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MECHANICS OF ESCAPE RESPONSES IN CRAYFISH (*ORCONECTES VIRILIS*)

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SUMMARY

Measurements of acceleration performance of crayfish (mean mass 0·018 kg) were made during lateral giant mediated tail flips (LG tail flips) and truncated tail flips at 15 °C. The LG tail flip power stroke was composed of a lift-off phase, when crayfish accelerated vertically from the substrate, and a free swimming phase. The total duration of the power stroke was 44 ms, followed by a recovery stroke lasting 173 ms. Truncated tail flips were used in acceleration and swimming by crayfish free of the substrate. Power strokes had a mean duration of 36 ms, and recovery strokes 92 ms. Net velocities, acceleration rates, and distances travelled by the centre of mass were similar for both types of tail flips. Thrust was generated almost entirely by the uropods and telson. Velocities and angles of orientation to the horizontal of abdominal segments were similar for both types of tail flip. Angles of attack were large, varying from 30° to 90°. Pressure (drag) forces were considered negligible compared to inertial forces associated with the acceleration of added water mass. Thrust forces, energy and power were determined for exemplary tail flips. Thrust was 0·92 and 0·42 N for LG tail flip lift-off and swimming phases respectively, and 0·29 N for the swimming truncated tail flip. Rates of working were 0·39, 0·19, and 0·18 W respectively. The efficiency of converting muscle power to backward motion was estimated to be 0·5 for power strokes and 0·68 for complete swimming cycles. Comparisons with fish performance suggested fish would be less efficient (0·1–0·2). The low efficiency is attributed to energy lost in lateral recoil movements.

INTRODUCTION

High-speed acceleration is characteristic of escape responses of fish, cephalopods and arthropods (Lochhead, 1961, 1977; Packard, 1972). Acceleration mechanics and performance of fish and cephalopods have been studied in some detail (see Alexander, 1977; Webb, 1978*a*, for references). In contrast, little is known on arthropod acceleration escape mechanics. Studies have concentrated on walking, steady swimming using the legs as oars (see Gray, 1968; Alexander, 1977), and on the neurophysiology of crayfish and lobster escape responses (e.g. Wine & Krasne, 1972; Wine & Hagiwara, 1977; Wine, 1977*a*, *b*). Some insects use jet propulsion to escape threats (e.g. Hughes, 1958), but most arthropods swim using segmental appendages or the abdomen. In crayfish, lobsters and fish, escape responses are superficially similar in that large amplitude movements of an expanded caudal area are involved. However, crustaceans differ from fish in several key respects.

The size of the abdomen of a lobster or crayfish is small compared to the rest of the body (Lang *et al.* 1977). Therefore the volume of muscle will be relatively small compared to that of fish. The exoskeleton of crayfish and lobsters is also heavy so that the muscle available to accelerate the animal is low compared to the mass to be accelerated, i.e. percentage muscle mass is low compared to fish. Acceleration behaviour is presumed adaptive, in which case it would be expected that the mechanical efficiency of the crayfish propulsive system ('propeller efficiency') is relatively high to compensate for the small percent muscle mass. By implication, that of fish would be relatively low.

Fish appear to be relatively inefficient in acceleration fast-starts compared to steady swimming. In the latter, propeller efficiencies up to 0·95 are expected (Wu, 1971; Webb, 1975*b*). If the same propeller efficiency applied to fast-starts, and muscle stresses were about 90 kN m^{-2}, typical of working muscle (Alexander, 1973), then acceleration rates should be 5–10 times greater than observed. McCutchen (1977) has calculated Froude efficiency from the wake energy during turns, which are mechanically similar to fast-starts (Weihs, 1973). McCutchen found the Froude efficiency was about 0·44.

The apparent differences between fish and crayfish therefore suggest that a comparison of their acceleration performance would be appropriate to evaluate questions of functional design, particularly questions relating to efficiency of the propulsion system. The purpose of the study reported here was to obtain performance measures for crayfish acceleration tail flips comparable to those recently made on fish (see Webb, 1978*b*, for references) and to evaluate the mechanics of the propulsion system.

MATERIALS AND METHODS

Crayfish (*Orconectes virilis* Hagen) were collected locally and held in 200 l tanks flushed continuously with water at 50 l h^{-1}. Crayfish were acclimated to 15 °C and then held at 15 ± 0·2 °C for at least 2 weeks before testing. Dissolved oxygen levels were maintained close to air saturation by means of air stones. Crayfish were fed daily on freshly killed fish.

Ten healthy individuals were selected for experiments. Individuals were placed in an observation chamber 0·3 m in length, 0·3 m in height and 0·1 m in width. After 20 h acclimation to the chamber, a d.c. electric shock of 0·01 V m^{-1} was applied across the length of the chamber via aluminum screens covering each end. No limb autotomy occurred immediately following the stimulus, nor in the following 48 h, with a single exception. One crayfish shed its chelipeds after several hours. Data from this individual were rejected. The stimulus initiated a tail-flip escape response. Swimming tail flips were also observed when crayfish were chased with a rod. All swimming movements were recorded on movie film at a framing rate of 250 Hz. The film record included a 50 Hz calibration signal.

Forty-eight hours after an experiment, crayfish were weighed and length (uropods to rostrum) was measured. The body outline of stretched-straight crayfish was traced, and the projected area of propulsive abdominal segments was measured. Individuals were then deeply frozen in three positions covering the observed range of body positions during swimming (see Fig. 1). The centre of mass (centre of gravity

Table 1. *Physical characteristics of crayfish used in acceleration performance and swimming experiments*

(Means ±2 S.E. are shown.)

Length (cm)	8·3±0·6
Mass (g)	18·34±2·35
Flexor muscle mass (g)	2·98±0·41
Mean cross-sectional area of flexor muscle (cm^2)	0·67±0·05
Projected area of extended uropods (cm^2)	4·7±0·5
Total projected area of abdomen (cm^2)	9·6±0·9
Width of extended uropods (cm)	4·0±0·2
Centre of mass:	
(*a*) Abdomen fully extended	
Horizontal distance from rostrum (cm)	3·1±0·4
Vertical distance from dorsal surface (cm)	0·9±0·1
(*b*) Abdomen half extended	
Horizontal distance (cm)	3·0±0·3
Vertical distance (cm)	1·0±0·1
(*c*) Abdomen fully flexed	
Horizontal distance (cm)	2·9±0·1
Vertical distance (cm)	1·0±0·1

in air) was determined for these positions as the point of intersection of two plumb-lines on the lateral surface when crayfish were suspended from two points on the body. The centre of mass was assumed to be located in the median plane at this point. Crayfish were thawed sufficiently to bend the abdomen, and refrozen in new positions. This was repeated for the third position.

The flexor muscles of each crayfish were dissected and weighed on completion of measurements of the centre of mass. This muscle was also weighed for a second sample of crayfish of similar mean size in case freezing and thawing affected the measurement. No effect was found.

