

ESCAPE TRAJECTORIES OF THE BROWN SHRIMP *CRANGON CRANGON*, AND A THEORETICAL CONSIDERATION OF INITIAL ESCAPE ANGLES FROM PREDATORS

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Summary

Tail-flip escape trajectories of the brown shrimp *Crangon crangon* have been investigated in response to a natural predator, the cod *Gadus morhua*, and an artificial stimulus. Shrimps escaped by rolling to their left or right during the initial tail-flip of a response, and thereafter swam on their side. As a result of the laterally directed first tail-flip, initial escape angles always lay between 75° and 156° with respect to the (pre-escape) longitudinal axis (anterior=0°) of the shrimp. Symmetrical attacks from either head-on or tail-on produced escapes to the shrimp's left or right in equal proportions, although a contralateral bias did occur if the shrimp experienced a looming object from one side before a symmetrical attack was applied. Lateral attacks produced a significantly greater proportion of contralateral responses than ipsilateral ones. Empirical and theoretical analyses indicate that the initial escape direction is influenced by an interaction between the range of first tail-flip escape angles that the shrimp is capable of

performing and the risk of being intercepted by a predator during the initial stage of an escape. Thus, the unpredictability ('protean behaviour') of the response may be affected by the conditions of the interaction.

Subsequent tail-flips of an escape usually directed the response away from the stimulus, but sometimes escapes were instead steered to the side of the stimulus and then behind it. The probability of each type of escape occurring changed with attack direction.

The elements of protean behaviour that have been identified in both the initial and subsequent stages of the escape may prevent predators from learning a fixed pattern of response, but a trade-off occurs when escape trajectories infringe upon zones of high capture risk.

Key words: *Crangon crangon*, brown shrimp, escape trajectory, predator-prey interaction, protean behaviour, tail-flip.

Introduction

The escape response of an animal has the objective of minimising the probability of capture by an approaching predator. The initial stage of the escape must remove the prey from the path of the predator's initial strike. Thereafter, the effectiveness of the escape depends upon the animal following a trajectory that will minimise the chance of a pursuit occurring or of it being caught if the predator does decide to engage in a pursuit.

Escape trajectories may be affected by the types of refuge offered by the surrounding habitat and the prey's use of them. In cases where a specific point-source refuge is used, its location with respect to the animal's starting position will have a strong influence upon the direction of an escape. For instance, the semaphore crab *Heloecius cordiformis* and the fiddler crab *Uca pugilator* both escape directly towards their burrow (if it is nearby) when they are threatened (Nalbach, 1990; Land and Layne, 1995). Conversely, when no habitat refuge is available, animals must adopt alternative escape strategies. In this

situation, Weihs and Webb (1984) argue that trajectories that prolong a pursuit will maximise the energetic cost to the predator, eventually causing the attack to be aborted. Incorporating unpredictability (also known as 'protean behaviour'; see Chance and Russell, 1959) into the escape response may also be advantageous in such circumstances, since it confuses the predator and prevents it from pre-empting the movements of the prey (Driver and Humphries, 1988).

As a predator closes in on its prey, the latter may take evasive action and, in this situation, Howland (1974) showed that the relative velocity, turning radius and timing of the response are critical in determining the outcome of the interaction. For the prey to escape, it was shown that the prey's normalised velocity (i.e. prey velocity/predator velocity) must exceed the square root of its normalised turning radius.

In this investigation, escape trajectories of the brown shrimp *Crangon crangon* have been studied. Unlike some shrimps, *C. crangon* do not shoal (Tiews, 1970), but live dispersed on

open-sediment substrata that are devoid of specific point-sources of refuge. They range in length typically between 5 and 70 mm, have cryptic coloration, and bury themselves when they are not active on the sediment surface (Pinn and Ansell, 1993). Despite these 'primary defences' (Edmunds, 1974), *C. crangon* are preyed upon by a large number of species, particularly fish such as cod (*Gadus morhua*), whiting (*Merlangius merlangus*) and gobies (*Pomatoschistus minutus*) (Henderson and Holmes, 1989; del Norte-Campos and Temming, 1994; Berghahn, 1996). When attacked, shrimps attempt to escape by means of a tail-flip escape response. Such tail-flip responses are typical of many macrurous decapod crustaceans (Neil and Ansell, 1995) and are brought about by a series of flexion and re-extension movements of the abdomen (Webb, 1979; Daniel and Meyhöfer, 1989). In *C. crangon*, as in the more extensively studied crayfish and lobster species (e.g. Wine and Krasne, 1982; Newland et al., 1992), tail-flips are controlled by both giant and non-giant neuronal networks (Johnson, 1924) and can attain mean velocities of between 0.3 and 1.4 m s⁻¹, depending upon the size of the shrimp (Arnott et al., 1998).

The escape trajectories of *Crangon crangon* have been investigated in response to a natural predator, the cod *Gadus morhua*, as well as to an artificial stimulus consisting of a wooden rod accelerated towards the shrimp. Video analysis has been used to determine the initial (first tail-flip) and final (subsequent tail-flip) escape trajectories of *C. crangon* with respect to (i) the pre-escape body position of the shrimp and (ii) the direction of attack. These data have been subjected to circular statistical analysis (see Domenici and Blake, 1993) to determine whether shrimps escape along preferred escape trajectories. Protean aspects of the escape behaviour (Driver and Humphries, 1988; Domenici and Blake, 1993) have been analysed quantitatively, and a theoretical model has been devised to interpret the observed relationship between unpredictability during the initial phase of an escape and the conditions of the interaction. Some of these data have been presented previously in abstract form (Arnott et al., 1995).

Materials and methods

Animals

Brown shrimps (*Crangon crangon* L.) were caught 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 holding tanks (100 cm×50 cm×30 cm) with a 1–2 cm deep sand substratum. The shrimps were fed *ad libitum* every other day on chopped mussels and/or frozen mysids.

Juvenile cod (*Gadus morhua* L.) were caught at night in the same location using a beach seine net and immediately transferred to circular holding tanks (100 cm diameter, 70 cm water depth). The cod were fed daily on either frozen mysids or a mixture of live mysids and *Crangon crangon*.

Shrimp and cod holding tanks were provided with a constantly renewing supply of sea water maintained at approximately 13 °C and aerated with an air stone. Animals

were kept for at least 2 weeks before being used for experiments and for a maximum of 2 months.

Experimental protocol

Cod stimulus experiments

A series of experiments was conducted in an air-conditioned room (13 °C) to determine the escape trajectories of *Crangon crangon* from an approaching predatory cod. An experimental arena (30 cm diameter, 20 cm water depth) with a white base was illuminated from a distance of 3 m with shaded fluorescent lighting. Experiments were filmed (50 frames s⁻¹) from directly above using conventional video equipment (Vista NCD 360 TV camera, IMP Electronics V9000 time inserter, Panasonic AG-6024 VHS recorder). Before each experiment, a single shrimp (12–34 mm rostrum–telson length) and a single cod (63–105 mm total length) were placed in the arena and kept separate from one another for 15 min by covering the shrimp with an upturned, perforated container. Aeration was provided at this stage through an air stone. At the start of the experiment, the air stone was removed, and the container was lifted remotely by an attached string from behind a screen. Thirty shrimps were used (range of shrimp:cod length ratio combinations 0.12–0.35; mean 0.24), and one escape by each shrimp was analysed.

