The Journal of Experimental Biology 201, 1771–1784 (1998)
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JEB1395

TAIL-FLIP MECHANISM AND SIZE-DEPENDENT KINEMATICS OF ESCAPE SWIMMING IN THE BROWN SHRIMP *CRANGON CRANGON*

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Accepted 9 March; published on WWW 12 May 1998

Summary

Tail-flip escape swimming by the brown shrimp *Crangon crangon* has been investigated across a range of body lengths (11–69 mm) using high-speed video analysis. This has revealed several novel aspects of the tail-flip mechanism when compared with that of other decapod crustaceans that have been studied. (i) The pattern of body flexion in *C. crangon* produces movement of the cephalothorax as well as the abdomen about the centre of mass. (ii) Shrimps form a 'head-fan' with their antennal scales, in addition to the tail-fan formed by their uropods, apparently for generating thrust during tail-flips. (iii) Shrimps typically swim on their side rather than in an upright body position. It is suggested that these features may be interlinked and derive from habitat specialisation.

The kinematic properties of tail-flips were found to vary with shrimp size. As shrimp body length increased, the rate of body flexion and re-extension decreased whilst the duration of tail-flips increased. Mean (and maximum) velocity estimates ranged between 0.4 m s^{-1} (0.7 m s^{-1}) and 1.1 m s^{-1} (1.8 m s^{-1}) for shrimps of different sizes. The combined effects of escape behaviour and size-dependent variability in tail-flip kinematics will have important implications with regard to predation risk.

Key words: *Crangon crangon*, escape, caridean shrimp, giant fibres, size, swimming, tail-flip, kinematics.

Introduction

Many malacostracan crustaceans such as crayfish, lobsters and shrimps possess an elongated abdomen that can be used for propelling the animal through the water with a powerful tail-flip swimming action. This energetically expensive behaviour is primarily employed as a startle escape response when they are attacked by a predator, but may also occur in response to noxious substances, during feeding (Wine and Krasne, 1972; Bellman and Krasne, 1983) and during agonistic encounters (Edwards, 1995).

The propulsive forces generated during tail-flip swimming derive from a combination of reactive forces (added mass) and resistive forces (drag), with the first of these dominating instantaneous thrust, and a major contribution being made by the expanded uropods (Webb, 1979; Neil and Ansell, 1995). A hydrodynamic 'squeeze' force is also produced towards the end of the tail-flip as the abdomen and cephalothorax are brought towards one another (Daniel and Meyhöfer, 1989). Since the uropods generate a significant proportion of the thrust, the tail-flip of many decapods represents a 'single oar' rowing action that produces a combination of both translatory forces (displacing the centre of mass) and rotational forces (pitching the animal forwards). Calculations by Daniel and Meyhöfer (1989) indicate that total tail-flip force and the balance between translatory and rotational forces scale differently from one another with respect to animal size. Therefore, for an animal of given dimensions and with an isometric growth pattern, there is a particular size at which tail-flip performance will be optimal.

The neuronal control of tail-flip behaviour has been intensively studied, particularly in the crayfish *Procambarus clarkii*. In this species, both giant and non-giant neuronal networks may mediate the tail-flips. There are two pairs of giant fibres, the lateral giants (LGs) and the medial giants (MGs), that produce upward and posteriorly directed escapes, respectively (Wine, 1984; Krasne and Wine, 1988), and this pattern of behaviour is typical of several other decapod species (e.g. Webb, 1979; Jacklyn and Ritz, 1986; Newland and Neil, 1990*a*).

Among the crustaceans, a vast range of body morphologies, body sizes, habitat types and life styles exist. Adaptations of the tail-flip mechanism are required to accommodate these divergences. For example, at the neuronal level, whilst groups such as crayfish (Astacidea) and caridean shrimps (Caridea) possess two pairs of giant fibres (Johnson, 1924), mud shrimps (Thalassinoidea) possess just one pair (the LGs) and squat lobsters (Galatheidae) possess neither (Paul, 1990). Intraspecific differences also occur, as demonstrated at the behavioural level in the American lobster *Homarus*

americanus. Juveniles of this species have a comparatively large abdomen and small claws and respond to predators by tail-flipping, whereas adults have a comparatively small abdomen and large claws, and respond to predators with defensive displays (Lang *et al.* 1977).

In this investigation, we have examined tail-flip swimming in the brown shrimp *Crangon crangon*, an epibenthic caridean shrimp that is widespread in shallow soft-bottom bays and estuaries around Europe. It lives on or buried just beneath the sediment surface (Al-Adhub and Naylor, 1975; Pinn and Ansell, 1993), and ranges in total length between 5 and 90 mm, although maximum lengths of approximately 70 mm are more typical (Tiews, 1970). The species is heavily fished in some areas and forms an important prey item for a number of commercially important fish species (Tiews, 1970). As part of their defence against both predators (Tallmark and Evans, 1986) and approaching trawl gear (Berghahn *et al.* 1995), brown shrimps have a rapid tail-flip escape response. We have used high-speed video techniques (i) to examine the tail-flip mechanism of brown shrimps, and to compare and contrast this with respect to habitat type and with respect to other crustacean species, and (ii) to quantify the kinematic performance of tail-flip swimming with respect to body length. Our results confirm that size has a significant effect upon escape performance and reveal several novel aspects of tail-flip swimming and body orientation in *C. crangon* that distinguish their behaviour from that of larger, more heavily calcified crustaceans. These differences suggest that there is an intrinsic relationship between habitat type, tail-flip mechanism and body orientation that has important implications with regard to escape from predatory attacks.

Materials and methods

Animals

Brown shrimps *Crangon crangon* (L.) were caught during July 1993 and 1994, in a hand-held trawl net at a depth of less than 1 m in Dunstaffnage Bay on the west coast of Scotland and transferred to aquaria (100 cm×50 cm×30 cm with a 1–2 cm sand substratum) maintained at an approximate salinity of 30 ‰ and temperature of 13 °C (fluctuating with ambient sea conditions). For predator-evasion experiments, juvenile cod (*Gadus morhua*) were used as predators. O-group cod of between 61–107 mm (tip of snout to tip of caudal fin) were caught in July 1993 in Dunstaffnage Bay (<2 m depth) using a beach seine net. These fish were housed in 1 m diameter tanks with circulating sea water of the same salinity and temperature as that of the shrimps.

The shrimps were kept for approximately 2 weeks before being used in experiments, and were fed *ad libitum* every second day on chopped mussels and/or mysids. None of the experimental shrimps was in a berried condition (i.e. carrying eggs attached to its pleopods), and all of them had a hard exoskeleton and showed no obvious signs of poor health or damage. Total body lengths were determined by measuring the distance from the anterior tip of the rostrum to the posterior tip of the telson. Twenty-five shrimps of between 11 and 69 mm body length (wet mass 0.013–4.55 g) were used for high-speed video experiments. An additional 38 shrimps of between 6 and 36 mm body length (0.002–0.55 g) were used for predator-evasion experiments.

Morphometrics

Total body length (L) was measured to the nearest 0.1 mm as described above, except for the relationship between L and the abdomen length (A). In this case, L was measured to the base of the rostrum rather than to its anterior tip. Abdomen length was measured as the distance from the posterior edge of the carapace to the posterior tip of the telson along the midline of the shrimp's dorsal side.

The cross-sectional area of the abdominal muscle was determined in shrimps that had been preserved in a flat position (i.e. abdomen extended) for 24 h in formaldehyde solution (4 % v/v in sea water). Total length was measured both before and after fixing, but no shrinkage effects were detected as a result of the procedure. Transverse sections were cut half-way along the third abdominal segment and examined under a microscope (magnification ×6–25) linked to a video recording system (Kappa CF 11/2 camera, Panasonic NV-FS200 HQ VHS recorder). The cross-sectional area of the fast muscles (F, the flexor and extensor areas combined) was measured from digitised video images using NIH Image 1.55 computer software. The area attributable to superficial pleopod and slow muscles was not included in the analysis.

Wet mass of live shrimps (blotted dry) was measured on a balance to the nearest milligram.