A sample of crayfish of similar size to those used for swimming experiments was cut transversely into sections. Each section was weighed to determine the distribution of mass along the body. Tracings were made of the cross-sectional shape. For abdominal sections, these tracings were made with and without the enclosed flexor muscle in order to determine the cross-sectional area of that muscle.

Physical characteristics of the crayfish are summarized in Table 1.

Film records were analysed frame by frame to observe swimming kinematics. Motions of the centre of mass were recorded for all tail flips because the centre of mass is the point about which propulsion forces act. The mean location of the centre of mass was used because changes in position were not significant for the range of postures spanning swimming movements (Table 1). Data for distances travelled by the centre of mass were analysed using moving point linear regression to calculate net velocity and acceleration rate (see Webb, 1978*a*, for details). The duration of swimming movements was recorded from the times when the uropods were stationary relative to the body (*a*) with the abdomen extended and (*b*) with the abdomen fully flexed (power stroke) and (*c*) with the abdomen re-extended (recovery stroke).

Following this analysis, exemplary tail-flip responses were identified and re-analysed in detail to determine forces developed during swimming. Additional measurements made for each abdominal segment were (*a*) velocity with respect to

the centre of mass, (*b*) angle of attack to incident water flow and (*c*) orientation angle to the horizontal. The velocity of each segment relative to the water (resultant velocity) was obtained by difference from (*a*) its velocity relative to the centre of mass and (*b*) the velocity of the centre of mass. This method has been used in analysing swimming of insects (Nachtigall, 1960, 1965).

Drag of crayfish was calculated during deceleration glides following swimming strokes (Gero, 1952; Vlymen, 1970), and expressed as a function of the mean velocity during 4 ms deceleration periods.

RESULTS

Locomotory movements

Escape responses and swimming movements of crayfish have been classified by Wine & Krasne (1972). Responses observed in the present experiments were all tail flips of the type initiated via the lateral pair of giant axons (LG tail flips) and truncated tail flips. The former were observed in crayfish accelerating from the substrate. Truncated tail flips were observed in crayfish suspended in the water column.

Body movements during an LG tail flip are illustrated in Fig. 1. Prior to stimulation, crayfish showed typical defensive display stances with the tail (abdomen and uropods) fully extended. Following stimulation, the tail was flexed in a single rapid movement, with the uropods moving first ventrally and forward, and then dorsally to touch the thorax. This stroke had a mean duration of 44 ms (Table 2). On completion of the power stroke, the uropods were flexed. They remained flexed as the tail was slowly extended during a prolonged recovery stroke lasting 173 ms. Crayfish did not continue swimming following tail extension in these experiments.

Although the LG tail flip power stroke was a single smooth movement, the motion of the centre of mass was more complex. This was because the uropods, the anterior of the body, and chelae remained in contact with the substrate for the first half of the stroke (24 ms in Fig. 1). During this part of the LG tail flip power stroke, the thorax rotated upwards and slightly forward about the rostrum. The abdomen bent ventrally, bringing the uropods forward. Thus the centre of mass was accelerated vertically upwards accelerating the crayfish from the substrate.

During the second part of the LG tail-flip power stroke (24–48 ms in Fig. 1) the crayfish continued to move vertically upwards (but while decelerating) lifting the body completely clear of the substrate. The uropods continued to move forward, generating thrust, so that the crayfish began to accelerate backwards. The body axis remained rotated with respect to the horizontal axis returning to the horizontal during the recovery stroke.

The LG tail-flip power stroke must be divided into two functional phases: (*a*) lift-off and (*b*) swimming. These two places are obviously important for a negatively buoyant (Pond, 1975) benthic animal to permit escape and free swimming away from the substrate.

Truncated tail flips were used to accelerate from rest in the water column (acceleration strokes) and for swimming with repeated power and recovery strokes (swimming strokes). Body movements relative to the centre of mass were essentially the same for all truncated tail flips. A typical example of a swimming stroke is shown in

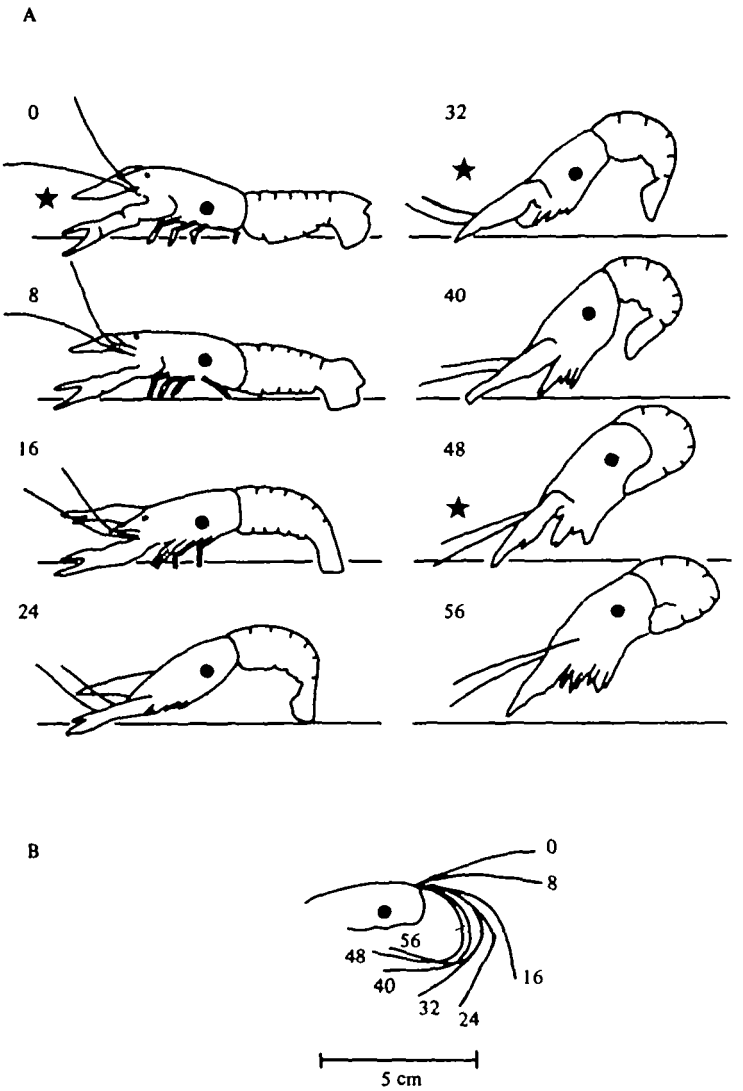

Fig. 1. Tracings from movie film of a crayfish during an LG tail flip. (A) Outlines of body form. (B) Superimposed outlines of the posterior to show abdomen motions (dorsal surface) relative to the centre of mass. Alternate frames are shown at 8 ms intervals. Solid circles show the centre mass. Stars indicate body patterns used to measure the centre of mass (see Materials and Methods).