Artificial stimulus experiments

A further series of experiments was performed using an artificial stimulus rather than cod to provoke escapes by *Crangon crangon*. Temperature, illumination and filming procedures were the same as in the cod experiments. Experiments were conducted in a 1 m diameter holding tank filled with sea water to a depth of 40 cm. A white base plate (75 cm diameter) was placed inside the tank and supported 15 cm off the bottom. The base plate was therefore covered with water to a depth of 25 cm and had a gap of 12.5 cm between its edge and the side of the main holding tank. For each experiment, an individual shrimp (25–40 mm rostrum–telson length) was placed on the base plate and covered with an upturned container to allow the shrimp to settle. After 15 min, this was removed, and the shrimp was startled by rapidly accelerating a hand-held wooden rod (2 cm diameter) towards it. Before each 'strike', the tip of the rod was held under the surface of the water, approximately 20 cm away from the shrimp, at a vertical elevation of approximately 30–45°. The only parts of the experimenter visible to the shrimp were his head and hands, which were behind and directly in line with the stimulus rod. Trials were rejected if the rod made direct contact with the shrimp or the base plate, or if the approaching stimulus was not in direct line with the shrimp's body. The stimulus induced single (not analysed) or multiple tail-flip swimming bouts, at the end of which the shrimp either landed back on the base plate or swam beyond it and sank down to the bottom of the holding tank. In the former instance, the shrimp was stimulated again after 1–2 min to induce another tail-flip swimming bout. In the latter instance, experiments

on that shrimp were terminated and another shrimp was introduced to the arena. Thirty-nine shrimps were used, each performing between one and four escapes ($N=76$ escapes in total).

Attacks were applied in a random order from five directions: approximately 0° (head-on, $N=12$), 45° ($N=17$), 90° ($N=16$), 135° ($N=18$) and 180° (tail-on, $N=13$). These angles were defined more precisely following video analysis (see below).

Application of an asymmetrical prior stimulus

Preliminary experiments with *Crangon crangon* revealed that the initial tail-flip of an escape is typically directed towards the shrimp's left or right side (described in the Results section). However, if an object is brought slowly towards one side of a shrimp, a slight lean towards the opposite side can be detected (Fig. 1). A series of 20 trials was conducted on separate shrimps to determine whether this leaning response correlated with the side to which an escape would occur if a head-on stimulus was subsequently applied.

Shrimps were introduced individually to the artificial stimulus arena and a lateral 'prior stimulus' was applied by bringing the stimulus rod slowly towards one side of the shrimp until a leaning response was induced. The rod was then withdrawn slowly (during which time the leaning response persisted), and an attack from approximately head-on (0°) was applied. The frequency of escapes to the same (ipsilateral) or opposite (contralateral) side of the shrimp with respect to the prior stimulus was recorded from the video tapes.

Experiments on blinded shrimps

Five shrimps were blinded by painting over both eyes with multiple layers of artist's black oil paint. All shrimps survived this treatment and subsequently lost the paint layer when they moulted. Blinded shrimps were attacked from various angles with the artificial stimulus rod to determine whether tail-flip escape responses could be evoked in the absence of visual stimuli.

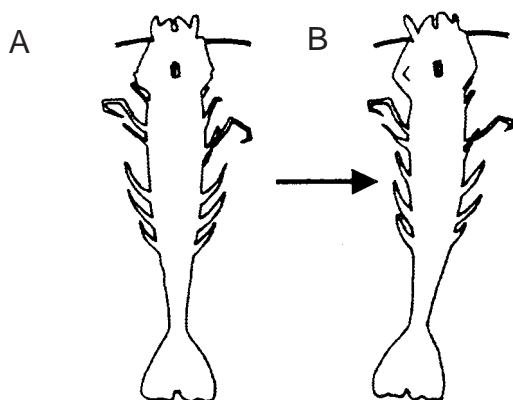


Fig. 1. Diagram showing leaning behaviour of *Crangon crangon* in response to a gradually applied lateral 'prior stimulus'. (A) Dorsal profile of a shrimp whilst motionless on the substratum in the absence of a prior stimulus. (B) Dorsal profile after applying a prior stimulus (arrow) from the shrimp's left side.

Analysis

Video analysis

Only multiple tail-flip escapes initiated away from the side of the arena have been analysed. In experiments with the cod stimulus, escape trajectories were plotted frame by frame (20 ms intervals) from a monitor (JVC) onto an acetate sheet by recording the position of the shrimp's approximate centre of mass. This is located on the ventral edge of the joint between the cephalothorax and abdomen (Arnott et al., 1998). The points were subsequently digitised on an x,y plotter and downloaded onto a personal computer (PC). In the artificial stimulus experiments, sequences of video frames were captured on a PC monitor and x and y coordinates were digitised manually from these using a program written in Visual Basic. Escape paths were plotted until the shrimp hit the side-wall of the arena (cod experiments), swam off the edge of the base plate (artificial stimulus experiments) or resettled on the base plate (both sets of experiments).

Correction was made for spherical aberration during playback by filming and digitising measured dimensions within the arena. Distances were calibrated against a 10 cm marker placed on the base plate of each respective experimental arena.

Reaction distances

The frame immediately prior to that in which movement by the shrimp was first detected was designated frame zero. For each escape, the position of the snout of the cod or the tip of the artificial stimulus was digitised from frame zero. The distance from this point to the position of the shrimp's centre of mass was measured as the reaction distance.

Convention used for measuring angles

Where necessary, both cod and artificial stimulus responses have been reflected so that all data are expressed as if attacks were from the shrimp's right side.

The attack angle of the stimulus has been measured with respect to the shrimp's longitudinal axis (Fig. 2A) such that 0° represents a head-on attack and 180° represents a tail-on attack. Escape angles (see below) have been measured both with respect to the shrimp's longitudinal axis (ϵ_{body} ; anterior= 0°) and with respect to the stimulus (ϵ_{attack} ; stimulus= 0°). All angles between 0° and 180° in a clockwise direction are assigned positive values, and those between 0° and 180° in an anti-clockwise direction are assigned negative values. When comparisons are made between the absolute values of negative and positive angles, the mathematical convention of moduli is used (e.g. $|90^\circ|$ describes both the angles $+90^\circ$ and -90°). In cases where reference is made to escape trajectories reported by other authors, values are expressed using the convention described here for ease of comparison.

With normalised data, where all attacks are expressed as if from the shrimp's right side, responses in which the shrimp escaped to its left are termed contralateral escapes and those to its right are termed ipsilateral escapes.

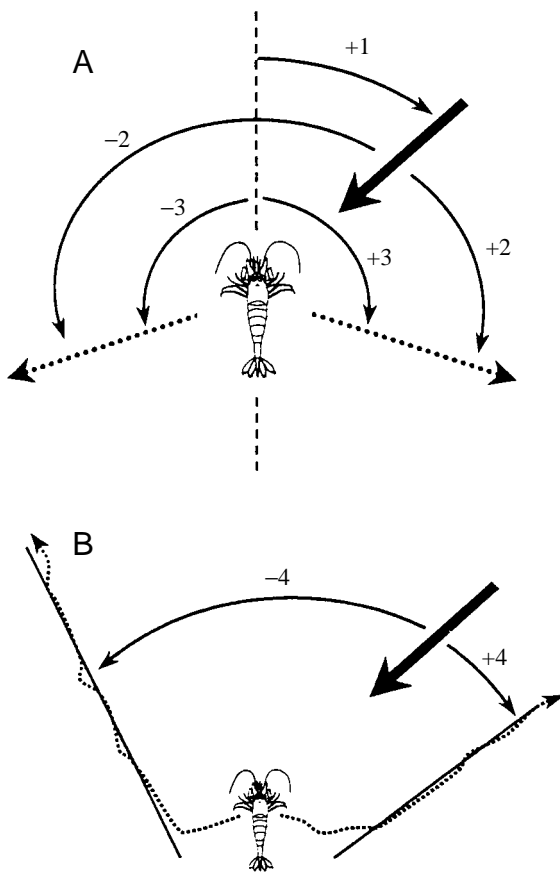


Fig. 2. Methods used for measuring angles (curved arrows) with respect to the stimulus (thick solid arrow), the shrimp's longitudinal axis (dashed line) and the shrimp's escape path (dotted arrow). All escape angles between 0° and 180° in a clockwise direction were assigned positive values, whilst those between 0° and 180° in an anticlockwise direction were assigned negative values. (A) Diagram representing the first tail-flip of an ipsilateral (to the right) and a contralateral (left) escape response. Angle 1, attack angle (normalised to the shrimp's right side where necessary); angle 2, initial ϵ_{attack} angle (the initial escape angle relative to the attack angle); angle 3, initial ϵ_{body} angle (the initial escape angle relative to the longitudinal axis of the shrimp's body). (B) Diagram showing the paths of an entire ipsilateral (right) and an entire contralateral (left) multiple tail-flip escape. A straight trajectory (solid line) was fitted to the final escape path, and the final ϵ_{attack} angle (angle 4) was measured with reference to this path. Angle 3 was measured from both cod and artificial stimulus data. Angles 1, 2 and 4 were only measured from the artificial stimulus data.