Protocol for high-speed video experiments

All experiments were conducted in an experimental arena (diameter 1 m, seawater depth 17 cm) in an air-conditioned room at 13 °C and were filmed from directly above using a NAC high-speed video camera linked to a NAC HSV400 video recorder. This provided a view of the horizontal position of the shrimp within the arena ('camera view'). A mirror was placed on the bottom of the arena at 45 ° to the camera to provide a view of the shrimp's vertical elevation above the substratum ('mirror view'). A 5 or 10 cm marker on the bottom of the arena provided calibration marks on the video films. Illumination was provided by a synchronised strobe, and the light from this was orientated along the axis of the camera lens by reflecting it in a half-silvered mirror angled just in front of the camera lens. The base of the arena was covered with reflective material (3M Scotchlite) to produce a sharp silhouette image of the shrimp in the camera view. A silhouette image was also obtained in the mirror view by placing an upright board covered in 3M Scotchlite at the opposite end of the arena from the mirror. All experiments were recorded at 200 frames s^{-1} on the high-speed video recorder.

For each experiment, a shrimp was removed from its holding tank by pressing lightly down on its carapace and then lifting it between two fingers. This method tended to inhibit the tail-flip escape response (a similar response has been noted in

crayfish; see Krasne and Wine, 1975) and therefore enabled shrimps to be moved without inducing muscle fatigue. The shrimp was placed on the bottom of the experimental arena and covered for 10 min with an upturned transparent plastic container in which perforations had been made. During this period, the water was aerated with an air-stone. At the start of an experiment, the video recording equipment was turned on and the plastic container and air-stone were removed. Tail-flip escape responses were induced, either by a rapid flick with a submerged finger placed 5–10 cm from the shrimp or by rapidly propelling a partially submerged rod (2 cm diameter) towards the shrimp. No direct physical contact was made with the shrimp or substratum; the stimulus therefore comprised mainly visual and water-borne vibrational cues. Experiments on dead animals confirmed that no passive movement of the shrimp was created by water displacement arising from either of the stimuli. Each shrimp was made to perform between 1 and 5 multiple tail-flip swimming bouts, during which no obvious signs of physical exhaustion were visible.

Protocol for predator-evasion experiments

An additional set of experiments was conducted using 38 shrimps (6–36 mm) and 38 cod (61–107 mm). The experiments were conducted at 13 °C in a circular arena with a white reflective substratum, a diameter of 30 cm and a water depth of 20 cm. Predatory encounters between cod and shrimps were filmed with a camera placed directly above the arena, and recorded on a conventional video recorder (Panasonic AG-6024) at a frame rate of 50 frames s^{-1}. A time inserter (IMP Electronics V9000) was used for inserting elapsed time (0.01 s) onto the video recordings.

For each experiment, a single shrimp and cod were placed in the arena and allowed to settle for 15 min. An upturned opaque container with perforations in it was placed over the shrimp during this period, and aeration was provided by means of an air stone. At the start of the experiment, the air was turned off and the container was lifted remotely from behind a screen using an attached string. Experiments were filmed for 1 h or until the shrimp had been consumed by the cod.

Estimation of the centre of mass

The centre of mass in *Crangon crangon* was determined by suspending frozen specimens between two opposed points formed by fine pins mounted on a pair of forceps. Shrimps were frozen (−10 °C) with their abdomen fully extended (i.e. in their normal resting body posture) or with their abdomen fully flexed in order to determine the shift in position of the centre of mass during the course of a tail-flip. In each case, the position of the pins on the shrimp was adjusted in air until the animal could be placed in any pitch orientation without pivoting under its own weight. The centre of mass was then assumed to lie on the axis between the pin attachment points.

Using this method, the centre of mass was found to lie within the ventral half of the first abdominal segment when the shrimp was in a fully extended position. When the body was fully flexed, the centre of mass shifted slightly to a position level with the coxa of the fifth pereiopod. Therefore, a single intermediate point on the postero-ventral corner of the shrimp's cephalothorax was used for digitising the estimated centre of mass from video film (see below).

Analysis of high-speed video recordings

Only escapes in which the shrimp performed more than one tail-flip during an escape swimming bout were analysed (this was the typical response to the type of stimulus used). Of 89 multiple tail-flip swimming bouts that were filmed, 25 were selected for kinematic analysis on the basis that the shrimp was swimming above and parallel to the substratum (identified from the mirror view of the shrimp). High-speed video sequences were replayed frame by frame onto a monitor (JVC) from which reference points on the shrimp's body were digitised on an attached digitising tablet (NAC). These data were analysed using MOVIAS 3.00-4 (NAC) and Excel 5.0 (Microsoft) software.

Movement in the horizontal plane was analysed by digitising four points from the camera view of the shrimp's lateral aspect (Fig. 1A; note that shrimps usually swam on their side; see Results section). These were: 1, the eyes; 2, the leading edge of the abdomen at its mid-point of flexion; 3, the posterior tip of the sixth abdominal segment; and 4, the estimated centre of mass. Points 1, 3 and 4 could be accurately identified by the fact that they occur at angled joints between the antennal scales and the cephalothorax (point 1), the sixth abdominal segment and the telson (point 3), and the cephalothorax and the abdomen (point 4). Although these angled joints were not visible in all images throughout a tail-flip cycle, once they had been identified for a particular shrimp, points in adjacent frames could be located by means of their respective distances from the anterior or posterior tips of the shrimp. In the first 1–3 frames of an escape swimming sequence, the camera view of the shrimp comprised images of the dorsal (or partial-dorsal) aspect as it performed a lateral rolling manoeuvre (described below). In such instances, the points were digitised along the midline of the shrimp (or estimated midline for partial-dorsal aspects). Escape sequences were analysed from the frame immediately preceding the shrimp's initial movement until the frame in which one of the digitising points on the shrimp's body moved out of the camera's field of view. The 25 sequences analysed consisted of two (N=9), three (N=9), four (N=5) or five (N=2) tail-flips, but in some cases, these only included the flexion phase of the last tail-flip.

The body angle of the shrimp was defined as the angle subtended by points 1, 2 and 3 (Fig. 1A). Changes in this angle (Δ angle) between successive frames were used to determine maximum angular velocity and maximum angular acceleration during flexion or re-extension phases of the tail-flip (i.e. the peak value attained over a 5 ms interval). The mean angular velocity for a complete flexion or re-extension movement of the abdomen was calculated as: (total Δ angle)/(total time taken). Negative angular values were assigned to flexion movements and positive angular values to body re-extension movements.

Displacement of the shrimp was determined by measuring

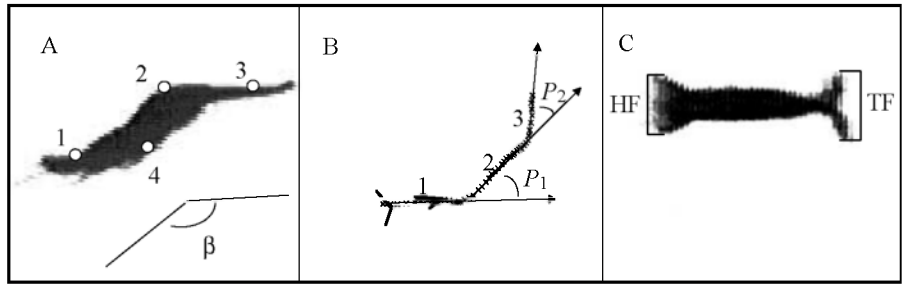

Fig. 1. High-speed video analysis. (A) Lateral aspect (camera view) of an escaping shrimp showing the four points that were digitised. 1, eyes; 2, leading edge of the abdomen at its mid-point of flexion; 3, posterior tip of the sixth abdominal segment; 4, centre of mass. The body angle of the shrimp (β) was measured as the angle subtended by points 1, 2 and 3. (B) Digitised points (crosses) of the shrimp's centre of mass showing horizontal displacement during tail-flips 1–3 of an escape. Stick diagrams join points 1 (uppermost), 2 and 3 (lowermost) at two positions during tail-flip 1. The pitch angles (P_1, P_2) between successive tail-flips were measured as the angle subtended by the fitted lines, with positive values assigned to pitch in the rostral direction (as in this example). (C) Dorsal aspect (mirror view) of an escaping shrimp showing measurement of the head-fan (HF) and tail-fan (TF) width.

the distance travelled by the digitised positions of the estimated centre of mass between one frame and the next. Distance travelled per tail-flip was calculated as the cumulative sum of these values over a complete body flexion/re-extension cycle. The mean velocity during an entire multiple tail-flip swimming bout was calculated as: (cumulative distance travelled)/(time elapsed). Velocity over 5 ms time intervals was determined from the distance moved by the centre of mass between one image and the next. Maximum velocity values for each tail-flip in an escape swimming bout were derived from the peak values reached (over a 5 ms interval) during body flexion. Acceleration values have not been included because of the increased error associated with calculating such second-order differentials (see Harper and Blake, 1989).