Fig. 2. During power strokes the uropods were extended and the tail rapidly flexed similar to the second phase of the LG tail flip (Lindberg, 1955; Wine & Krasne, 1972). Acceleration strokes were completed in 43 ms, comparable to LG tail-flip power strokes. Subsequent swimming truncated tail flips were of progressively shorter duration (Table 2). The overall mean duration for power strokes was 36 ms.

The uropods were flexed on completion of the truncated tail flip power stroke and remained flexed as the tail was extended. Differences between successive recovery strokes were not significant. The mean extension time was 92 ms (2–3 times the

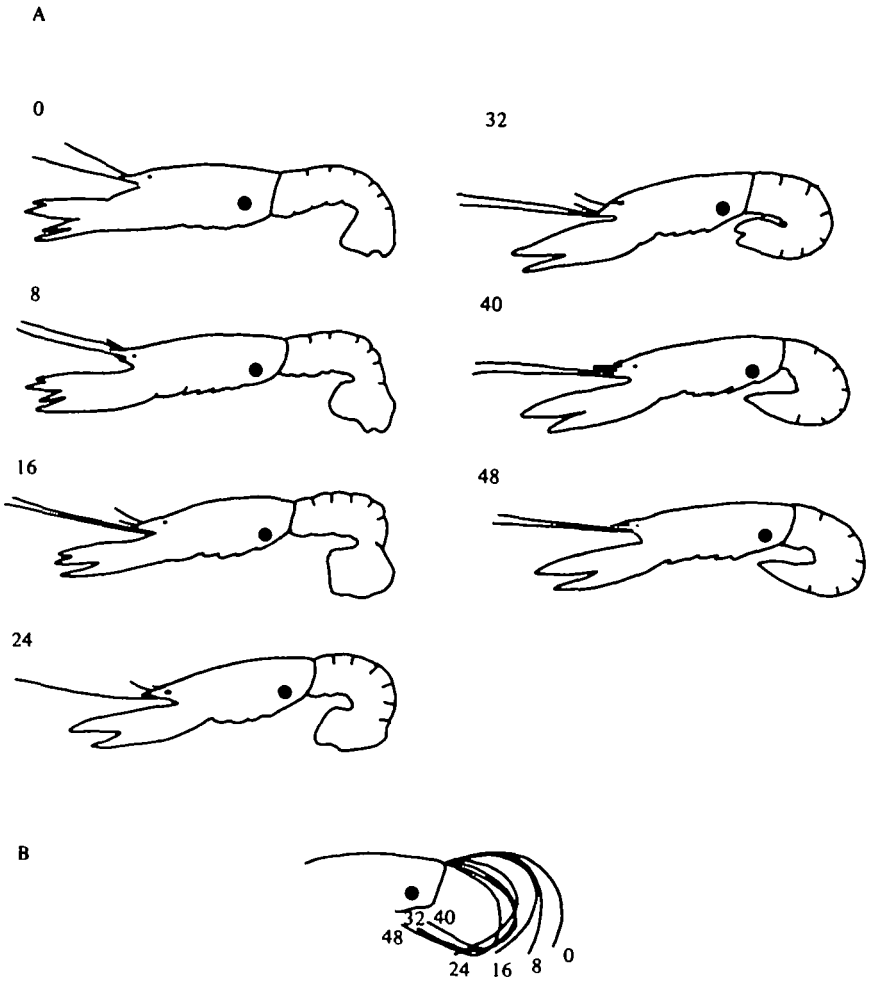

Fig. 2. Tracings from movie film as in Fig. 1, of a crayfish during a swimming truncated tail flip. (A) Outlines of body form. (B) Superimposed outlines of the posterior to show abdomen motions (dorsal surface) relative to the centre of mass.

power stroke). Swimming movements were repeated up to 25 times, but crayfish usually struck the chamber walls after 4 or 5 strokes.

During repeated swimming strokes, crayfish moved primarily backwards in a more or less horizontal plane. Couples generated by the uropods rotated the tail upwards to a small extent so there was usually a small vertical movement. However this was a very small percentage of the horizontal motion. During recovery strokes crayfish continued to glide backwards and, because of their negative buoyancy, downwards.

Net performance

The overall performance of LG and acceleration truncated tail flips is summarized in Fig. 3 and Table 2. Net motions are analysed here for the centre of mass resolved along its path and hence show the resultant effect of forces accelerating the crayfish.

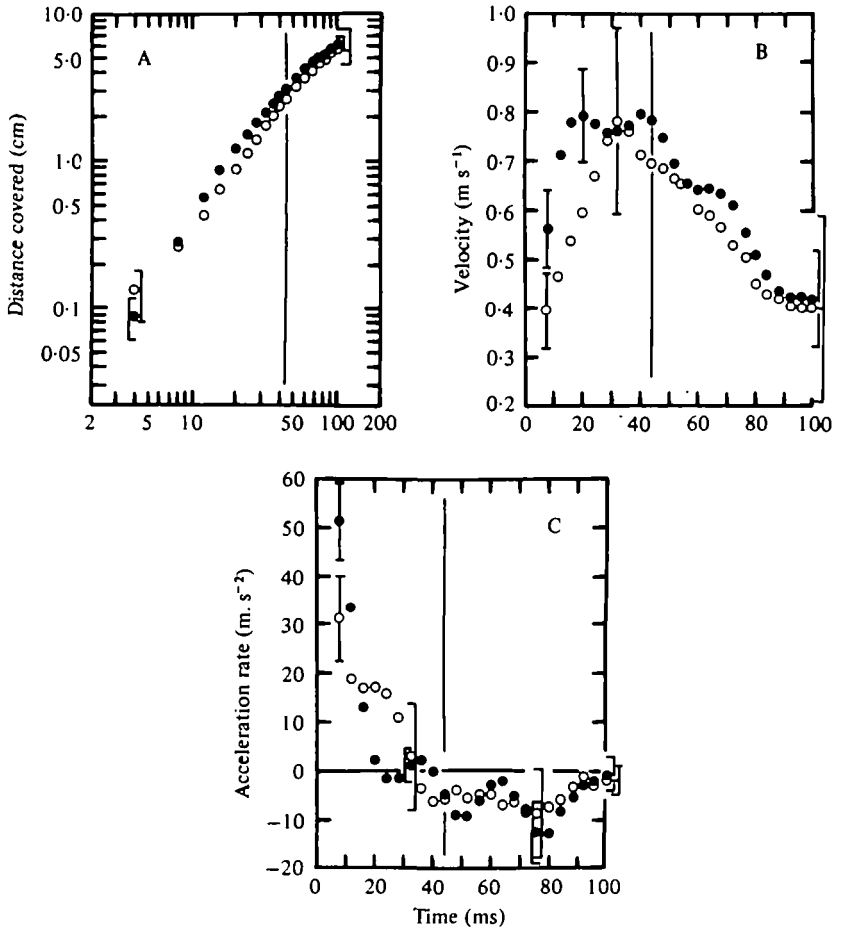

Fig. 3. Time relations for (A) distance covered, (B) velocity, and (C) acceleration rate for the centre of mass of crayfish in LG tail flips (open circles) and truncated tail flips (closed circles). For clarity, error bars (± 2 S.E.) are omitted for most points. They are included to show the magnitude of variation for first and last points, maxima and minima in (A)–(C), and some data close to zero acceleration rate in (C). The solid vertical line shows the time to the end of the power stroke for the LG tail flip and the first truncated tail flip. Note in (A) the double logarithm scale, and alternate data points only during the recovery stroke.

