. Angelfish are herbivorous fish characterized by specializations for efficient low-speed swimming (Blake, 1983*a*) while foraging among the weeds, but also show high fast-start performance for escaping from predators. Fish from complex habitats often possess a well-defined 'two-gear' system (low speed and burst speed) in contrast to pelagic fish which most often swim at intermediate speeds.

Pike and angelfish both live in complex habitats and show similar swimming performance (turning radius, acceleration), yet they have very different morphologies. Pike are elongated, with a narrow head, a large tail and posteriorly placed median fins, while angelfish are disk-shaped, have centrally placed median fins and a large tail. Their designs are well suited for complex environments, where BCF transient swimming and MPF swimming are necessary. In both species, large posterior body depth contributes to good BCF transient swimming performance. Good MPF performance is ensured by large, laterally placed pectoral fins in angelfish, and by large pectoral and pelvic fins in pike. Angelfish and pike can utilize median and paired fins in hovering and swimming backwards. There is no optimal design for MPF swimmers, as they are not subject to the same design constraints encountered by BCF periodic swimmers, which show convergence of body form aimed at minimizing drag (Blake, 1996). The differences in the morphology of angelfish and pike may be correlated to their different lifestyles and to factors that are not necessarily linked to locomotor performance. Webb (1984*b*) showed that the low

body profile of pike contributes to their high prey capture rate, because their body shape induces very short reaction distances in their prey. In contrast, large body depths such as that of angelfish may act as a deterrent for predators that are gape-limited (Hambright, 1991; Brönmark and Miner, 1992).

Fast-starts in predator–prey encounters

Predator attacks

Timing is one of the most important components in predator–prey encounters. Attack speed is not necessarily correlated with successful prey capture. Dill (1974) showed that the prey's reaction distance increases with the speed and the depth of the body profile of a predator. A rapid approach by the predator may trigger an early response in the prey, allowing it to escape. Therefore, the fast-start performance of attacking predators is often sub-maximal (Webb, 1984*b*; Harper and Blake, 1991). As a result of the dependence of prey reaction distance on both predator speed and body profile, predators with a narrow body depth, such as pike, can afford to attack at relatively high speed without inducing an early response in the prey (Webb, 1984*b*).

Other factors are also important in capturing prey. If the mouth is opened too early, the predator may fail to capture its prey (Rand and Lauder, 1981). In addition, predators aim at the centre of mass of their prey (Webb and Skadsen, 1980). Webb and Skadsen (1980) suggested that the centre of mass is the best target for a predator, since it can be readily located from the prey geometry and it is the point of a prey that moves the least during escapes.

The orientation of the predator relative to the prey before an attack tends to be perpendicular in most cases (Webb and Skadsen, 1980). Webb and Skadsen (1980) argue that such an orientation would keep the escape paths of the prey aligned to the predator's strike. This would be true if prey consistently escaped with turning angles of 90°. However, Domenici and Blake (1991) and Eaton and Emberley (1991) showed that turning angles in escape responses are much more variable. Attacking prey from the side may offer other advantages, such as maximizing the body surface of prey at which to aim. This mechanism would be related to prey shape, although the maximum body depth of most species is at their centre of mass. Indeed, striking angles may also be species-specific (Hoogland *et al.* 1956) and possibly influenced by gape limitation in addition to prey shape and other design factors, such as false eye spots (e.g. McPhail, 1977).

Prey escapes

Various factors contribute to escape performance in fish: distance travelled, speed and acceleration (Webb, 1976; Harper and Blake, 1990), turning angle and turning radius (Webb, 1976; Eaton and Hackett, 1984; Domenici and Blake, 1991), response latencies (Eaton and Hackett, 1984), reaction distance (Dill, 1974) and sensory responsiveness (Blaxter and Fuiman, 1990). Since the aim of this paper is to review performance

and kinematic data, we will discuss the relevance of linear and angular variables within the context of prey escape.