Rotation in the shrimp's pitch plane between successive tail-flips was estimated by fitting a straight line through the horizontal trajectory of the centre of mass for each tail-flip. The angle between successive tail-flip trajectories was measured as the pitch angle, with positive angles assigned to rotation in the rostral direction and negative angles to rotation in the caudal direction (Fig. 1B).

The shrimp's antennal scales (scaphocerites) and uropods pivoted laterally during tail-flips, expanding during body flexion to form a head-fan and tail-fan respectively. These movements were analysed in a selection of sequences by digitising the most lateral point of each antennal scale or uropod (as seen from the shrimp's dorso-ventral aspect) and measuring the linear distance between the opposite points (Fig. 1C).

During tail-flips, thrust is produced when appendages are moved through the water with respect to the centre of mass (Webb, 1979). In 12 sequences, the positions of points 1 and 3 with respect to point 4 (centre of mass) were determined at the beginning and end of each flexion phase. From these data, the distance moved during body flexion by the head-fan and tail-fan with respect to the centre of mass was calculated (note that points 1 and 3 are located at the base of the head-fan and tail-fan respectively).

Analysis of predator-evasion recordings

Predator-evasion experiments were used to provide supplementary mean velocity measurements for shrimps responding to a natural predator. Recordings were analysed from sequences in which shrimps performed multiple tail-flip escapes in response to an approach by a cod. The estimated centre of mass of the shrimp was traced frame by frame from a video monitor (JVC) onto an acetate overlay. These x,y coordinates were digitised, and distances between successive points were calculated. Mean horizontal velocity was calculated as a function of cumulative displacement divided by time elapsed.

Statistical analyses of data

Statistical calculations were performed using Minitab 10Xtra (Minitab Inc.) software or according to Zar (1996). Muscle area and wet mass relationships were examined using linear regression of $\log_e$-transformed data. Deviation of regression slope coefficients from values expected for isometric growth (2.0 for muscle area, 3.0 for wet mass) was investigated using t-tests.

Comparisons between first tail-flip *versus* second tail-flip measurements for an escape swimming bout were conducted using two-tailed paired t-tests (where percentages were compared, data were arcsine-transformed). Relationships between shrimp body length and various tail-flip measurements were determined using regression models. Linear regressions were fitted to data on the duration of tail-flip phases (duration of entire tail-flips and of body flexion and re-extension phases). For data on displacement per tail-flip, mean velocity and maximum velocity, three types of regression models were tested. These were (i) a linear regression, (ii) a linear regression of the log-transformed data, and (iii) a quadratic regression. The most appropriate model was then determined for each set of data by plotting the residuals of the regression values and assessing their deviation from zero. In all instances, the quadratic model produced the best fit, and therefore only these regressions are presented.

Results

Morphometrics

The ratio of abdomen length to total length (A:L) remained stable at approximately 0.77±0.02 (mean ± S.D., N=503) for shrimps of all lengths.

The cross-sectional area of the fast muscle within the third abdominal segment was only measured in shrimps between 20 and 50 mm total length. Within this range, fast muscle area (F, mm^2) was related to total length (L, mm) by:

$$F = 0.009L^{1.987} \ (N=16,\ r^2=0.97,\ P<0.0001)\ . \qquad (1)$$

The scaling factor of 1.987 was not significantly different from 2.0 (t-test, $t_{15}=0.144$, $P>0.50$).

The relationship between shrimp total length and shrimp wet mass (M, g) was described by the function:

$$M = 5.52\times10^{-6}L^{3.217} \ (N=90,\ r^2=0.996,\ P<0.0001)\ . \qquad (2)$$

In this instance, the scaling factor was significantly greater than 3.0 (t-test, $t_{89}=9.65$, $P<0.001$).

Description of tail-flips

Flexion and re-extension movements

Shrimps responded to a vibrational or visual stimulus by performing either a single tail-flip, comprising a single cycle of abdominal flexion and re-extension, or more typically, a series of multiple tail-flips (termed an escape swimming bout). Escape latencies (the time between the first visible movement of the stimulus until the first visible movement of the shrimp) were between 10 and 15 ms.

The kinematic variables of an escape swimming bout performed by an 11 mm total length shrimp are shown in Fig. 2 and are analysed in detail below in relation to body length and tail-flip number. Broadly speaking, the flexion and re-extension movements were similar between the first and subsequent tail-flips within a swimming bout and for shrimps of all sizes. They resulted in both point 1 (the eyes) and point 3 (the telson) pivoting with respect to point 4 (the centre of mass) during the tail-flip cycle, producing a 'jack-knife' pattern of movement. The pivoting movements of point 1 were not as great as those of point 3, as shown by an analysis of 12 of the sequences (shrimp total body lengths 33–69 mm). Expressed as a percentage, the distance (with respect to point 4) travelled by point 1 divided by the distance travelled by point 3 ranged between 33 and 91 % (mean 55 %) during the tail-flip 1 flexion and between 29 and 88 % (mean 44 %) during the tail-flip 2 flexion. The difference between tail-flip 1 and 2 was not significant (paired t-test, $t_{11}=1.40$, $P=0.19$).

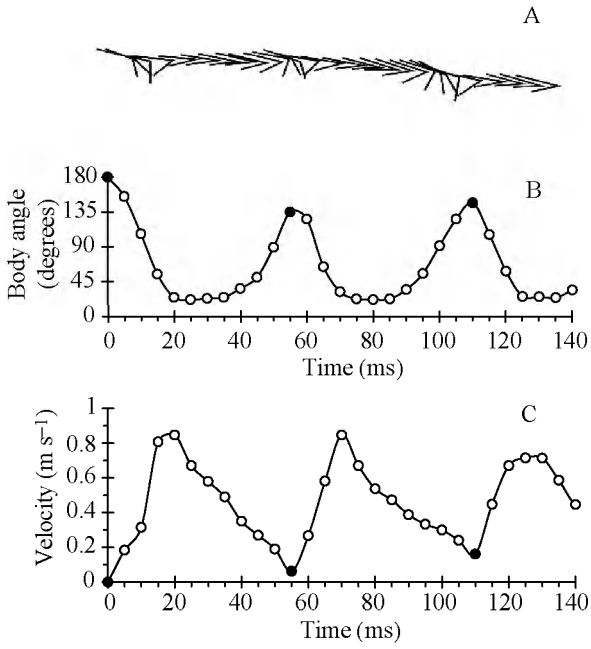

Fig. 2. (A) Sequence of superimposed stick diagrams digitised from high-speed video (camera view: points 1, 2 and 3 of an 11 mm shrimp) during the first three tail-flips of an escape swimming bout. Point 1 (eyes) is uppermost, and the direction of travel is from left to right. Graphs show the corresponding changes in body angle (B) and velocity of the centre of mass (C). Filled symbols represent the beginning of each flexion phase.

The flexion phase of the tail-flip (see 0–30 ms of Fig. 3) was brought about predominantly by movements within the anterior portion of the abdomen, with the mid-point for flexion being located at a point between abdominal segments 2 and 3. Virtually no movement occurred at the joint between the sixth abdominal segment and the telson. During the re-extension phase of the tail-flip (see 40–110 ms of Fig. 3), the anterior abdominal segments were extended earlier than the posterior segments, and the joint between segment 6 and the telson was held in a flexed position until the next flexion phase was initiated. Movement about this latter joint was probably brought about (at least in part) by passive forces exerted by the incident flow of water.