Attack angles

With the cod stimulus, it was sometimes impossible to determine a narrowly defined attack angle because turning manoeuvres performed by the cod resulted in a wide visual angle being presented to the shrimp. Therefore, escape from cod were separated into two categories; those in response to cod approaching from the (normalised) right anterior quadrant (i.e. attacks from between 0° and 90°), and those in response to approaches from the (normalised) right posterior quadrant (90 – 180°).

With the artificial stimulus, the five attack categories termed 0° , 45° , 90° , 135° and 180° had measured attack angles (from the video recordings) with mean values (\pm S.D.) of $3\pm 2^\circ$, $48\pm 5^\circ$, $90\pm 6^\circ$, $139\pm 7^\circ$ and $176\pm 4^\circ$, respectively.

Initial ϵ_{body} angle (cod and artificial stimuli)

The initial escape angle with respect to the shrimp's body orientation (initial ϵ_{body} angle) was determined by fitting a regression line from the shrimp's centre of mass on frame 0 (when stationary) through its position on frames 2 and 3 (i.e. after escaping, on average, for 30 and 50 ms, respectively, along an approximately linear trajectory). The angle between the fitted line and the orientation of the shrimp on frame 0 (anterior= 0°) was measured as the initial ϵ_{body} angle (Fig. 2A).

In an earlier study, Arnott et al. (1998) determined that the time interval of 50 ms falls within the first tail-flip of an escape by *Crangon crangon*, and original data from their high-speed video recording ($200 \text{ frames s}^{-1}$) sequences have been used to estimate the potential error arising from the lower filming speed (50 frames s^{-1}) used in this study. Regressions were fitted to x , y coordinates digitised from the first 11 high-speed video frames (5 ms intervals) from 18 separate escapes (shrimp rostrum–telson lengths 11–50 mm). The initial ϵ_{body} angles determined from these were compared with those derived from regressions fitted to data from frames 1, 7 and 11 only. Angles compared in this manner agreed within a range of 4° of one another, with a mean difference of 2.1° .

Initial ϵ_{attack} angle (artificial stimulus)

The initial escape angle with respect to the attack angle (initial ϵ_{attack} angle) was determined in the same manner as the initial ϵ_{body} angle, with the exception that angles were measured with respect to the attack angle of the artificial stimulus on frame 0 (Fig. 2A). Initial-toward responses were defined as those in which the initial ϵ_{attack} angle was less than $|90^\circ|$ and initial-away responses as those in which the initial ϵ_{attack} angle was greater than $|90^\circ|$.

Final ϵ_{attack} angle (artificial stimulus)

After the first one or two tail-flips of an escape swimming bout, shrimps escaped along an approximately linear path. A straight line was fitted to this final escape trajectory, and the final escape angle with respect to the attack angle (final ϵ_{attack} angle) was measured as the angle between the fitted line and the attack angle of the artificial stimulus on frame 0 (Fig. 2B). Final-toward responses were defined as those in which the final ϵ_{attack} angle was less than $|90^\circ|$ and final-away responses as those in which the final ϵ_{attack} angle was greater than $|90^\circ|$.

Graphical representation of circular data

Escape angle frequencies have been represented (see Fig. 6) using radial plots (arranged into 10° sectors) in which the distance from the origin is proportional to the frequency of escapes in the specified direction. When pooling data from different attack categories, equal weighting has been applied (by considering percentages rather than actual frequencies) to

prevent bias arising from differences between category sample sizes.

Statistical analyses

Differences between reaction distances in response to various stimuli and attack directions were tested using a nested analysis of variance (ANOVA) (performed using Minitab 10X software, Minitab Inc.) after \log_e -transformation of the data to meet normal distribution criteria. Randomness in the frequency of escapes to the shrimps' contralateral and ipsilateral sides was analysed using a binomial test (Zar, 1996). A logistic regression was fitted to the relationship between the probability of a final-toward response occurring and the initial ϵ_{attack} angle of an escape (see Fig. 7). The significance of the fit was analysed by means of a χ^2 -test (regression) and χ^2 -test performed using SPSS 5.0.2 software, SPSS Inc.).

Escape angles were analysed using circular statistical methods (Batschelet, 1981) and, where appropriate, calculations were performed using Oriana 1.0 software (Kovach, 1994). Circular distributions of escape angle data were tested for randomness using Rayleigh's test of uniformity. Homogeneity between the distribution of escape angles in response to different attack categories was analysed using the Watson-Williams test. Where this revealed a significant difference between more than two groups of data, subsequent pairwise comparisons have not been performed because no standard procedure for this appears to exist.

Domenici and Blake (1993) fitted unimodal von Mises (circular normal) functions to escape trajectory data to test whether apparent bimodal escape preference distributions differed significantly from a unimodal model. This method has been applied here (see Fig. 6) by fitting von Mises curves to final ϵ_{attack} angle data after applying grouping corrections to allow for differences in the number of observations between each attack category (Batschelet, 1981). The significance of the fitted curves was tested using χ^2 goodness-of-fit tests (Zar, 1996).

Results

General description of tail-flip escapes

Shrimps responded to both the cod and artificial stimuli by performing a tail-flip swimming bout. The first tail-flip of a bout was preceded by a lateral roll of the shrimp's body about its antero-posterior axis, causing the shrimp to escape from the substratum on its side in a predominantly horizontal direction (Fig. 3). The detailed kinematics of the tail-flip are described elsewhere (Arnott et al., 1998). Thereafter, shrimps remained on their side whilst swimming and were able to steer in the horizontal plane by altering the degree of pitch rotation between successive tail-flips. If a large steering manoeuvre occurred, it tended to take place at the end of the first tail-flip, altering the shrimp's direction of travel by up to 70° . No escapes were observed in which shrimps tail-flipped in an initial backward or forward direction. At the end of a swimming bout, shrimps settled on the substratum in an upright body position.

Escapes in response to the cod (range of mean approach velocities $0.1\text{--}1.0\text{ m s}^{-1}$) occurred either as the fish was

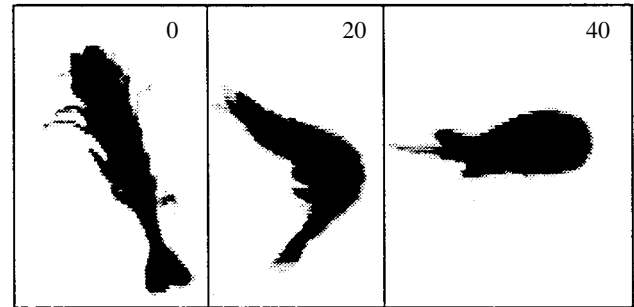


Fig. 3. High-speed video sequence showing the first tail-flip of an escape response by *Crangon crangon* (modified from Arnott et al., 1998; filmed at 200 frames s^{-1} , every fourth frame shown). The image on the left shows the shrimp motionless on the substratum (viewed from directly above). The second and third images show the shrimp rolling onto its right side during the initial tail-flip of a laterally directed escape response. Numbers indicate time elapsed (in ms) since the first frame.

swimming directly towards the shrimp or as the fish lunged forwards in an attempt to capture it. Escaping shrimps did not alter their trajectories as they approached the side wall of the arena, sometimes colliding with it.