Performance was remarkably similar for various swimming patterns. The largest differences occurred because of the LG tail flip lift off which gave the centre of a mass a large (vertical) velocity early in the power stroke. However, this high velocity was maintained as the direction of motion shifted to the horizontal. The lift-off phase also achieved higher maximum acceleration rates. Truncated tail flip maximum acceleration rates were comparable to fish (Webb, 1978*a*), but exceed those reported for cephalopods (Trueman & Packard, 1968; Packard, 1969). Acceleration movements propelled the crayfish a total distance of 0·031 m in the LG tail flip power stroke, and 0·026 m in the truncated tail flip power stroke. These distances are 1·5–2 times greater than distances travelled by cephalopods and fish in the same time (Trueman & Packard, 1968; Packard, 1969; Webb, 1978*a*). Maximum velocities during the crayfish power strokes were also superior to those attained by cephalopods and fish in the

Table 2. *Summary of net acceleration performance along the path of the centre of mass of crayfish at 15 °C to the end of power and recovery strokes*

(Means ±2 S.E. are shown.)

	Status at end of power stroke					Status at end of recovery stroke	
Stroke	Duration (ms)	Maximum acceleration rate ($m\ s^{-2}$)	Mean acceleration rate ($m\ s^{-2}$)	Maximum velocity ($m\ s^{-1}$)	Distance covered (cm)	Duration (ms)	Distance covered (cm)
LG tail flip	44±4	50·9±8·1	6·61±1·94	0·868±0·067	3·1±0·3	173±39	7·6±1·0
First truncated tail flip	43±13	37·0±12·0	10·3±7·0	0·842±296	2·6±1·0	99±4	5·4±2·0
Second truncated tail flip	39±6	42·5±21·0	7·85±2·36	0·871±0·411	2·7±1·4	97±9	5·6±1·6
Third truncated tail flip	30±5	—	—	—	—	86±14	—
Fourth truncated tail flip	29±5	—	—	—	—	85±26	—

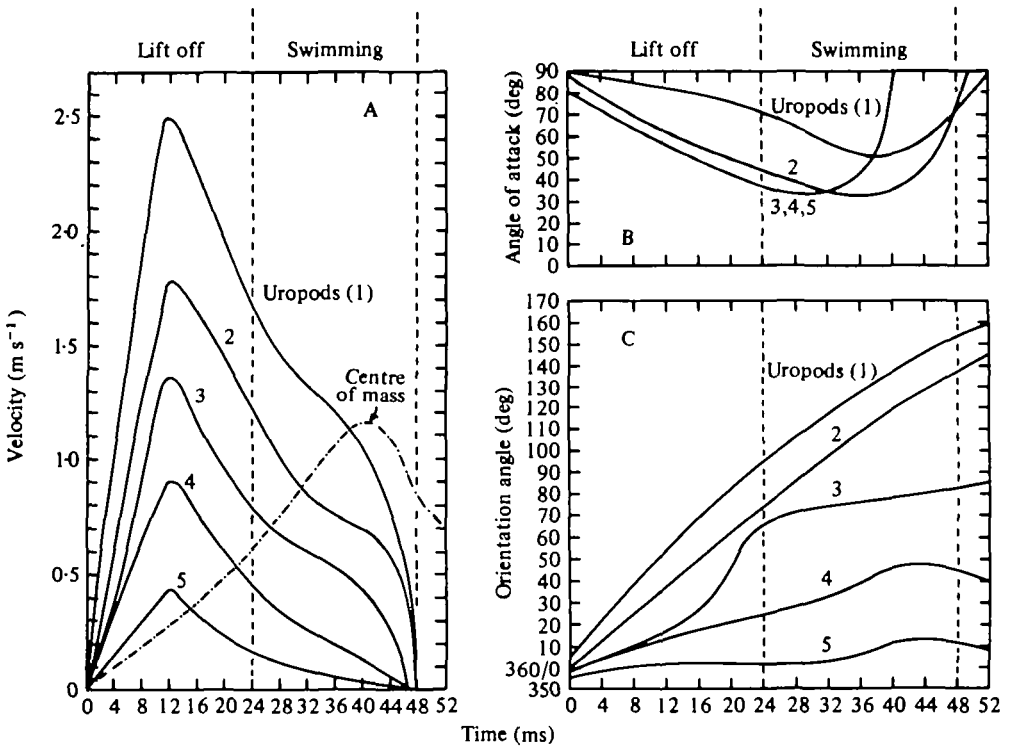

Fig. 4. Kinematics of abdominal segments (numbered from the uropods = 1) during an LG tail flip. (A) Velocity of segments relative to the centre of mass, and the velocity of the centre of mass relative to the water. (B) Angles of attack of abdominal segments to the incident water flow. (C) Orientation angles of segments relative to the horizontal axis. Curves were fitted by eye to data obtained from movie film at 250 frames s^{-1}. Horizontal lines delineate lift-off and swimming phases.