Articulation of the uropods and antennal scales

During the flexion phase of the tail-flip, both the antennal scales and the uropods underwent lateral pivoting movements to form expanded propulsive surfaces (the head-fan and tail-fan surfaces respectively). In a 31 mm total length shrimp, both fans had a maximum width of approximately 10 mm (Fig. 4). Full expansion of the tail-fan occurred within 5–10 ms of the start of flexion, and within 10–15 ms for the head-fan, but each fan remained maximally spread for less than 5 ms (the duration of a single frame). Towards the end of the flexion phase, both fans were gradually retracted so that, by the start of body re-extension, the width of the tail-fan (as seen from the dorso-ventral aspect) was only 15–20 % of its maximum, whilst that of the head-fan was between 40 and 60 % of its maximum. The difference between the minimum widths is due to the fact that shrimps not only retract the uropods laterally but also fold the opposing ventral surfaces together beneath the telson into a streamlined position. Reduction in the width of the head-fan occurred primarily as a result of pivoting the antennal scales medially rather than by folding them.

Orientation of the body during tail-flip swimming

In the majority of escapes filmed (84 %), the first tail-flip of a swimming bout was accompanied by a lateral roll of the shrimp's body about its antero-posterior axis so that the animal escaped either to its left or right side (Fig. 5). This rotation was evident within the first 1–3 frames in which movement was

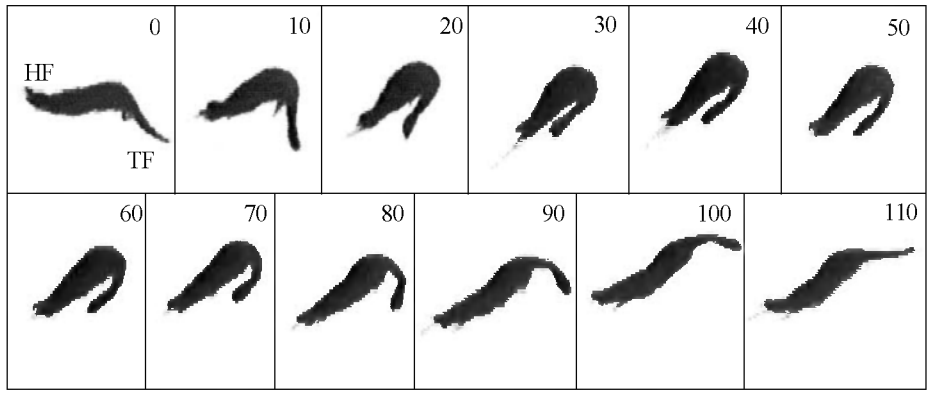

Fig. 3. High-speed video images (every second frame shown) of tail-flip 2 in an escape swimming bout. The shrimp is viewed from its lateral aspect with the head-fan (HF) to the left and tail-fan (TF) to the right at time zero. Numbers refer to the time elapsed (in milliseconds) since the first frame. 0–30 ms, flexion phase; 40–110 ms, re-extension phase.

detected (i.e. within 5–15 ms of the onset of movement) and caused subsequent tail-flips to take place with the shrimp swimming on its side in a horizontal direction.

In some responses (16 %), lateral roll was much less pronounced or absent, and the first flexion of an escape response was instead performed with the shrimp orientated in an upright position, producing a predominantly vertical trajectory. In these cases, a roll was usually executed during the first re-extension (typically accompanied by pleopod movements), so that subsequent tail-flips of the escape then also took place with the shrimp swimming on its side in a horizontal direction. These mainly vertical escapes occurred in response to both rostrally and caudally applied stimuli.

In three instances (3 %) in which an escape involved an initial vertical rather than lateral displacement, no roll occurred at all, even during the first re-extension. Instead, the shrimp rotated rostrally (i.e. pitched forward) during the first re-extension and continued doing so during the second flexion, causing it to perform a partial forward somersault. Subsequent tail-flips then took place above the substratum in a predominantly horizontal direction but, instead of the shrimp swimming on its side, it swam with its cephalothorax positioned lowermost and its abdomen uppermost.

Following a sideways roll during the first tail-flip, subsequent tail-flips often involved a smaller degree of roll which tended to direct the shrimp slightly downwards rather than maintaining a constant vertical elevation. This looping movement resulted in periodic contact with the substratum which, on a sand or mud bottom, caused intermittent puffs of sediment to be produced. Similar observations were made by Tallmark and Evans (1986).

Pitch movements during subsequent tail-flips of an escape response

When a shrimp was swimming on its side (the typical escape mode observed), horizontal displacement during each flexion phase occurred along an approximately linear trajectory. Horizontal steering was achieved by rotation in the pitch plane between one tail-flip and the next, thereby adjusting the direction of travel. When changes in direction did take place, the largest adjustments tended to be performed during the first few tail-flips of an escape, after which steering adjustments were minimal. Larger changes in direction were observed when pitching rostrally (up to 70–80 °) than when pitching caudally (up to 10–15 °).

During the re-extension phase immediately preceding a large rotational pitch in the rostral direction, a single beat of the pleopods sometimes occurred, possibly assisting in bringing about the change of direction (this can be seen in Fig. 5).

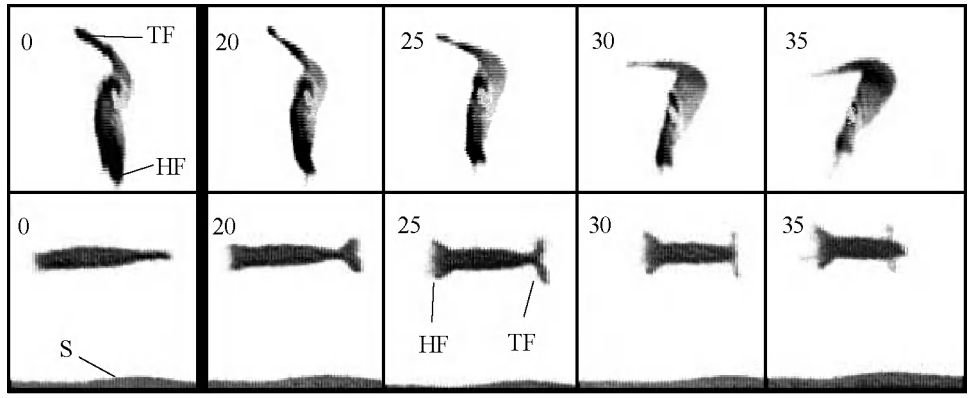

Fig. 4. High-speed video images showing expansion of the head-fan (HF) and tail-fan (TF) during an escape swimming bout. Top row: camera view of the shrimp (view from vertically above the arena). Bottom row: concurrent mirror view (looking horizontally) showing the shrimp approximately 5 cm above the substratum (S). The initial pair of images (left-hand column) show the re-extension phase of tail-flip 1, during which the head-fan and tail-fan are retracted into a streamlined position. During the subsequent flexion phase of tail-flip 2 (columns 2–5), the head-fan and tail-fan are rapidly expanded. Numbers refer to time elapsed (in milliseconds).

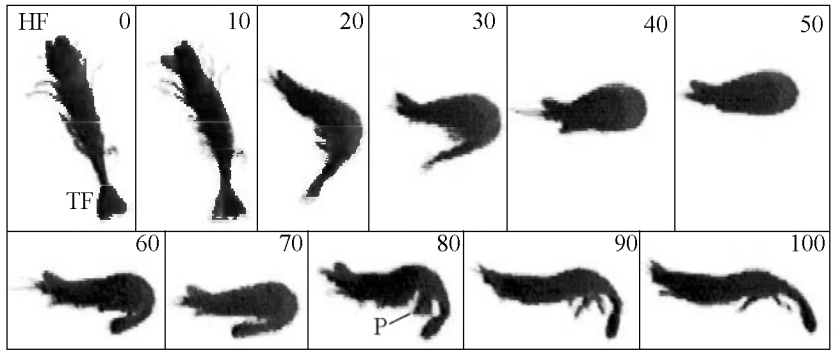

Fig. 5. High-speed video images from the camera view of the shrimp (view from vertically above the arena, every second frame) showing laterally directed body roll during the first tail-flip of an escape response. Numbers refer to time elapsed (in milliseconds). The shrimp starts at time zero from an upright position, stationary on the substratum. HF, head-fan; TF, tail-fan. In this example, movement of the pleopods (P) can also be seen during the re-extension phase (80–100 ms).

Movement in the shrimp's yaw plane

Rotation of the shrimp in the yaw plane was not examined in detail, but this does occur and adds to the complexity of tail-flips. Yaw rotation was especially evident during the re-extension phase of tail-flips. In many of the escapes, when shrimps were swimming on their side, yaw rotation resulted in the shrimp's longitudinal axis being at an angle (rather than parallel) to the horizontal, with the tail-fan elevated a greater distance above the substratum than the head-fan.