Harper and Blake (1991) showed that the velocity and acceleration of escaping fish is on average higher than that of the same individuals when striking at prey. This is possibly due to the employment of sub-maximal performance by attacking predators, as the reaction distance of the prey would increase with attack speed (Webb, 1984*b*). In addition, Frith and Blake (1995) suggested that the superior acceleration rate achieved during the initial stages of a C-start when compared with an S-start can be explained in part by the greater maximum angles of attack, higher lateral and perpendicular velocities and larger maximum forces produced by the caudal fin.

In the case of prey, it seems reasonable to suggest that the best strategy would be to escape at the highest speed and acceleration possible. However, the linear performance of escaping fish is not always maximal. Webb (1986*b*) found that the prey speed was often sub-maximal in responses to predator attacks that were not followed by chases. Therefore, motivation may play a role in determining the fast-start performance of escaping prey. Domenici and Blake (1993*b*) found that the speed of large angelfish is compromised at large angles of escape. Turning angles are an important factor for escaping predators. The 'choice' of turning angles determines fixed preferred escape trajectories (Domenici and Blake, 1993*a*). Particular trajectories may maximize parameters related to escape success (e.g. sensory awareness, Domenici and Blake, 1993*a*; distance from the threat, Weihs and Webb, 1984; Domenici and Blake, 1993*a*).

An additional angular parameter is the orientation of the prey relative to the attacking predator. Domenici and Blake (1993*a*) found that angelfish usually escape away from a stimulus when this is at 60–120° to the side of the fish. If the stimulus is frontal or caudal to the fish, escape trajectories are randomly distributed around 360°, possibly because of a decrease in left–right discrimination when the stimulus is more in line with the longitudinal body axis. In these situations, the prey may end up escaping towards the predator's mouth. This finding must have some implication in the relative orientation of predators and prey in the wild. Webb and Skadsen (1980) suggested that predators tend to attack prey perpendicularly. It would be interesting to investigate to what extent this orientation results from the predator's attack tactics or if it is also influenced by the prey's defensive strategies. In schooling fish such as herring, the trajectories of escape responses in which the initial turn (during stage 1) is towards the stimulus are corrected to the extent that the final angle of escape (at the end of stage 2) is directed away from the stimulus (Domenici and Batty, 1994). Domenici and Batty (1994, 1997) suggested that this behaviour may be due to the influence of schooling neighbours, most of which show stage 1 angles away from the stimulus.

Concluding remarks

The study of fast-starts has progressed considerably in the

past decade. Recent studies of escape responses have shown a remarkable variability in kinematics (Foreman and Eaton, 1993; Domenici and Blake, 1991, 1993*a*). This is due to the development of image-processing systems which allow the analysis of a large number of escape responses within a relatively short time. Escape responses were shown to imply turns which vary from 0 to 180° on either side of the fish (Foreman and Eaton, 1993; Domenici and Blake, 1993*a*). In addition, escape angles were shown to be related to stimulus angle (Eaton and Emberley, 1991; Domenici and Blake, 1993*a*). Video analysis linked with electromyograms has allowed the evaluation of the relationship between kinematics and muscle activity (Foreman and Eaton, 1993; Jayne and Lauder, 1993). Jayne and Lauder (1993) have shown that only the onset of stage 1 EMG activity is synchronous along the fish, while stage 1 EMG offset as well as stage 2 EMG on- and offset show significant posterior propagation. Foreman and Eaton (1993) have shown that the ipsilateral contraction during stage 1 is not necessarily followed by a contralateral contraction, confirming previous kinematic studies (Domenici and Blake, 1991; Kasapi *et al.* 1993).