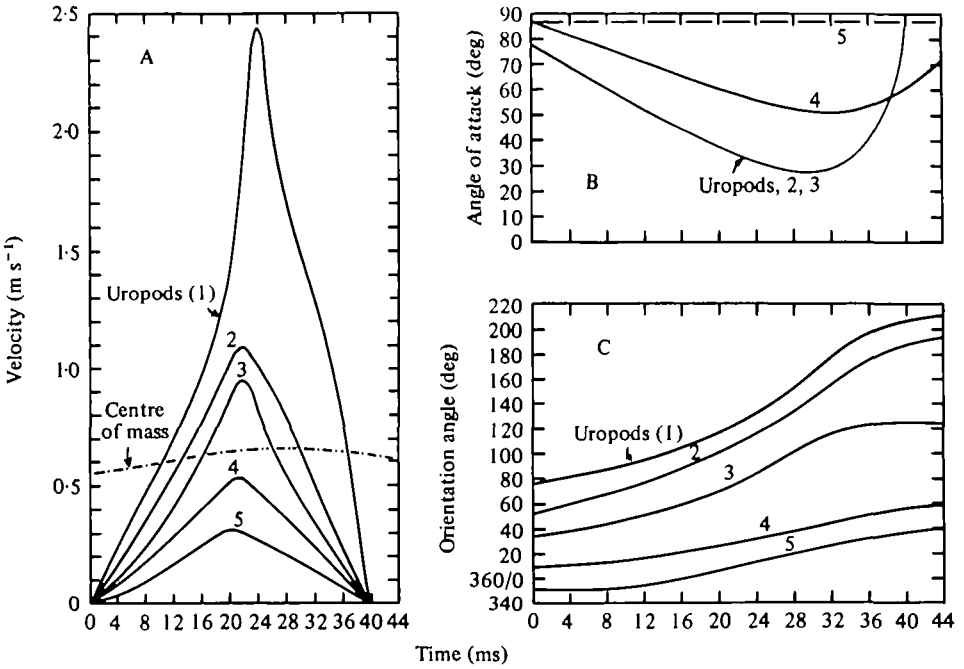

Fig. 5. Kinematics of abdominal segments during a swimming truncated tail flip. (A) Velocity of segments relative to the centre of mass relative to the water. (B) Angles of attack to the incident water flow. (C) Orientation angles to the horizontal axis.

same time. However, both these latter groups achieve greater performance than crayfish over longer periods of time. In fish, this occurs because a recovery stroke is absent. For cephalopods, the jet period is longer than the crayfish power stroke, and the recovery period relatively shorter.

Velocity and orientation of propulsive segments

In a discussion of the mechanics of swimming, the usual convention is to define the trailing edge as the zero position along the body. Therefore segments along the abdomen are defined with respect to the trailing edge, with the uropods and telson representing segment 1.

Results for velocity (relative to the centre of mass), angle of attack and orientation of the first propulsive segments are shown in Fig. 4 for an exemplary LG tail-flip sequence. Segments more proximal than 5 did not have significant motion different from the thorax. The velocity of other abdominal segments increased rapidly, reaching a maximum before lift-off was complete (Fig. 4A). Velocities decreased rostrally along the abdomen. During the swimming phase, only the uropods had an average velocity greater than the centre of mass. Therefore, only the uropods would contribute to net thrust during that phase. Angles of attack were large at the start of the power stroke, decreasing from maxima of about 90° to minima of about 33° in the swimming phase and thereafter increasing again. Angles of attack also decreased rostrally (Fig. 4B). Orientation angles increased from about zero to maximum values at the end of the power stroke. These angles also decreased rostrally.

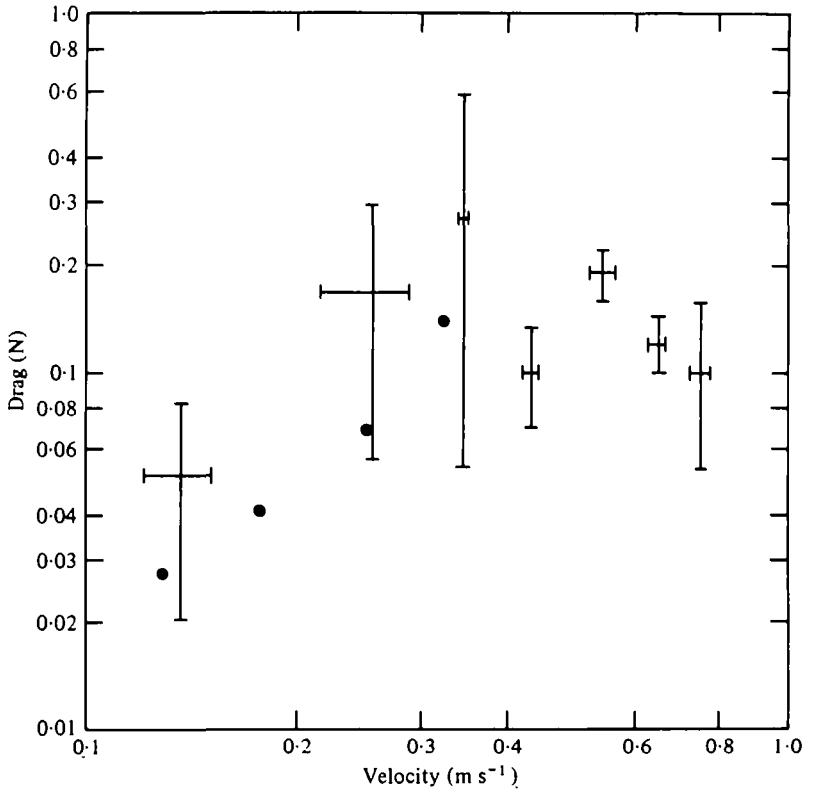

Fig. 6. The relationship between the drag of decelerating crayfish during recovery strokes and mean velocity. Vertical and horizontal bars represent ±2 S.E. Solid circles show drag for dead *Austropotamobious pallipes* towed backwards (Pond, 1975).

Results are shown in Fig. 5 for a typical swimming truncated tail-flip power stroke. The pattern and magnitudes of velocities and orientation angles were very similar to the LG tail flip power stroke. However, although the pattern of changes in the angle of attack was also similar, they increased rostrally in the truncated tail flip, opposite to the LG tail flip. The uropods and telson again had mean velocities substantially greater than the centre of mass, and the second segment also had a small excess velocity. Therefore thrust will be dominated by uropods and telson, with a minor contribution from the second propulsive segment.

The data for the two swimming sequences show that crayfish exercise control over the orientation of the abdominal segments. This is shown by the differences in angle of attack along the abdomen in the power strokes analysed. In addition, angles of attack of propulsive segments 3–5 were similar for the LG tail flip, but for truncated tail flip, 1–3 were similar. It seems probable that crayfish can modulate thrust forces by controlling the angle of attack and the orientation angle of abdominal segments.

Acceleration truncated tail flips were similar to swimming truncated tail flips except that velocities of propulsive segments relative to the water had higher mean values. This was not because abdominal segments had a larger velocity about the centre of mass. Rather, the centre of mass was accelerated from zero in acceleration strokes, but was already in motion during swimming strokes so that mean resultant velocities

were lower in the latter. Angles of attack and orientation angles did not differ substantially for acceleration and swimming truncated tail flips.

Drag

Results from the calculation of drag, determined from rates of deceleration of crayfish during recovery strokes, are shown as a function of the mean velocity in Fig. 6. Drag increased with velocity up to 0·3 m s^{-1} in the same way as that measured by Pond (1975) for dead *Austropotamobious pallipes* (length 0·015 m) moving backwards. At higher velocities, drag was essentially independent of velocity, presumably because of changes in body shape towards higher drag shapes (body extended) at lower velocities. Over the velocity range 0·3–0·8 m s^{-1} drag averaged 0·12 N.