Tail-flip kinematics

Duration of tail-flip

Tail-flips of the smallest shrimps (11 mm total length) had typical durations of between 30 and 50 ms, whereas those of larger shrimps (55–69 mm) were between 65 and 140 ms. Total tail-flip duration, flexion duration and re-extension duration all increased as positive linear functions of shrimp body length (Fig. 6A–C; Table 1). The ratios of flexion duration to total tail-flip duration for tail-flips 1 and 2 had values of 0.47±0.10 and 0.39±0.08 (mean ± S.D.), respectively, and did not change significantly with body length (*t*-tests on regression slopes; t_{24}=1.83 and t_{19}=0.53 respectively, both *P* values >0.05).

Within each escape swimming bout, there was no significant difference between the total duration of tail-flip 1 and that of tail-flip 2 (paired *t*-test, t_{19}=1.56, *P*=0.14). The flexion phase of tail-flip 2 had a significantly shorter duration than that of tail-flip 1 (paired *t*-test, t_{24}=2.70, *P*=0.012), probably in part because the body started from a fully extended position at the beginning of tail-flip 1 compared with a partially extended position in subsequent tail-flips. However, the re-extension phase of the tail-flip 2 had a significantly longer duration than that of tail-flip 1 (paired *t*-test, t_{19}=2.44, *P*=0.025).

Body angle measurements

Consecutive flexion and re-extension movements of the abdomen during a tail-flip swimming bout resulted in cyclic changes in the body angle (Fig. 2B). Tail-flips usually resulted in full flexion of the abdomen, causing the tail-fan to come into close or direct contact with the cephalothorax. Regression analysis on the pooled data showed that there was no significant change in minimum body angle with total body length (*t*-test on slope of line, t_{49}=1.52, *P*=0.14). For all tail-flips analysed (tail-flips 1–5), the mean body angle when in a fully flexed position was 25.0±4.9 ° (mean ± S.D., *N*=62). There was no significant difference between the minimum body angle at the end of the first and second flexions of an escape (paired *t*-test, t_{24}=1.68, *P*=0.11).

The maximum body angle attained at the end of the re-extension phase of a tail-flip was more variable (range 75–165 °). The mean angle of all pooled data (tail-flips 1–5) was 128.2±20.3 ° (mean ± S.D., *N*=60), but a significant

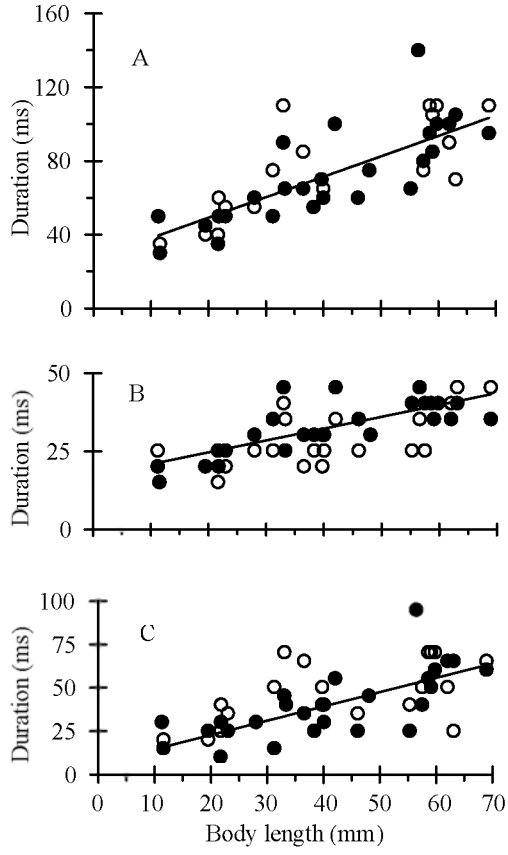

Fig. 6. Relationships between shrimp total body length and the duration of tail-flip phases. (A) Duration of an entire tail-flip (flexion + re-extension). (B) Duration of the flexion phase. (C) Duration of the re-extension phase. Filled symbols represent tail-flip 1; open symbols represent tail-flip 2. Regressions (see Table 1) are either for the pooled data (A) or only for the first tail-flip data (B,C), depending upon the results of paired *t*-tests (see text).

Table 1. *Regression parameters derived for kinematic relationships with shrimp total length*

Regression model Parameter Data used for fitting regression	*a*	*b*	*c*	Regression ANOVA *P*	 r^2	Figure
Linear regressions						
Duration (ms)						
Entire tail-flip (tail-flips 1 and 2)	1.11		27.0	<0.001	0.57	6A
Flexion 1	0.34		16.9	<0.001	0.56	6B
Flexion 2	0.40		12.5	<0.001	0.53	–
Re-extension 1	0.82		6.23	<0.001	0.49	6C
Re-extension 2	0.56		22.6	<0.01	0.27	–
Maximum body angle (degrees)						
End of re-extensions 1–5	0.41		113	<0.004	0.12	–
Mean angular velocity (degrees s^{-1})						
Flexion 1	70.9		−7777	<0.001	0.61	7A
Flexion 2	29.0		−4639	<0.002	0.34	7A
Re-extension 1	−37.4		4360	<0.001	0.37	7A
Re-extension 2	−33.6		3833	<0.001	0.32	7A
Maximum angular velocity (degrees s^{-1})						
Flexion 1	93.1		−12 336	<0.001	0.52	7B
Flexion 2	70.9		−8929	<0.001	0.35	7B
Re-extensions 1 and 2	−55.8		7106	<0.009	0.32	7B
Maximum angular acceleration (degrees s^{-2})						
Flexions 1 and 2	2486		−228 573	<0.001	0.57	7C
Quadratic regressions						
Displacement per tail-flip (mm)						
Tail-flips 1–5	2.88	−0.02	−14.6	<0.001	0.60	8A
Mean velocity (m s^{-1})						
Entire escape swimming bout	0.0415	−0.0004	−0.008	<0.001	0.77	8B
Maximum velocity (m s^{-1})						
Flexions 1–5	0.0596	−0.00051	0.082	<0.001	0.58	8C

L, total body length (mm).
For linear regressions, $y=aL+c$; for quadratic regressions, $y=aL+bL^2+c$.
Figure refers to the figure number in which the regression is shown fitted to the data.

increase with shrimp total body length was detected (Table 1). The predicted values from the regression indicated that the mean angle increased from 118 to 141 ° with an increase in body length from 11 to 69 mm, but this relationship accounted for very little of the overall variability (r^2=0.12). There was no significant difference between the maximum body angles at the end of re-extensions 1 and 2 (paired *t*-test, t_{19}=1.51, *P*=0.14).

Mean and maximum angular velocities of the body

The mean angular velocity during the flexion phase of tail-flip 1 was between -6.3×10^3 and -7.8×10^3 ° s^{-1} in small (11 mm) shrimps compared with between -3.2×10^3 and -4.4×10^3 ° s^{-1} in large (>60 mm) shrimps. Maximum instantaneous values attained (over a 5 ms interval) during flexion were between -1.0×10^4 and -1.3×10^4 ° s^{-1} in small shrimps and between -6.1×10^3 and -7.8×10^3 ° s^{-1} in large shrimps.

Flexion rates were linearly related to shrimp total body length. The mean and maximum angular velocities achieved during flexion 2 were slower than during flexion 1 (paired *t*-tests: t_{24}=5.67, *P*<0.0001; t_{24}=5.56, *P*<0.0001 for mean and maximum angular velocities respectively). Therefore, separate regression lines were fitted to these data (Fig. 7A,B), all of which had significant slopes (Table 1).