Domenici and Batty (1994, 1997) have observed the occurrence of two escape types with difference latencies and kinematics in herring. Intracellular recordings of the Mauthner cell are needed to establish whether these two escape types correspond to differential neural control, the longer latency possibly being associated with non-Mauthner-cell commands. Future studies of escape responses should consider applying startle stimuli from various directions in order to reveal variations in kinematics among different species. In addition, the simultaneous use of electromyography and video analysis (as in Foreman and Eaton, 1993) should be employed to investigate the variability in stage 1 and stage 2 muscular activity and the potential contribution of passive elastic elements in fast-starts. While the contribution of passive elastic elements has been investigated in steady swimming (Wainwright *et al.* 1978), there is no such study for fast-starts. Given the amount of bending experienced by fish during fast-starts (particularly during escape responses), such studies would be welcomed. An integrative approach would allow the investigation of the potential trade-off occurring in turning angles between maximizing energy storage in bending the body and optimizing swimming trajectories to escape from predators.

More effort needs to be put into understanding the relationship between the kinematics and physiology of S-starts (Fig. 5). Webb and Skadsen (1980) observed two kinematic types of S-starts, but their correlation with muscle activity is still unknown. In addition, nothing is known regarding the neural control of S-starts and whether escape responses described as S-starts by some authors (Webb, 1976; Harper and Blake, 1991) differ neurophysiologically from C-type escape responses.

Our knowledge of fast-start performance has made considerable advances in the last few years. The use of high-speed video-recording and subcutaneous accelerometry has allowed much improvement in the evaluation of fast-start performance, particulary for acceleration. Harper and Blake (1989) suggested that many previous studies of fast-start performance may have considerably underestimated acceleration. Fast-start performance was hypothesized to trade off with both cruising performance and manoeuvrability (Webb, 1984*a*). Recent studies on the performance of species previously considered to be manoeuvre specialists (Domenici and Blake, 1991, 1993*b*; Kasapi *et al.* 1993) have shown that specialization for good manoeuvrability does not compromise fast-start performance. Although data on the turning radius of various pelagic fish (Table 2) suggest that fast-start performance may be relatively poor in species with good cruising performance, no study has yet investigated the acceleration performance of pelagic species during fast-starts. Table 1 shows that more than half of all fast-start studies on performance have focused on two species, rainbow trout and pike. Since fast-start behaviour is present in most fish species, as shown by the widespread presence of Mauthner cells in fish (Eaton and Hackett, 1984), and its variability is starting to become apparent, fast-start kinematics and performance should be studied in a much wider variety of species of different shapes and sizes.

Since fast-start behaviour is utilized mainly for prey capture and predator evasion, studies linking kinematics and performance with behaviour and ecology could lead to a better understanding of predator–prey relationships. For instance, integrating the scaling of fast-start performance with behaviour and ecology may be essential for understanding important ecological parameters such as prey size distributions of piscivorous predators. In addition, although there are various studies of predator–prey interactions in the laboratory (e.g. Webb, 1984*b*, 1986*b*), the relative importance of various kinematic and performance variables in the field is unknown.

Fast-start swimming is a promising area of study since it allows the integration of various levels of biology, from neurobiology to biomechanics and ecology. While the study of animal locomotion is often compartmentalized into sub-areas, such as muscle mechanics, kinematics and neurophysiology, a multidisciplinary approach can be valuable in understanding fast-start swimming. Unlike other locomotory activities, such as steady swimming, fast-start swimming is utilized by fish mainly in a specific behavioural context (predator–prey interactions) of great ecological importance. This should be taken into consideration in studies of fast-starts at any level of complexity. For example, neurobiological studies of the directionality and timing of the Mauthner cells must take into account that escape responses are utilized by fish in order to avoid predation (Eaton and Hackett, 1984). Studies of muscle mechanics should take into account the behavioural consideration that fast-start performance is not necessarily maximal since maximal escape or capture success may imply sub-maximal speeds (Webb, 1986*b*; Domenici and Blake, 1993*b*). Carling *et al.* (1994) apply a multidisciplinary approach to the study of steady swimming in the lamprey.

Their approach includes various levels of complexity, from neural commands to the mechanical properties of the lamprey, muscular activity, hydrodynamics and finally to the kinematics describing the forward swimming. Such an integrative approach to animal locomotion is very promising. In the case of fast-starts, the levels of complexity can be expanded to include the specific behavioural context of predator–prey encounters as well as the ecological context of predator–prey relationships.

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