DISCUSSION

Mechanics

The angles of attack for abdominal segments were large. They exceeded stalling angles measured for lifting surfaces such as hydrofoils (Prandtl & Tietjens, 1934; von Mises, 1945). For reasonably steady motions, such as those predominating in rowing (Nachtigall, 1960, 1965), the large angles of attack would imply that thrust was generated by a resistance (pressure drag) mechanism. However, when an object accelerates in a fluid, an added mass of that fluid is accelerated with the object (e.g. Batchelor, 1967; Yih, 1969; Lighthill, 1970). The inertial effects due to acceleration of this added mass can dominate resistance to motion when acceleration rate is high, of short duration, and in a dense medium such as water (see Prandtl & Tietjens, 1934; Siekman, 1963; Schlichting, 1968; Batchelor, 1967; Yih, 1969; Weihs, 1972, 1973 for theory; Johnson, Soden & Trueman, 1972; Webb, 1975*b*, 1978*b* for results from calculations). It can be shown that the added mass inertial force for the uropods during swimming would be about an order of magnitude greater than the resistance drag force. Thus from Fig. 5 the maximum resultant velocity of the uropods is 1·77 m s^{-1} based on measurements made at 4 ms intervals. The drag force on the uropods, f_{Du}, moving at this velocity, normal to the flow, is:

$$f_{Du} = \tfrac{1}{2}.\rho.A.\mathbf{w}^2 C_{Du}, \tag{1}$$

where A is the uropod area, $\mathbf{w}$ the resultant velocity, ρ the density of water, C_{Du} the drag coefficient. For the uropods, with a length/breadth ratio of 0·3, C_{Du} will be 1·16 (von Mises, 1945). Then f_{Du} is 0·86 N at this instant.

The inertial force f_{Iu} is given by (Weihs, 1973)

$$f_{Iu} = m\frac{d\mathbf{w}}{dt} \tag{2}$$

and for the uropods

$$m = (\pi \mathbf{s}^2)/4, \tag{3}$$

where m is the added mass of water per unit length, t time, $\mathbf{s}$ span.

Then f_{Iu} is 8·5 N for this instant and is about one order of magnitude greater than f_{Du}. All other instances give larger differences, so that for a complete propulsive cycle $f_{Iu} \gg f_{Du}$ and f_{Du} can be neglected.

Therefore, the normal force f_N on each propulsive segment is given by (Weihs, 1973):

$$f_N = m\frac{d\mathbf{w}}{dt}\sin\alpha, \tag{4}$$

where α is the angle of attack.

f_N can be resolved into components acting in the horizontal plane, f_X and in vertical plane, f_Y:

$$f_X = f_N \sin\phi, \tag{5}$$

$$f_Y = f_N \cos\phi, \tag{6}$$

where ϕ = orientation angle.

The total forces F_X and F_Y in the X and Y planes are obtained by numerical integration of equations 5 and 6 for all propulsive segments. In practice, only the uropods and telson (propulsive segment) had significant positive resultant velocities, and analysis could be limited to them.

The energy expended and rate of working of the crayfish can be calculated from F_X and F_Y and velocity (see Lighthill, 1971; Weihs, 1972, 1973).

The above approach is appropriate for free swimming but not for the LG tail-flip lift-off when crayfish simply push off the substrate. Indeed, $\mathbf{w}$ is maximum during lift-off and $\sin\alpha$ and $\sin\phi$ have large enough mean values to suggest F_X should be large. However, there is negligible motion of the centre of mass in the horizontal plane, and what motion there is tends to be opposite to F_X. Furthermore, there is no relative motion between the uropods and telson and the water lifting the posterior in the vertical plane so that the hydromechanical force F_Y must be negligible. Nevertheless, the centre of mass accelerates vertically upwards, and therefore, the LG tail flip lift off phase must be treated differently.

The force required for lift off F_L, can be obtained from:

$$F_L = \int_0^l k.M.a.dl, \tag{7}$$

where l is the position along the body measured from the trailing edge, a the mean acceleration, M the mass, k the proportionality constant for added mass.

Data for M and a are shown as a function of l in Fig. 7.

The value of k varies with body shape. For a cylinder accelerating in water, k is 2, for a sphere 1·5, a streamline body, 1·2 and for a flat plate added mass is obtained from equation 3 (Prandtl & Tietjens, 1934; Gero, 1952; Lang, 1966).

The value for a cylinder was taken for the abdomen, and a value of 1·5 for the thorax which is more elongated in the vertical plane. This was assumed to include the walking legs.

Various forces, work performed and rates of working were calculated from equations 5–7 using data in Figs. 4–7. Results are summarized in Table 3. These results can be compared with the expected performance based on comparative observations and the net motions of the crayfish.

During the LG tail-flip lift-off, energy was expended at a rate of 0·36 W which represents 121 W (kg muscle^{-1}) at 15 °C. Typical rates of working are about 100 W (kg muscle^{-1}) at 15 °C (Bainbridge, 1961; Alexander, 1977; Goldspink, 1977). This value is for muscle working for periods substantially longer than 20 ms. Then a lower mean rate of working would be expected so the value for crayfish is not unreasonable.

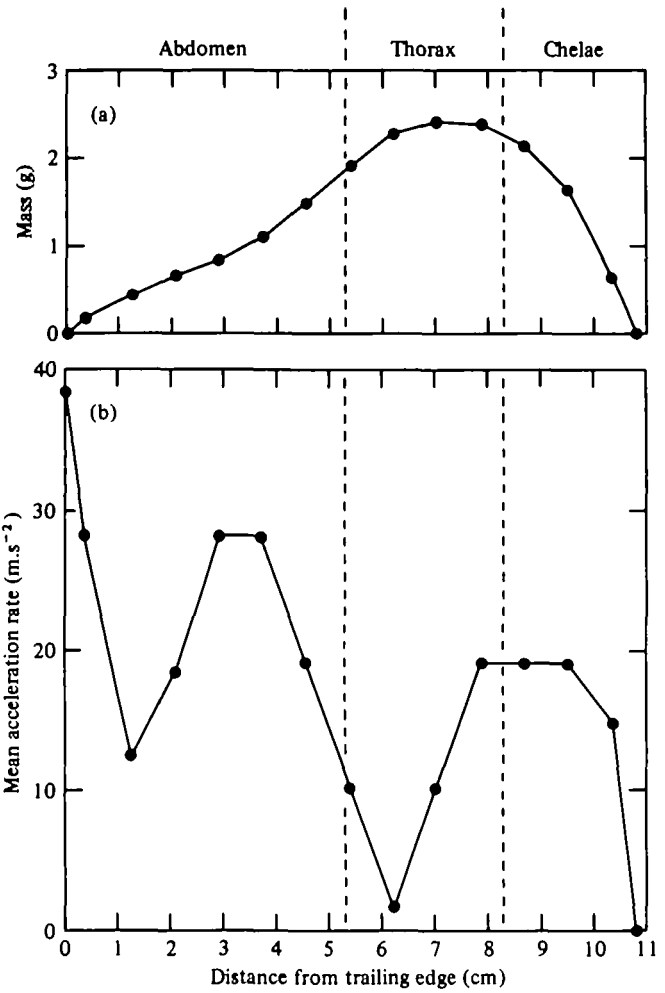

Fig. 7. Relationships between mass and mean acceleration rate during an LG tail-flip lift-off, shown as a function of position along the body of crayfish. Vertical dotted lines delineate various body portions.