Mean angular velocity during the re-extension phase of a tail-flip was slower than that during the flexion phase (paired *t*-tests on absolute values: t_{24}=7.41, *P*<0.0001 for tail-flip 1, and t_{19}=5.18, *P*<0.0001 for tail-flip 2). Linear regressions (Fig. 7A,B; Table 1) indicated that both the mean and maximum angular velocities decreased significantly with body length. Mean angular velocities during re-extension decreased from between $+2.9\times10^{31}$ and $+4.2\times10^3$ ° s^{-1} in small shrimps to between $+1.2\times10^3$ and $+2.2\times10^3$ ° s^{-1} in large shrimps, whilst maximum values decreased from between $+4.1\times10^3$ and $+9.1\times10^3$ ° s^{-1} to between $+3.0\times10^3$ and $+5.0\times10^3$ ° s^{-1} respectively. The mean angular velocity during re-extension of tail-flip 1 was slightly greater than that for tail-flip 2 of a swimming bout (paired *t*-test: t_{19}=2.18, *P*=0.042), but there was no significant difference in the maximum angular velocities attained (t_{24}=1.63, *P*=0.12).

Maximum angular acceleration of the body angle during the flexion phase

Maximum angular acceleration values for the flexion phase of tail-flip 1 changed linearly from approximately -2×10^5 ° s^{-2} in small shrimps to approximately -5×10^4 ° s^{-2} in large ones (Fig. 7C; Table 1). There was no significant difference in this measure between the flexion phases of tail-flip 1 and tail-flip 2 in a swimming bout (paired *t*-test: $t_{24}=0.65$, $P=0.52$).

Swimming kinematics

Distance travelled per tail-flip

The displacement the centre of mass in tail-flip 1 increased as a positive function of total body length from 10–30 mm for small (11 mm) shrimps to 50–120 mm for large (>60 mm) shrimps. The relationship between total body length and distance travelled by the centre of mass per tail-flip was described by a quadratic regression (Fig. 8A) in which both the positive (value *a* in Table 1) and negative (value *b* in Table 1) slope coefficients were significant ($t_{59}=3.62$, $P<0.001$ and $t_{59}=2.01$, $P<0.05$ respectively). Over the size range of shrimps used in the experiments (11–69 mm), the fitted regression line predicts a rise in displacement with total body length to a peak value of 94 mm for a 69 mm shrimp. However, transformed into body length equivalents, the peak value predicted was 1.8 body lengths for a 28 mm shrimp compared with minimum values of 1.4 body lengths for both 11 mm and 69 mm shrimps (the highest measured value was 2.8 body lengths by a 33 mm shrimp).

The distance travelled by the centre of mass during tail-flip 2 of a swimming bout was not significantly different from that in tail-flip 1 (paired *t*-test, $t_{19}=1.81$, $P>0.05$), and values for subsequent tail-flips were also similar. Values have therefore been pooled in the above regression analysis.

Mean velocity of the centre of mass during multiple tail-flips

The mean velocity of the centre of mass measured from high-speed video recordings agreed very closely with the mean velocity for escapes in response to predatory cod measured from conventional video recordings (50 frames s^{-1}), and these

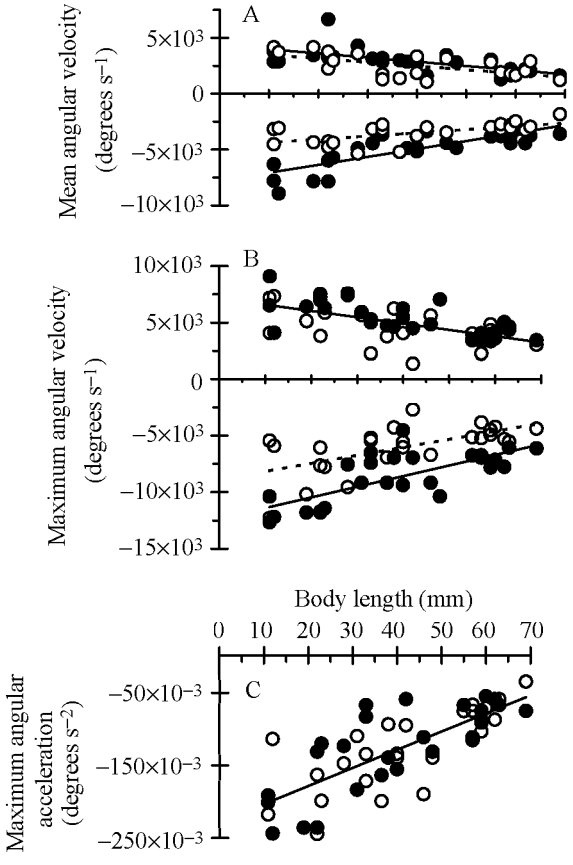

Fig. 7. Body angle measurements during tail-flip 1 (filled symbols) and tail-flip 2 (open symbols). (A) Mean angular velocity of flexion phases (negative values) and re-extension phases (positive values). (B) Maximum instantaneous angular velocity attained during flexion and re-extension phases. (C) Maximum instantaneous angular acceleration attained during flexion phases. Fitted regressions are for the pooled data unless tail-flip 1 and tail-flip 2 values differed significantly in paired *t*-tests (see text). Solid line, pooled data or (when significantly different) tail-flip 1 data. Dashed line, tail-flip 2 data. Fitted lines were derived from the linear regression parameters given in Table 1.

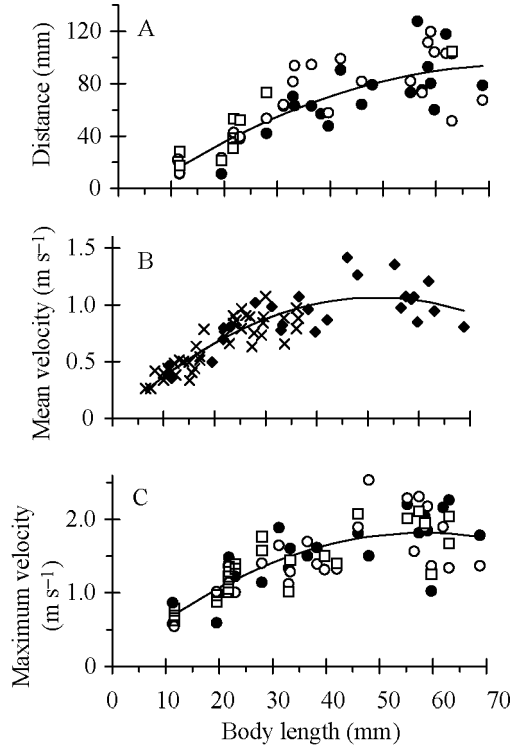

Fig. 8. Displacement variables of the shrimp's centre of mass. (A) Horizontal displacement per tail-flip. (B) Mean velocity over entire tail-flip swimming bouts. (C) Maximum velocity attained during flexion phases. Crosses in B represent recordings at 50 frames s^{-1} with a natural stimulus (cod); other symbols in A–C are from high-speed video recordings (200 frames s^{-1}) using an artificial stimulus. Filled circles, tail-flip 1; open circles, tail-flip 2; squares, subsequent tail-flips; diamonds, entire swimming bout. Fitted lines were derived from quadratic regressions (see Table 1).

data have therefore been pooled. The lowest mean velocity measured was 0.26 m s^{-1} by an 8 mm shrimp, and the highest was 1.42 m s^{-1} by a 46 mm shrimp. There was a tendency for values to decline in the largest (>60 mm) shrimps, although only a few shrimps were filmed within this size range. A quadratic regression fitted to the data (Fig. 8B; Table 1) had both positive and negative slope coefficients that were significant (t_{62}=6.65, P<0.0001 and t_{62}=9.52, P<0.0001 respectively), and had a predicted peak value of 1.07 m s^{-1} (at a body length of 52 mm). In terms of body length equivalents, mean velocity decreased with body length from approximately 37 body lengths s^{-1} in the smallest shrimps and 14 body lengths s^{-1} in the largest.

Maximum velocity of centre of mass during the flexion phase of the tail-flip

The lowest maximum velocity of the centre of mass for a single tail-flip was 0.59 m s^{-1} by a shrimp of 20 mm, and the highest was 2.31 m s^{-1} by a shrimp of 57 mm. A quadratic regression fitted to the data (Fig. 8C; Table 1) had both positive and negative slope coefficients that were significant (t_{71}=5.19, P<0.0001 and t_{71}=3.57, P<0.001 respectively) and had a predicted peak value of 1.8 m s^{-1} (at a shrimp length of 58 mm). In terms of body length equivalents, maximum velocity decreased with body length from approximately 60 body lengths s^{-1} in the smallest shrimps to 25 body lengths s^{-1} in the largest.