Shrimps responding to the artificial stimulus (approximate range of mean approach velocities $1.0\text{--}2.5\text{ m s}^{-1}$) displayed similar escape patterns to those responding to the cod stimulus. However, shrimps that were blinded only rarely responded ($<5\%$ of attacks, trajectories not analysed) unless the stimulus rod made direct contact with the shrimp or the base plate of the experimental arena.

Pre-escape events

Reaction distances (cod and artificial stimulus)

Direct physical contact between the stimulus source and the shrimp's body did not occur in any of the escapes analysed (although it was not possible to determine whether contact with the antennae occurred). Reaction distances ranged from 0.1 to 4.1 cm with the cod stimulus and from 1.4 to 15.0 cm with the artificial stimulus and did not differ significantly with shrimp length or, in the cod experiments, with different predator:prey length ratio combinations ($P>0.25$ for all regressions). With cod, mean reaction distances (\pm S.D.) were 1.1 ± 0.5 cm ($N=20$) and 1.4 ± 0.3 cm ($N=10$) for anterior and posterior attacks respectively. With the artificial stimulus, mean reaction distances were 5.6 ± 0.5 cm, 4.7 ± 0.5 cm, 6.4 ± 0.3 cm, 6.5 ± 0.3 cm and 5.1 ± 0.3 cm for attack categories progressing from 0° to 180° (see Materials and methods). Reaction distances in response to the cod were significantly shorter than those in response to the artificial stimulus (nested ANOVA, $F_{1,5}=140.2$, $P<0.0001$), but for escapes grouped within each stimulus type, there was no significant difference between the various attack angle categories ($F_{5,99}=1.82$, $P>0.05$).

Initial escape events

Contralateral versus ipsilateral escapes (cod stimulus)

Of the 20 escapes in response to cod attacking from the

shrimp's anterior quadrant, 11 (55%) were directed to the contralateral side of the stimulus whilst the remaining nine (45%) occurred to the ipsilateral side (Fig. 4A). This general pattern did not differ significantly between small (0.12–0.21) shrimp:cod length ratio encounters and large (0.21–0.35) ones (binomial comparative trial χ^2 -test, $\chi^2_1=3.23$, $P=0.07$). Overall, shrimps escaped to the contra- and ipsilateral sides in a random, unpredictable manner (binomial test, $P=0.41$, $N=20$).

In attacks from the shrimp's posterior quadrant, all 10 shrimps escaped towards the contralateral side (Fig. 4B), and this was significantly different from a random distribution (binomial test, $P=0.001$, $N=10$).

Contralateral versus ipsilateral escapes (artificial stimulus)

Attacks from both 0° and 180° (Fig. 5A,E) resulted in escapes that were randomly distributed between the shrimps'

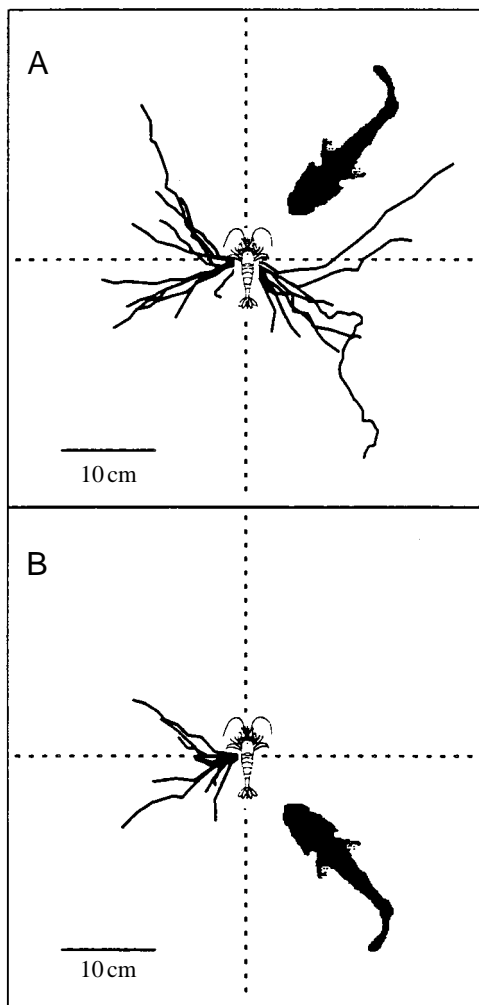


Fig. 4. Superimposed escape trajectories of *Crangon crangon* in response to a cod approaching from (A) the shrimp's (normalised) right anterior quadrant and (B) the shrimp's (normalised) right posterior quadrant. Graphic overlays (not to scale) indicate the shrimp's pre-escape position and the attack quadrant from which the cod approached.

contralateral and ipsilateral sides (binomial tests; 50% contralateral, $P=0.61$, $N=12$ for 0° attacks; 62% contralateral, $P=0.50$, $N=13$ for 180° attacks).

Attacks from 45° resulted in 13 escapes (76%) that were directed towards the shrimps' contralateral side and four (24%) towards the ipsilateral side (Fig. 5B). This is significantly different from a random distribution ($P=0.02$, $N=17$), indicating a contralateral bias in the escapes.

When attacked from 90° and 135° (Fig. 5C,D), shrimps showed an even stronger preference for escaping to their contralateral side, producing no ipsilateral escapes at all ($P<0.0001$ in both cases, $N=16$ and $N=17$, respectively). Therefore, the 'discrimination zone' in response to the artificial stimulus spanned attack angles of 45 – 135° .

In cases when a particular attack angle produced both contralateral and ipsilateral responses, the overall pattern of escapes was not affected by the fact that more than one response was recorded for some of the individual shrimps (data from first escape data only versus later escapes: 0° and 180° data, $\chi^2_1=0.019$, $P>0.75$; 45° data, $\chi^2_1=1.022$, $P>0.25$).

Prior-stimulus effects (artificial stimulus)

In 18 out of 20 instances in which an asymmetrical prior stimulus was applied before a shrimp was attacked from 0° , escapes were directed towards the contralateral side of the prior stimulus (i.e. the side to which the shrimp leaned). In contrast to 0° attacks with no prior stimulus, these responses deviated significantly from a random distribution (binomial test, $P=0.0002$).

Initial ϵ_{body} angles (cod and artificial stimulus)

Absolute values of initial ϵ_{body} angles ranged between $|75^\circ|$ and $|156^\circ|$. For separate attack categories within the cod and artificial stimulus groups, initial ϵ_{body} angles were non-randomly distributed (Rayleigh's test of uniformity; $P\leq 0.001$ or $P\leq 0.01$ in all instances, contralateral and ipsilateral escapes treated separately).