An alternative approach is to estimate muscle stress which seems to vary little among animals (Weis-Fogh & Alexander, 1977). The flexor muscles, with a mean cross-sectional area of $0{\cdot}67 \times 10^{-4}$ m^2 develop at least 0·96 N, or 14 kN m^{-2}. Maximum muscle stresses of 400 kN m^{-2} are reasonable (Weiss-Fogh & Alexander, 1977). Therefore muscle performance required to provide the computed external forces and power during lift-off are within the expected capabilities of animals. No consideration is given to hydromechanical efficiency of the propulsion system in these calculations. Obviously it is not appropriate for a simple push from a solid substrate, when a numerical value would be 1·0.

During the swimming phase of the LG flip, F_X was calculated to be 0·42 N. The abdomen is fairly well curved during this phase, so that crayfish present a reasonably streamlined profile to the incident flow. The added mass should be about 20% of the body mass (Gero, 1952; Lang, 1966).

Then a force of 0·42 N should accelerate the crayfish (total mass 0·022 kg) at a mean rate of 19·1 m s^{-2}. This compares with a mean observed rate of 18·6 m s^{-2}.

Table 3. *Results from calculation of total forces (F), energy (E) and power (P) for typical crayfish LG tail flips and tuncated tail flips*

(Subscripts X and Y refer to horizontal and vertical planes.)

	LG tail flip lift-off	LG tail flip swimming	Truncated tail flip
$F_X(N)$	0	0·42	0·29
$F_Y(N)$	0·96	0·088	−0·094
Horizontal distance travelled (m)	Function of l	0·0107	0·0246
Vertical distance travelled (m)	Function of l	0·0120	Negligible
Time (ms)	24	24	40
E_X (J)	0	0·0046	0·0072
E_Y (J)	0·0087	−0·0011	0
P_X (W)	0	0·19	0·18
P_Y (W)	0·36	−0·045	0

F_Y for the LG tail flip swimming phase was 0·088 N. This should be sufficient to accelerate the crayfish in the vertical plane from a velocity of 0·60 m s^{-1} to 0·68 m m^{-2}. In practice, crayfish decelerated during this phase. Presumably this was because the dorso-ventral axis presents an unfavourable profile to the flow. Then drag would rise rapidly during the tail-flip swimming phase. The kinetic energy at the end of lift-off was 0·004 J, and thrust accounted for a further 0·001 J. Therefore, the energy expended against this drag must be of the order of 0·005 J. This approximates the work done against a mean drag force of 0·42 N, which just exceeds that measured for crayfish moving backwards (Fig. 6). This higher value is not unreasonable for the drag normal to the long axis of the body.

The mean F_X for the truncated tail flip was 0·29 N. This force must be sufficient to overcome drag plus the inertial resistance of the crayfish accelerating from 0·54 to 0·66 m s^{-1}, at a mean acceleration rate of 6·7 m s^{-2}. The changes in body shape during recovery strokes are similar to those during power strokes. Therefore the mean drag force was assumed to be 0·12 N, equal to that calculated for deceleration glides during recovery strokes (Fig. 6). The mean acceleration would thus be expected to be 7·8 m s^{-2} accelerating the crayfish to 0·68 m s^{-1}. This is in reasonable agreement with observations.

Thrust is generated primarily by the uropods which are located at some distance from the centre of mass. Therefore, F_Y should be associated with pitching couples. In practice pitching movements were small, except in the LG tail flip lift-off. Pitching movements appear to be reduced by the ability of crayfish to rotate the uropods and telson so that they move fairly close to parallel to the body longitudinal axis (Fig. 2). Such rotation is lower in the LG tail-flip swimming phase, but here such couples are opposite to those initiated in lift-off. Although it was not possible to demonstrate quantitatively, the chelae also appear to have a major steering function, controlling body orientation.

Efficiency of the propulsion system

The efficiency of the propulsion system (propeller efficiency, η_P) of swimming crayfish is defined here by

$$\eta_P = \frac{\text{energy or power to overcome drag.}}{\text{energy or power input}} \tag{8}$$

During the LG tail-flip lift-off η_P will be numerically 1·0. As a result, it is possible to determine an *in situ* value for muscle rate of working of 121 W kg^{-1}. Throughout the present experiments, crayfish were stimulated to perform maximally. Therefore it is reasonable to assume that muscle power was similar for all the swimming movements. Then, using this value for muscle power output, a measure of propeller power input is obtained. Power input is therefore taken to be of the order of 0·36 W (Table 3).

The rate of energy expenditure for thrust for the remainder of the swimming phase of LG tail flip was 0·19 W. Assuming the muscles continue to work maximally, η_P must be about 0·5. Similarly, the truncated tail-flip power stroke analysed expended thrust energy at a rate of 0·18 W, so η_P is of the same order. Truncated tail flips are also used for continuous swimming. Then the energy expended to overcome drag must include that for the recovery stroke in addition to the power stroke (Nachtigall, 1960, 1965; Alexander, 1968). The overall mean data given in Tables 2 and 3, can be used to calculate η_P for complete truncated tail flips. The mean velocity during both power and recovery strokes exceeds 0·3 m sec^{-1}, and hence drag is expected to be 0·12 N as discussed above. The mean distance travelled during a complete cycle was about 0·078 m. Therefore the mean energy expended against drag would be 0·0096 J.* The muscles work at an average rate of 0·36 W for 0·04 s, expending 0·014 J during the power stroke. η_P will be about 0·68. These values for η_P are comparable to those obtained for rowing insects (Nachtigall, 1965).

Comparison with acceleration locomotion of other animals

Many aquatic animals, covering a size range from copepods (Vlymen, 1970) to tuna (Fierstine & Walters, 1968) can accelerate at impressive rates. Among larger animals, fish, cephalopods and crustaceans include high-speed acceleration in their locomotory repertoire as an escape mechanism. Most comprehensive information is available for these groups, which are discussed here.