There was no significant difference between the maximum velocity achieved by the centre of mass during the first and second tail-flips of each escape (paired t-test, t_{24}=0.26, P=0.80). Subsequent tail-flips (up to the fifth of an escape swimming bout) were also very similar, and so these data have been pooled in the regression analysis.

Discussion

Thrust-producing mechanisms during tail-flip swimming

In crayfish (Wine and Krasne, 1972; Wine, 1984) and nephropid lobsters (Newland *et al.* 1988; Newland and Neil, 1990*a*), tail-flips mediated by medial giant fibres (in response to a sudden frontal attack) and by the non-giant circuitry produce a curling of the tail-fan under the body as flexion is propagated along the abdomen. This results in little or no pivoting of the cephalothorax about the centre of mass. In this 'single oar' propulsion system, the majority of thrust is produced by movements of the abdomen through the water and is due to the inertial forces associated with the acceleration of the added mass of water (Webb, 1979). These forces are largely attributable to movements of the tail-fan, which has a large surface area, is furthest from the point of flexion and has a high velocity relative to the animal's centre of mass. Daniel and Meyhöfer (1989) have also shown that, in the dock shrimp *Pandalus danae*, an additional and significant source of thrust is created by 'squeeze forces' towards the end of flexion as trapped water is ejected from between the abdomen and cephalothorax.

Tail-flip flexion in *Crangon crangon* is mainly confined to the anterior region of the abdomen, causing both it and, to a lesser degree, the cephalothorax to pivot about the shrimp's centre of mass in a 'jack-knife' manner. This jack-knife mechanism, which was common to all forms of tail-flip escape swimming observed in this study and to shrimps of all lengths, regardless of stimulus direction, resembles more closely the flexion pattern of mysid tail-flips (Neil and Ansell, 1995). In such cases, it would appear that thrust is generated using a 'twin oar' system, since thrust may be produced both by the expanded head-fan and tail-fan. Another contributing factor of jack-knife tail-flips may derive from greater squeeze forces (Daniel and Meyhöfer, 1989) produced by the channelling of water trapped between the abdomen and the cephalothorax.

The jack-knife tail-flip mechanism is promoted by the lightly armoured chelipeds and carapace of *C. crangon*, making the mass of the cephalothorax more equal to that of the abdomen and bringing the centre of mass close to the point of flexion. In lobsters and crayfish, the mass of the cephalothorax and the heavily armoured claws suppresses the jack-knife form of tail-flip so that it only occurs (mediated by the lateral giant fibres) in response to a sudden attack from the animal's rear (Wine and Krasne, 1972; Neil and Ansell, 1995).

Neuronal control of Crangon crangon *tail-flips*

The question of the involvement of the giant fibres in *C. crangon* tail-flips remains to be addressed. This shrimp certainly possesses both medial and lateral giant fibres (Johnson, 1924), and the types of stimuli employed, visual and vibrational, are known to be sufficient to activate giant fibres in other crustaceans (Wine, 1984). Furthermore, short response latencies (10–15 ms) were typical of the escapes observed, suggesting that the giant fibres were involved, but this must be interpreted with caution because a more precisely defined stimulus is needed to measure this parameter specifically.

Unlike the clear differences between lateral- and medial-giant-mediated tail-flips in crayfish and lobsters (Wine and Krasne, 1972), both frontal and rear attacks to *C. crangon* produced fairly similar types of responses. Within the lateral and vertical escapes produced, there was no obvious difference in the trajectories between the frontal and rear attacks (although this was not assessed in detail). Therefore, if the two giant fibre systems of *C. crangon* are responsible for conveying anterior and posterior stimuli to the abdominal flexor motor system, then their output connections would be expected to have a greater degree of similarity than in crayfish.

In frontal attacks, there is a clear difference between the escape trajectories of *C. crangon* compared with crayfish and lobsters in that the former do not produce escapes propelled directly backwards along the substratum. Whilst this may in part be due to differing electrophysiological connections, the body posture of *C. crangon* probably also plays an important part in excluding this behaviour. Shrimps normally adopt a resting posture with their entire abdomen in a fully extended position and flat against the substratum. This causes the initial thrust produced by both the head-fan and tail-fan at the

beginning of an escape to be directed downwards against the substratum, creating vertical lift.

Several differences were detected between the kinematic properties of tail-flip 1 and tail-flip 2 of an escape. Tail-flip 1 had a longer flexion and shorter re-extension phase than tail-flip 2 and produced higher angular velocities. Some of these differences are undoubtedly caused by the fact that tail-flip 1 started from a fully extended body position in contact with the substratum, but some differences may also be attributable to the involvement of giant fibres in the first flip, with a non-giant pathway mediating later flips. Confirmation of this requires direct recordings by electrophysiological methods.

Size-dependent kinematic variability

Daniel and Meyhöfer (1989) calculated that, for a shrimp of given dimensions and with an isometric growth pattern, there is a unique body length that maximises the tail-flip kinematic performance. This arises because of the non-uniform scaling relationships between the stress limits of the abdominal muscle, the body dimensions and the translational and rotational components of tail-flip thrust.

In *C. crangon*, the abdomen to total length (*A*:*L*) ratio and the cross-sectional area of abdominal fast muscle (*F*) were both found to scale isometrically with respect to total length. Despite these isometric dimensions, wet mass increased at a rate greater than that expected for isometric growth. A possible cause for this may be that the shrimp's more dense exoskeleton becomes proportionally thicker as length increases, as suggested by the fact that the underwater wet weight of *C. crangon* scales to the power 3.48 (Kils, 1981). This may decrease the efficiency of tail-flips as shrimps increase in length.

In their study of *Pandalus danae*, Daniel and Meyhöfer (1989) predicted that the duration of the flexion stage of the tail-flip should increase in an approximately linear manner as shrimp body length increases (derived from Fig. 9 of Daniel and Meyhöfer, 1989), and this was found to be true for *C. crangon* (Table 1; Fig. 6B). They also predicted an increase in tail-flip performance with shrimp length until a peak value was reached (in the case of *P. danae*, at a body length of 60 mm). The curves fitted to the mean and maximum velocity values in *C. crangon* (Table 1; Fig. 8B,C) clearly indicate that tail-flip performance increases as the smallest individuals increase in length, at least between 5 and 50 mm. Some caution is required in interpreting the maximum velocity values of the smallest shrimps since, at these sizes, underestimation of the peak velocity attained may occur. This is because velocity was measured from only eight images per tail-flip compared with as many as 24 images per tail-flip in larger shrimps (because of the size-dependent differences in tail-flip duration). The potential error arising from this source was tested using a simulation in which a mathematically derived curve (with the same shape as the tail-flip velocity data) was repeatedly 'sampled' at different rates per cycle, starting from different points along the curve. From the simulation, peaks were estimated to lie between 88.7 % and 96.9 % (median 94.7 %) of their true value (calculated from the curve function) at six samples per cycle compared with 98.8 % (median 99.5 %) at 24 samples per cycle. In our high-speed video results, the predicted maximum velocity of the smallest shrimps (11 mm) was approximately 0.68 m s^{-1} compared with 1.82 m s^{-1} for the larger, fastest shrimps. In the worst case of underestimation, the value for the smallest shrimps would actually be 0.76 m s^{-1} (0.71 m s^{-1} with median error). The error arising from the lower sampling rate frequencies of small shrimps will therefore have a negligible effect on the conclusions drawn from the results.

The fitted mean and maximum velocity curves for *C. crangon* (Table 1; Fig. 8B,C) suggest that a peak in tail-flip performance may occur in shrimps of between 52 and 58 mm. However, the data presented here provide inconclusive proof of these peaks because of the small number of shrimps longer than 60 mm that were filmed and because shrimps approaching the maximum reported size for the species (80–90 mm; Tiews, 1970) were not available for study.