Results from circular statistical analysis of the initial ϵ_{body} angles are summarised in Table 1. If escapes towards the contralateral or ipsilateral side are considered separately, the values indicate that a large change in the attack angle results in a comparatively small, although significant, change in the initial ϵ_{body} angle. In contralateral responses to the artificial stimulus, mean directions of the initial ϵ_{body} angles decreased from -130° to -97° as the attack angle increased from 0° to 180° (Watson-Williams test between all five categories, $F_{4,56}=12.9$, $P<0.0005$). Significant differences also occurred among the ipsilateral escapes; the mean angles changed from $+124^\circ$ to $+144^\circ$ as the attack angle increased from the front (0°) to the side (45°) of the shrimp, and then reverted to $+99^\circ$ when ipsilateral escapes reappeared in response to rear (180°) attacks ($F_{2,12}=17.1$, $P<0.0005$). An exception occurred with contralateral escapes from cod since the mean initial ϵ_{body} angles did not differ significantly between anterior (mean -106°) and posterior (-98°) attacks (Watson-Williams test, $F_{1,19}=1.41$, $P>0.20$). This is

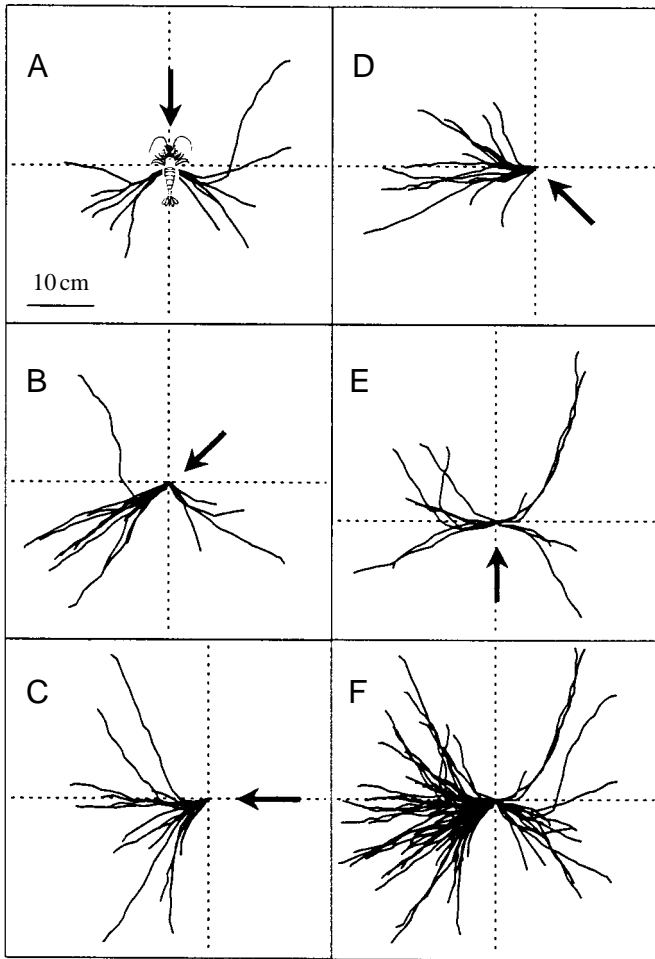


Fig. 5. Superimposed escape trajectories of *Crangon crangon* in response to artificial stimuli approaching from (A) 0°, (B) 45°, (C) 90°, (D) 135°, (E) 180° and (F) all data combined. The pre-escape position and orientation of *C. crangon* are shown in A and apply to all plots. Trajectories are plotted as if attacks (arrows) were from the shrimp's right side. The scale is the same throughout (shrimp outline is not to scale).

probably a result of the broader categorisation of the cod attack angles.

A small degree of modification was also evident when comparing the symmetry of contralateral *versus* ipsilateral initial ϵ_{body} angles. Attacks that were parallel with the shrimps' longitudinal axis produced symmetrical initial ϵ_{body} angle distributions, whereas those offset from it produced asymmetrical distributions. Mean angles were +124° and -130° for 0° attacks (moduli not significantly different; Watson-Williams test, $F_{1,10}=1.1$, $P>0.25$), and +99° and -97° for 180° attacks ($F_{1,11}=0.1$, $P>0.50$). However, attacks from 45° resulted in ipsilateral escapes with a mean angle of +144° and contralateral escapes with a mean angle of -127° ($F_{1,15}=15.2$, $P<0.005$). For cod attacking from the shrimps' anterior quadrant, mean angles for the ipsilateral and contralateral escapes were +126° and -106° respectively ($F_{1,18}=10.2$, $P<0.005$).

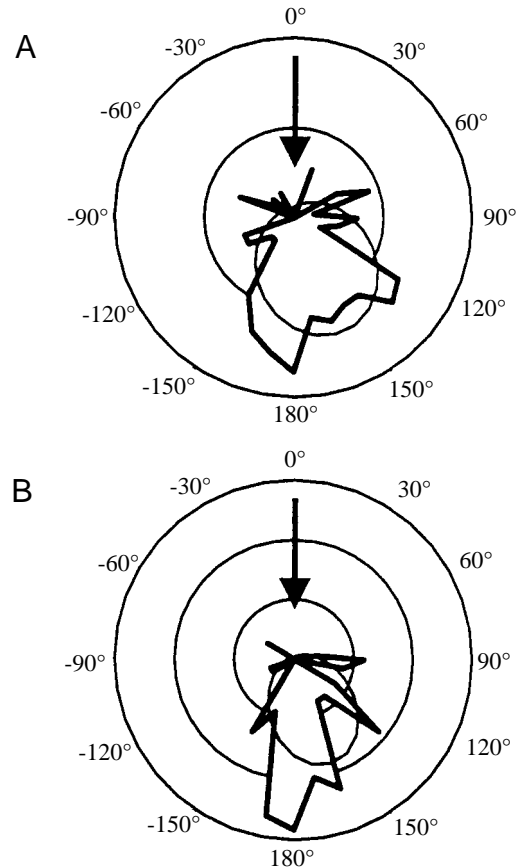


Fig. 6. Circular frequency distributions of final ϵ_{attack} angles (final escape angle relative to attack angle) (arranged into class lengths of 10°) in response to the artificial stimulus. Distributions are displayed as if all attacks were from the shrimp's right side, and equal weighting has been applied to each attack category when pooling the data (to allow for different numbers of observations). (A) Distribution of all pooled data ($N=76$). (B) Distribution of pooled data from contralateral responses to 45°, 90° and 135° attacks ($N=47$). Arrows indicate the direction of attack. Grid circles represent 5%. The fitted elliptical curves are derived from unimodal von Mises functions and do not differ significantly from the observed distributions.

Initial ϵ_{attack} angles (artificial stimulus)

No initial tail-flips occurred directly towards the stimulus, and the initial ϵ_{attack} angle with the lowest absolute value was |63°| (in an ipsilateral escape from a 45° attack). Initial-away responses (i.e. those with an initial ϵ_{attack} angle greater than |90°|) occurred in 83% of the escapes (significantly different from random, binomial test, $P<0.0001$, $N=76$). Initial-toward responses (initial ϵ_{attack} angle less than |90°|) that did occur were mainly in response to 180° attacks (nine of 13 instances). The overall distribution of initial ϵ_{attack} angles did not differ significantly between shrimps of different lengths (χ^2 -test, $\chi^2_4=4.85$, $P=0.303$).

Circular statistical parameters of the initial ϵ_{attack} angles are shown in Table 1. Pooling of all data produced a non-random distribution (Rayleigh's test, $P<0.001$; mean angle +147±55°, mean ± S.D.) reflecting the predominance of initial-away

Table 1. Circular statistical analysis of initial and final escape angles (as if all stimuli were from the shrimps' right)

Stimulus	Attack direction	Side	<i>N</i>	Initial ϵ_{body} (degrees)	Initial ϵ_{attack} (degrees)	Final ϵ_{attack} (degrees)
Cod	Anterior quadrant	Ipsi	9	+126±14	ND	ND
	Anterior quadrant	Contra	11	-106±13	ND	ND
	Posterior quadrant	Contra	10	-98±11	ND	ND
Artificial	0°	Ipsi	6	+124±9	+121±10	Random
	45°	Ipsi	4	+144±9	+96±10	Random
	180°	Ipsi	5	+99±12	-79±14	Random
	0°	Contra	6	-130±8	-130±7	Random
	45°	Contra	13	-127±6	+175±7	-172±31
	90°	Contra	16	-117±14	+153±14	+163±46
	135°	Contra	18	-102±16	+119±16	+143±35
	180°	Contra	8	-97±13	+84±11	Random
	0–180 (pooled)	All	76	ND	+147±55	+161±55
	45–135 (pooled)	Contra	47	ND	ND	+164±40

Angles are circular means \pm s.d.