Macrurous decapods and cephalopods swim using an intermittent thrust system with a power or jet stage and a recovery stage. This is necessitated in cephalopods using jet propulsion by the need to refill the mantle cavity with water. Crustacea have evolved a body plan that is typically asymmetrical in the vertical plane, the plane of body bending. This body plan makes it difficult to generate thrust when the abdomen is both flexing and extending, restricting crayfish and lobsters to swimming based on intermittent power strokes. Fish are symmetrical about the axis of body bending and are therefore capable of developing thrust continuously. This is extremely important, because it allows fish to continue to accelerate for longer than a crayfish, and therefore allows fish to achieve swimming speeds that exceed those of similar sized crayfish. For example, 'stride length' of fish is 0·6–0·8 body lengths (Wardle, 1975). For crayfish, stride length was comparable at 0·66 body length. However, crayfish stride frequency was about 8 Hz at 15 °C. Wardle (1975) shows that a fish large enough to eat a crayfish should be able to beat its tail at about 15 Hz in sprint swimming. However, this is 30 power strokes/s, compared with 8 power strokes/s in crayfish. Therefore it is obvious that crayfish cannot, and indeed they do not, outswim fish. However, it is important to recognize that crayfish are typically nocturnal

* This value exceeds the energy expended during the power stroke for the truncated tail flip analysed in detail because the distance covered during recovery for this single stroke was 0·03 M.

and hide during the day, and an escape response is often the last resort (Lindberg, 1955). Perhaps the vertical component of the LG tail flip is more important because it is a relatively unexpected response contributing to predator confusion.

Thrust generation is clearly dominated by inertial forces in escape responses of fish, cephalopods, and macrurous decapods. This is obvious for cephalopods using jet propulsion (see Siekman, 1963; Johnson *et al.* 1972 for details of theory). Added mass inertial effects dominate for high rates of acceleration over the short time periods observed for accelerating fish and crustacean decapods (Prandtl & Tietjens, 1934 Batchelor, 1967; Yih, 1969). This is independent of whether propulsive segments move at small angles to the incident flow as in fish (Weihs, 1972, 1973), or at large angles as in crayfish discussed above. The difference in angle of attack between fish and crayfish is of course due to the differences in basic morphology.

A major difference among fish, cephalopods and crustaceans is the amount of muscle involved in acceleration compared to the mass to be accelerated (percent muscle mass). The crayfish used in the present experiments had 16% muscle, and the body was propelled at least 0·025 m in 0·044 s (Table 2). Decapod cephalopods, with the best cephalopod acceleration performance, have from 30 to 45% muscle (Trueman & Packard, 1968; Packard, 1969). *Loligo vulgaris* (0·35 kg, 20 °C) accelerates over about 0·015 m in 0·044 s starting from rest (Johnson *et al.* 1972; their fig. 2). Teleost fish have 30–55% muscle, depending on species. The distance travelled in a standing start is also about 0·015 cm in 0·044 s for fish tested at 15 °C (Webb, 1978*a*). This distance varies little among species.

Given these observations, it must be concluded that muscle power of fish and cephalopods is low, and/or the resistance to motion is high, and/or propeller efficiency is low. There are no grounds to assume that muscle power is low compared to crustacea. In terms of reducing drag the shape of swimming macrurous decapods is, at best, as good as that of fish and cephalopod decapods (see Packard, 1972). Therefore it seems likely that propeller efficiency is low in converting muscle power into longitudinal motion: i.e. in converting muscle motion into the biologically useful component for free swimming in these animals.

Low efficiency of jet propulsion is well known. This is because kinetic energy losses are high when thrust is generated by accelerating a small mass of water to a high velocity (e.g. Alexander, 1977). In contrast, fish are popularly assumed to be efficient swimmers, and in steady swimming, η_P may be as high as 0·95 (Wu, 1971). Thus a low η_P during acceleration fast-starts appears surprising.

An estimate of the efficiency may be obtained by assuming fish muscle works at the same rate as calculated above for crayfish muscle. Consider a salmonid fish, of the same mass as the crayfish used. Muscle represents 50% of the body mass and half the muscle works in each acceleration tail stroke. The fish could do work at a rate of 0·55 W. Energy would be expended at a rate of 0·058 W to accelerate the fish, plus 20% added mass over 0·015 m in 0·044 s. Then η_P should be about 0·1. It should be pointed out that the period of 0·044 s covers the first tail beat which is less efficient than the second. Although fish accelerate at high rates during the first stroke, the optimal swimming shapes with higher efficiency are found during the second stroke (Weihs, 1973). The mean acceleration rate to the end of the major acceleration period (second stroke) of several teleost species of various sizes is about 10 m s^{-2}. A fish

completing the first tail beat in 0·044 s would complete the second in a further 0·032 s, and travel a distance of about 0·037 cm (Webb, 1978*a*). Then, for a mass equal to the crayfish, energy would be expended at a rate of 0·11 W, and η_P will then be about 0·2 averaged for both tail beats. This efficiency is still low.

A question remains: why are fish inefficient in acceleration? McCutchen (1977) determined a Froude efficiency of 0·44 for *Brachydanio rerio* during acceleration turns. Thus approximately 44% of muscle energy should be available for thrust of which roughly 25–50% must be wasted in fish motions in directions other than that of mean progression (i.e. recoil). Lateral recoil movements are small compared to forward motion (see figures in Hertel, 1966; Weihs, 1973; Webb, 1975*a*; Eaton, Bombardieri & Meyer, 1977). However, DuBois, Cavagna & Fox (1976) have measured forward and lateral acceleration rates for *Pomotamus saltatrix* (bluefish) during fast-starts. Lateral acceleration rates were about twice the forward acceleration, and apparently alternated direction with each tail beat. Webb (1978*a*) found that *Esox* had the same fast-start performance as other fish, in spite of having the highest percent muscle, and the largest caudal area to develop thrust. *Esox* lacks large anterior body mass or depth and as a result lateral recoil movements are large compared to other teleosts. Webb attributed the low performance of pike, in comparison with that expected, to a substantial loss of energy in lateral recoil movements. Therefore, it appears that fish are unable to accelerate forward without expending large amounts of energy in recoil movements. As a result, only a small proportion of muscle energy is translated into forward progression.

Crayfish (Table 3) and steadily swimming fish (Lighthill, 1970) are also subject to recoil movements. Steadily swimming fish reduce the problem of recoil movement energy losses by having a large anterior depth and mass (Lighthill, 1970) and/or including more than half a propulsive wavelength along the body (Webb, 1975*b*). The former morphological factor also aids reducing recoil in acceleration. However, during acceleration the body is most commonly bent into a C-Shape (Eaton *et al.* 1977), and movements are lateral and of large amplitude. Then large unbalanced recoil forces are unavoidable (Weihs, 1973). Crayfish utilize both vertical and horizontal forces in LG tail flips to lift off the substrate and initiate swimming. Hence recoil forces are not 'wasted'. In truncated tail flips, recoil forces are apparently minimized because drag is high in opposition to the applied force. Finally, recoil forces are only about one fifth to one third the horizontal force during swimming because the uropods and telson can be more effectively rotated normal to the direction of motion.

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