Orientation of the body whilst tail-flipping

In the majority of tail-flips analysed, *C. crangon* performed a pronounced roll about its longitudinal axis during the first flexion of an escape response. If this did not occur, and the shrimp escaped with an initial vertical trajectory, it usually rolled onto its side during the first re-extension phase. The division between these two types of behaviours is not absolute since different degrees of initial roll were observed. In both cases, however, shrimps then swam on their side in a horizontal direction during subsequent tail-flips before righting themselves again as they settled back onto the substratum. Incidents in which shrimps did not escape on their side at all (i.e. when they swam in a head-down, tail-up position) were rare. This strong tendency for *C. crangon* to swim on their side contrasts with the typical tail-flip behaviour of many decapod crustaceans (e.g. Wine and Krasne, 1972; Webb, 1979; Sillar and Heitler, 1985; Jacklyn and Ritz, 1986; Wilson and Paul, 1987; Spanier *et al.* 1991; Newland *et al.* 1992*a*), which generally tail-flip in an upright position and have dynamic self-righting mechanisms that maintain this orientation during an escape (Newland and Neil, 1990*b*; Newland *et al.* 1992*b*).

Body roll during the first tail-flip of an escape in *C. crangon* is fundamental in re-directing the vertical thrust from jack-knife tail-flips to produce a horizontal escape trajectory. Without it, shrimps would continue to tail-flip vertically (if no somersault is performed), translating them away from the refuge provided by the sediment, against which they are cryptic and within which they are able to hide by quickly burying themselves once they resettle (Pinn and Ansell, 1993). Escaping too far off the substratum may also be disadvantageous because the silhouette image of the shrimp created against the water surface will make it conspicuous to visual predators (Thetmeyer and Kils, 1995). A further advantage offered by the body roll is that it can occur to the shrimp's left or right in an unpredictable ('protean') manner,

a factor that may assist in evading an attacking predator (Driver and Humphries, 1988).

An initial roll towards one side of the body has also been shown to take place in mysid shrimps (Kaiser *et al.* 1992; Neil and Ansell, 1995) which, as described above, also use jack-knife tail-flips and form an expanded head-fan. The relatively small size of *C. crangon* (and mysids) and their comparatively thin (i.e. light) exoskeleton are probably important features that enable them to adopt these characteristics. Larger crustaceans with heavily calcified exoskeletons have to generate a greater proportion of vertical thrust when tail-flipping in order to maintain height above the substratum. This is facilitated by being in an upright position because the rotational forces generated during abdominal flexion (Daniel and Meyhöfer, 1989) create vertically directed thrust and, in the case of heavily calcified scyllarid lobsters, because their large antennal scales act as 'ailerons' (Jacklyn and Ritz, 1986).

A jack-knife tail-flip mechanism and swimming on one side of the body seem to be incompatible with anachoresis (i.e. living within crevices or burrows) since tail-flip movements would become obstructed by the walls of a narrow passageway. The use of jack-knife tail-flipping, head-fan formation and swimming on one side therefore appear to be intrinsically linked adaptations adopted by small crustaceans living in relatively unconfined habitats.

Steering of tail-flips in the animal's roll plane

In laterally directed escapes, the sideways roll was often evident within the first few frames in which movement was detected (Fig. 5). It is not obvious how these rotational forces were brought about. Neil and Ansell (1995) noted that, when the mysid *Praunus flexuosus* rolled on to its side during its first tail-flip, the antennal scales and uropods were expanded asymmetrically and acted as rotors which contributed towards the forces bringing about the body roll. Occasionally, asymmetrical spreading of the antennal scales or uropods was observed in *C. crangon*, but this was not noticeable in many of the escapes and was not necessary for body roll to occur.

An alternative may be that the roll is brought about by asymmetrical muscle activity in the shrimp's abdomen. Newland and Neil (1990*b*) have shown that, during tail-flip swimming in *Nephrops norvegicus*, dynamic righting reactions in the animal's roll plane are brought about primarily by rotation of the abdomen relative to the cephalothorax. *C. crangon* possess a set of oblique fast muscles spanning this joint (S. A. Arnott, personal observations), and it is possible that these serve to tilt the shrimp away from the upright rather than towards it at the beginning of an escape.

Another possible contributor to roll is suggested by the observation that, in the palinurid lobster *Jasus lalandii*, asymmetrical movements of the swimmerets can cause movements in the animal's roll plane during tail-flips (Cattaert *et al.* 1988). In the video sequences of *C. crangon*, the pleopods were obscured from the camera's view by the abdomen during the initial stages of an escape. However, when shrimps performed an initial vertical flexion and then rolled onto their side during the re-extension phase, pleopod movement was sometimes visible. This suggests that the pleopods may assist in bringing about body roll, at least under some circumstances.

In scyllarid lobsters, roll manoeuvres are controlled during the glide phase of tail-flips (i.e. at the end of the flexion phase), once the animal is swimming within the water column, by asymmetrically raising or lowering their antennal scales (Jacklyn and Ritz, 1986). Whether *C. crangon* are able to use a similar form of steering during subsequent tail-flips is uncertain.

Steering in the animal's pitch plane

When *C. crangon* do perform a body roll during their first tail-flip and then swim on their side, control of rotation in the shrimp's pitch plane brings about horizontally directed steering. During the largest steering manoeuvres in the rostral direction, a backward beat of the pleopods was often observed during the preceding re-extension phase (Fig. 5). This may serve to prevent the cephalothorax from pivoting about the centre of mass as the abdomen re-extends, thereby adjusting the shrimp's orientation in preparation for the next flexion phase and directing it along a new trajectory. However, large pitching manoeuvres also occurred without the assistance of pleopod activity. In these cases, spatial and temporal adjustments in muscle activation patterns within the abdomen may have contributed to the pitching movements, as occurs in larger decapods (Wine, 1984; Newland and Neil, 1990*a*). Additionally, the head-fan was not always fully retracted during the re-extension phase of a rostrally directed pitch movement, and this may also have affected the shrimp's pitch orientation. At present, tail-flip steering in *C. crangon* remains poorly understood and warrants further investigation.

Comparison of swimming kinematics

Neil and Ansell (1995) compared the tail-flip performances reported in the literature for six species of decapods, two species of mysids and one species of euphausid across a range of body lengths covering 10–270 mm. Maximum velocities ranged from $0.6\,m\,s^{-1}$ for the nephropid lobster *Nephrops norvegicus* (Newland *et al.* 1988) to $2.8\,m\,s^{-1}$ for the caridean shrimp *Pandalus danae* (Daniel and Meyhöfer, 1989), with most species having peak velocities of less than $1\,m\,s^{-1}$. Among these species, *Crangon crangon* ranks as a relatively fast tail-flip swimmer according to the maximum velocity of $1.8\,m\,s^{-1}$ for a 58 mm shrimp predicted by the regression equation in Table 1, but it is difficult to make accurate comparisons because of the different frame rates and conditions used in the various studies.

In comparison with one of the common predators of *C. crangon*, the cod *Gadus morhua* (Tiews, 1970; Pihl, 1982; Berghahn, 1996), the results presented here suggest that shrimps will not be able to escape a pursuing cod by using speed alone. Juvenile cod are able to consume shrimps up to 36 % of their own body length (Arnott, 1996). According to Wardle (1975), a cod with a length of 100 mm can achieve a

maximum velocity of up to $1.7\,m\,s^{-1}$, which is faster than shrimps in the edible range 10–36 mm ($0.6–1.6\,m\,s^{-1}$). More significant is the fact that the maximum velocity of cod continues to increase with length so that, for a cod of 300 mm, Wardle (1975) predicts a value of $3.3\,m\,s^{-1}$. This is considerably faster than *C. crangon* of any length. Furthermore, because the tail-flip velocity of *C. crangon* may level off in shrimps larger that 50 mm, one might expect the escape success of a large shrimp being attacked by a large cod to be lower than for a small shrimp being attacked by a proportionally smaller-sized cod. The inability of *C. crangon* to out-compete predators in a 'straight-line race' suggests that other strategies such as manoeuvrability (Howland, 1974; Webb, 1976; Weihs and Webb, 1984), unpredictability (Driver and Humphries, 1988; Domenici and Blake, 1993) and hiding on or within the substratum will also be important in determining the outcome of encounters with predators.

We are grateful to Dr R. S. Batty for generous provision of and assistance with the high-speed video equipment and to other staff and students at the Dunstaffnage Marine Laboratory (DML) for their support with the project. We also thank Dr B. Bergström and two anonymous referees for their suggestions on improving the manuscript. Measurements used for calculating the abdomen length to total length ratio of shrimps were kindly provided by Håkan Wennhage and Sven Nilsson. The project was funded by a Natural Environment Research Council CASE studentship (S.A.A.) between the University of Glasgow and DML.

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