Contra, contralateral escapes; Ipsi, ipsilateral escapes; *N*, sample size; ND, values not determined; Random, circular distributions in which $P > 0.05$ for Rayleigh's test of uniformity.

responses. Treated separately, initial ϵ_{attack} angles for ipsi- and contralateral escapes of each attack category were also non-randomly distributed ($P < 0.009$ in all cases), but shrimps did not maintain a constant ϵ_{attack} angle (i.e. it changed significantly as attack angle changed). As the attack angle increased from 0° to 180°, the mean directions of the initial ϵ_{attack} angles for contralateral escapes rotated from -130° to +84° (Table 1). Mean angles for ipsilateral responses also rotated, moving through +121°, +96° and -79° as the attack angle changed from 0° to 45° and 180° respectively. The values for both contralateral and ipsilateral escapes were highly heterogeneous in response to different attack angles

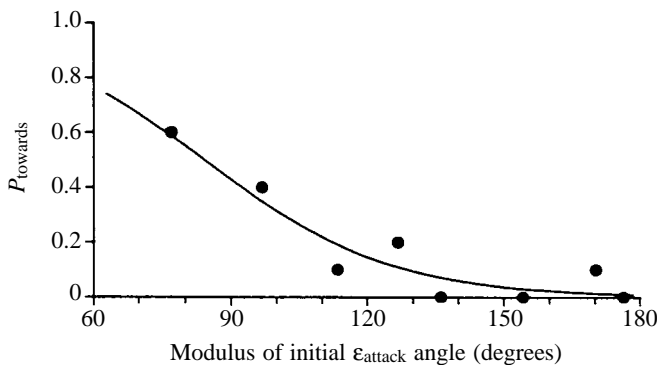


Fig. 7. Graph showing the relationship between the probability of a final-toward response occurring (P_{towards}) and the initial ϵ_{attack} angle (initial escape angle relative to attack angle) of an escape by *Crangon crangon*. The data points show probabilities derived from sequential groups of 10 observations ($N=6$ for the last point) arranged in order of ascending initial ϵ_{attack} angle. The fitted line is derived from a logistic regression with the form: $P_{\text{towards}} = e^z / (1 + e^z)$, where $z = 4.143 - 0.0492|\text{initial } \epsilon_{\text{attack}} \text{ angle}|$. The model explains 85.5% of the observed variation in P_{towards} .

(Watson–Williams test, $F_{4,56}=506$, $P < 0.0001$ and $F_{2,13}=242.8$, $P < 0.0001$ respectively).

Final escape angles

Final ϵ_{attack} angles (artificial stimulus)

There was no significant difference between the final ϵ_{attack} angle data derived from the first escape, the second escape and subsequent escapes performed by individual shrimps ($\chi^2_4=3.06$, $P > 0.50$). Pooled data for all the final ϵ_{attack} angles were non-randomly distributed (Rayleigh test of uniformity, $P < 0.001$), with a modal value at $\pm 180^\circ$ and a smaller peak occurring at $+130^\circ$. This apparent bimodal distribution did not differ significantly from a unimodal von Mises function fitted to the data (goodness-of-fit test, $\chi^2=2.81$, d.f.=3, $P > 0.25$; Fig. 6A), with the mean final ϵ_{attack} angle occurring at $+161 \pm 55^\circ$ (mean \pm s.d.).

Contralateral escapes in responses to 45°, 90° and 135° attacks (i.e. within the discrimination zone) differed in their final ϵ_{attack} angles (Watson–Williams test, $F_{2,44}=5.20$, $P < 0.01$), with mean values of -172°, +163° and +143° respectively (Table 1). When pooled, the predominance of final-away responses produced a non-random distribution (Rayleigh test of uniformity, $P < 0.001$; $164 \pm 40^\circ$, mean \pm s.d.) with major and minor peaks at $\pm 180^\circ$ and $+130^\circ$ respectively (Fig. 6B), although the distribution did not differ significantly from a unimodal von Mises function fitted to the data (goodness-of-fit test, $\chi^2=3.8$, d.f.=2, $P > 0.1$).

The majority (81%) of all escapes were final-away responses (i.e. final ϵ_{attack} angle greater than $|90^\circ|$), representing a significant preference (binomial test, $P < 0.001$, $N=76$). This pattern was consistent between shrimps of different lengths (χ^2 -test, $\chi^2_2=2.02$, $P=0.365$), but the likelihood of a final-toward response occurring increased as the initial ϵ_{attack} angle of an escape decreased (χ^2 -test on logistic regression fit, $\chi^2=19.4$, d.f.=1, $P < 0.0001$; Fig. 7).

Consequently, if the shrimp 'side-stepped' an attack during its first tail-flip, it was more likely then to steer behind the attacker than if the initial tail-flip was directed away along the line of the attack. Furthermore, since the initial ϵ_{attack} angle was mainly governed by the attack direction (see previous section), final-away responses were more common in response to attacks from 0° and 180° than in response to attacks from 45° , 90° and 135° . Among the 45° attacks, this trend was also evident since three of the four final-toward responses observed were produced by ipsilateral escapes in which the initial ϵ_{attack} angles were lower than for the contralateral escapes.

Discussion

The experiments performed here have revealed several novel features of *Crangon crangon* escape swimming that represent variations on the escape behaviour described for other decapods such as lobsters and crayfish (see Neil and Ansell, 1995). These adaptations of the *C. crangon* tail-flip can be related to its habitat and lifestyle, and impart a manoeuvrability that contributes to effective escape of these shrimps from predator pursuits (e.g. capture success per strike by juvenile cod is size-dependent and varies between 10 and 50%; Arnott, 1996). We have identified separate pre-escape, initial escape and final escape events, have described their distinct characteristics and suggest below that some of these can be related to a combination of anatomical and behavioural constraints acting upon the shrimp. Unpredictable elements of the escape response have been shown to be a prominent feature of *C. crangon* escape swimming and are probably important in preventing predators from learning a fixed pattern of response.

Pre-escape events

In experiments with both natural and artificial stimuli, *Crangon crangon* produced tail-flip escapes with trajectories that varied according to the angle of attack. To achieve this, shrimps must process sensory information about the attacker's position and integrate this with the motor control of their tail-flip swimming behaviour.

The stimuli presented to shrimps in these experiments consisted of a combination of mechanical (water-borne vibration) and visual cues. With cod stimuli, chemical cues may also have been detected by the shrimps and, although these may potentially heighten a shrimp's awareness, it is unlikely that these were used in rapid orientation responses (Atema, 1988; Breithaupt et al., 1995).

Crangon crangon are able to detect vibrational signals using direction-sensitive mechanosensory hairs distributed over their body surface (Heinisch and Wiese, 1987). In the absence of visual stimuli, water-borne mechanosensory cues from the artificial stimulus were usually insufficient to generate tail-flip responses. The importance of visual cues in initiating escapes (when no direct physical contact occurs) has also been shown by Berghahn et al. (1995) for *C. crangon* and by Wiese (1976) for the crayfish *Procambarus clarkii*.

The neuronal pathways mediating the escapes in the present study were not investigated. High-speed video observations using artificial stimuli reveal that tail-flip responses by *Crangon crangon* typically have short latencies, of the order of 5–10 ms (Arnott et al., 1998). This suggests the probable involvement of giant fibres in generating the responses, but no direct confirmation of this has been made.

Mean reaction distances of *Crangon crangon* were 1.1–1.4 cm with the cod stimulus and 4.7–6.5 cm with the faster-moving artificial stimulus (equivalent to less than 100 ms before contact). The values for the cod attacks are similar to the mean reaction distance of 1.5 cm reported for *Crangon alaskensis* escaping from fish predators (Nemeth, 1998b). Webb and Skadsen (1980) found that, during the last 80 ms of a strike, tiger muskies (*Esox* sp.) were unable to alter their attack direction. Therefore, delaying an escape until the last moment has the advantage of committing a predator to a strike and prevents it from compensating its attack direction in response to the escape.

The reaction distances in response to the artificial stimulus were significantly greater than in response to attacks from the cod. This was probably because acceleration of the artificial stimulus started at a distance of approximately 20 cm from the shrimp and achieved greater velocities. In contrast, the cod usually approached the shrimp slowly, and when a feeding strike occurred, it was initiated from a range of within a few centimetres. Similarly, one might expect small (i.e. slower) shrimps to react earlier than large shrimps, but no size-dependent effect was found, perhaps because of the imprecise and variable nature of the stimuli used in the experiments.

The results from this study are probably most representative of an *in situ* situation when shrimps are active on the sediment surface. When inactive and buried within the sediment, reaction distances may well be shorter than those reported here. Theoretical and empirical studies show that, in many animals, reaction distances decrease when crypsis and concealment are used to avoid detection (e.g. Heatwole, 1968; Ydenberg and Dill, 1986; Ellis et al., 1997).

Initial escape events (first tail-flip)

Initial escape constraints

Arnott et al. (1998) found that *Crangon crangon* occasionally direct the first tail-flip of an escape vertically, but this behaviour was not observed in the present study (it may be more appropriate when the shrimp is buried rather than on top of the substratum). Here, the first tail-flip of an escape was always laterally directed (with respect to the shrimp's body axis) and had an absolute initial ϵ_{body} angle of between $|75^\circ|$ and $|156^\circ|$. This creates a pair of lateral 'escape envelopes' (sectors each spanning 81° to the left and right of a shrimp) into which the first tail-flip of a response by *C. crangon* may be directed. Separating the envelopes are an anterior sector (initial ϵ_{body} angles $<|75^\circ|$) and a posterior sector (initial ϵ_{body} angles $>|156^\circ|$) into which the shrimp never escaped (Fig. 8A, stippled sectors). The boundaries between these regions are probably governed by anatomical constraints acting upon the

shrimp. In particular, the relative length of the shrimp's abdomen places a constraint on the proportion of forces that rotate the shrimp rostrally during body flexion (Daniel and Meyhöfer, 1989), thereby limiting the initial ϵ_{body} angle that can be achieved. The lack of escapes directly backwards into the posterior sector (initial ϵ_{body} angles $>156^\circ$) differs markedly from the escape trajectories observed in many other decapod crustaceans (e.g. Wine and Krasne, 1972; Newland and Neil, 1990). One reason for this is that flexion during tail-flips by *C. crangon* is confined to the anterior region of the abdomen, regardless of the attack direction (Arnott et al., 1998). This produces a 'jack-knife' tail-flip, whereas backward escapes require a progressive wave of flexion that propagates anteriorly from the telson towards the cephalothorax (Newland and Neil, 1990; Neil and Ansell, 1995).

When the first tail-flip of a response is considered with respect to the attack direction, a wide spread of trajectories occurred, but initial ϵ_{attack} angles never had an absolute value of less than $|63^\circ|$. This defines an 'exclusion envelope', a sector spanning 126° (63° either side of the attack direction) into which the shrimp never escaped, regardless of the attack angle (Fig. 8A, black sector). A significant feature of the exclusion envelope is that it is independent of the initial orientation of the shrimp and can, in fact, include escape directions that are available to it (i.e. ones within the escape envelopes). Therefore, the exclusion envelope does not represent an anatomical constraint, but instead reflects a behavioural 'choice' by the animal not to escape in certain directions relative to the stimulus. The restriction applies only to the first tail-flip of an escape since subsequent tail-flips may then steer the shrimp behind the attacker (see below).

If an initial tail-flip occurs directly towards an attacker, there is a high probability that the shrimp will be caught. However, as the initial ϵ_{attack} angle increases, the risk of this diminishes depending upon the relative velocity of the predator and prey (Howland, 1974; Webb, 1976), the size of the predator's mouth, the magnitude and range of the negative pressure created during the predator's feeding strike (Alexander, 1970; Hart and Hamrin, 1990; Norton, 1991, 1995; Nemeth, 1998a,b) and the responsiveness of the predator to the shrimp's movements (Webb, 1984). Therefore, the boundaries of the exclusion envelope may change in response to the type of stimulus encountered.

Interaction between the escape and exclusion envelopes

The two analyses of the initial escapes described above yield measures of the escape directions relative to the animal's body axis and relative to the attack direction. In this sense, they can be regarded as simultaneously acting 'rules' that apply to a given attack situation and dictate its outcome. The escape and exclusion envelopes are graphic representations of these rules that encompass all the measured experimental data (Fig. 8A). The interaction of these rules can be depicted as an overlay of the two envelopes, with the former being fixed and the latter rotating (Fig. 8B–F). At different angles of attack, the exclusion envelope either partly (Fig. 8C,F) or completely

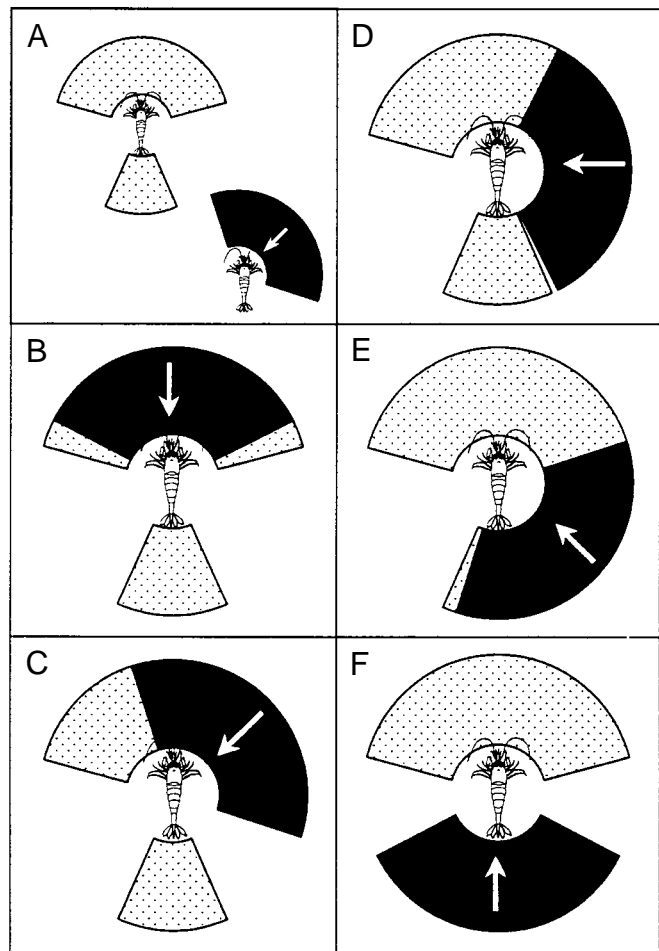


Fig. 8. Interactions between the escape and exclusion envelopes of *Crangon crangon* during its first tail-flip in response to the artificial stimulus. (A) The stippled sectors in A represent the range of initial ϵ_{body} angles (initial escape angle relative to the shrimp's longitudinal axis) that were never used by any of the shrimps. These leave two escape envelopes (unfilled sectors) to the shrimp's left and right side spanning $|75\text{--}156^\circ|$, into which the first tail-flip of an escape may be directed. The lower diagram in A shows the exclusion envelope (black sector) spanning 63° to either side of the approaching stimulus (white arrow). Shrimps never escaped into this region during the first tail-flip of an escape, regardless of the attack direction. The interactions of the escape and exclusion envelopes are shown with respect to one another in response to attacks from (B) 0° , (C) 45° , (D) 90° , (E) 135° and (F) 180° . The inset of the shrimp indicates its pre-escape position and orientation throughout.

(Fig. 8D,E) eclipses certain areas of the shrimp's escape envelope(s) and so prevents the overlapping initial ϵ_{body} angles from being used. As a consequence of this, a greater proportion of the contralateral escape envelope is available than of the ipsilateral envelope when attacked from 45° and 90° ; when attacked from 135° , the shrimp only has the option of escaping towards the contralateral side. When attacked from 0° (Fig. 8B) and 180° (Fig. 8F), the left and right escape envelopes are equally available, although in the latter case, both escape envelopes are partially eclipsed posteriorly by the

exclusion envelope. This indicates that the degree to which a predator may predict a shrimp's initial escape direction will depend upon its angle of attack.

Theoretical consideration of the escape and exclusions envelopes

A model has been devised to explore the theoretical basis of these initial escape 'rules' whereby the escape and exclusion envelopes interact with one another to determine the direction of the shrimp's initial roll. The model describes the initial movements of a shrimp escaping from an attack by a 'ram-feeding' predator (Norton, 1991, 1995). (The same general principles can be applied to 'suction' feeders, although the solutions are more complex because they require the addition of fluid dynamic calculations.)

In the model, at time $t=0$, when the shrimp initiates its escape, the midpoint of the leading edge of the predator's mouth is located in Cartesian coordinates at point $(0, 0)$ and the shrimp's centre of mass is located at point $(D, 0)$, where D represents the reaction distance. This starting position is equivalent to that described in an escape trajectory model of Howland (1974); however, in that model, the paths of the predator and prey were considered to move along arcs with defined radii, whereas in the present situation the predator and prey are considered to move along straight lines of attack and escape during the initial stages of the escape. This scenario is more appropriate here, since fish are unable to modify their attack direction during the final strike phase of an attack (e.g. Webb and Skadsen, 1980), and individual tail-flips in *Crangon crangon* follow approximately linear trajectories (turns mainly occurring between one tail-flip and the next; Arnott et al., 1998). In the model, the predator attacks the shrimp along the line of the x -axis, whilst the shrimp escapes along a straight line at any angle (θ) between 0° and 180° above the x -axis, where θ represents the initial ϵ_{attack} angle (Fig. 9A). Then, at

time t , the coordinates $(X_{p,t}, Y_{p,t})$ describing the position of the predator with respect to its starting position are:

$$X_{p,t} = tV_p, \quad (1)$$

$$Y_{p,t} = 0, \quad (2)$$

where V_p is the mean attack velocity of the predator (for simplicity, time-dependent variability in attack and escape velocities are not considered here). Similarly, the coordinates $(X_{s,t}, Y_{s,t})$ describing the position of the shrimp at time t with respect to its starting position are given by:

$$X_{s,t} = D - tV_s \cos \theta, \quad (3)$$

$$Y_{s,t} = tV_s \sin \theta, \quad (4)$$

where D is the reaction distance, θ is the initial ϵ_{attack} angle of the shrimp and V_s is the shrimp's mean escape velocity. From this, it is also possible to calculate $(X_{\text{rel},t}, Y_{\text{rel},t})$, which represents the relative position of the shrimp with respect to the predator at time t , where:

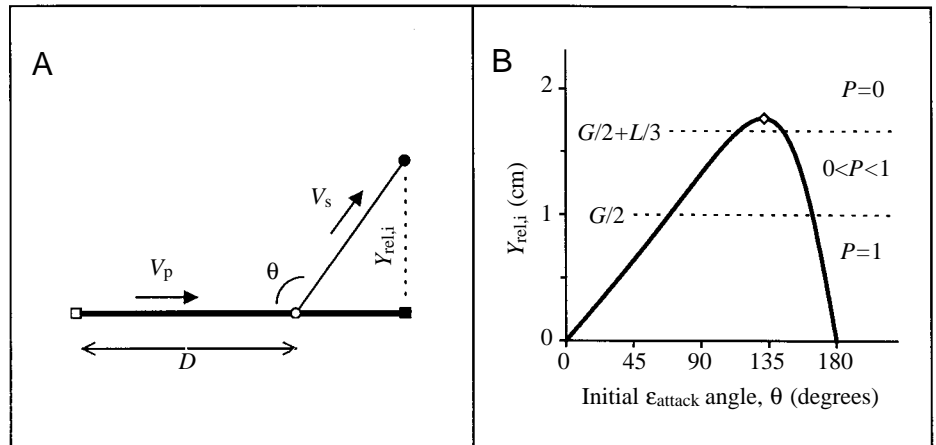
$$X_{\text{rel},t} = X_{s,t} - X_{p,t}, \quad (5)$$

$$Y_{\text{rel},t} = Y_{s,t} - Y_{p,t} = Y_{s,t}. \quad (6)$$

Two criteria can be used to determine whether the shrimp will escape during an actual strike. First, if the x component of the shrimp's velocity is greater than that of the predator's (i.e. if $-V_s \cos \theta > V_p$), the predator will never overtake the shrimp along the x -axis and the shrimp will escape. If this is not true, the second criterion depends upon the shrimp's position at the interaction time $t=i$, when the predator just starts to overtake it along the x -axis. When this occurs, the shrimp will escape only if it lies outside the predator's gape (i.e. if $Y_{\text{rel},i} > 0.5G$, where G represents the mouth gape), otherwise it will be caught. To resolve this, the fact that $X_{\text{rel},i} = 0$ at the time of interaction enables us to rearrange equation 5 such that:

$$i = D / (V_s \cos \theta + V_p) \quad (7)$$

Fig. 9. (A) An example showing the movements of a predator (squares, thick line) and an escaping shrimp (circles, thin line) according to equations 1–4 of the model described in the text. At time $t=0$ (open symbols), when the shrimp initiates its escape, the midpoint of the predator's mouth is located in Cartesian coordinates at $(0, 0)$ and is moving at a velocity V_p along the x -axis from left to right. The shrimp's centre of mass starts from position $(D, 0)$ and moves at a velocity V_s above the x -axis along an initial ϵ_{attack} angle (initial escape angle relative to attack angle) of θ . At time $t=i$, when the predator just starts to overtake the shrimp along the x -axis (filled symbols),



the shrimp's centre of mass is located at a distance $Y_{\text{rel},i}$ above the x -axis. (B) An example showing the relationship between the initial ϵ_{attack} angle of an escaping shrimp (body length $L=20$ mm) and $Y_{\text{rel},i}$ at the time of interaction along the x -axis (derived from equation 8 using the following values: attack velocity $V_p=1$ m s $^{-1}$; escape velocity $V_s=0.7$ m s $^{-1}$, derived from equation 9; reaction distance $D=2$ cm; predator's gape $G=2$ cm). The different regions of capture probability, P , depend on whether the shrimp's centre of mass or trailing body parts lie outside the predator's gape. The peak in the curve (diamond) occurs at the 'optimal' initial ϵ_{attack} angle (equation 10).

and this allows equation 7 to be substituted into equation 6 to give:

$$Y_{rel,i} = D \cdot V_s \cdot \sin\theta / (V_s \cos\theta + V_p). \quad (8)$$

Under a given set of circumstances, equation 8 gives the distance of the shrimp's centre of mass above the y -axis as the predator overtakes it along the x -axis, and thus reveals whether the shrimp lies within or outside the predator's gape. Webb and Skadsen (1980) showed that predatory fish tend to aim their attack towards a prey's centre of mass, and so if $Y_{rel,i} < 0.5G$, then the shrimp is assumed to be caught with a probability $P=1$. An additional consideration is that the shrimp may be captured by another part of its body trailing behind its centre of mass. The length of the trailing body parts fluctuates as the shrimp performs tail-flip swimming movements, causing the risk of capture to fluctuate, but the maximum trailing edge occurs when the body is in a fully flexed position. Measurements from high-speed video images in Arnott et al. (1998) indicate that this distance is approximately one-third of the shrimp's body length (L). Therefore, if the shrimp's centre of mass is outside the predators gape on the y -axis, but $Y_{rel,i} < (0.5G + L/3)$, then the shrimp will be caught with a probability $0 < P < 1$.

As may be expected, equation 8 indicates that the outcome of an encounter will depend upon the predator's attack velocity and on the shrimp's body length, escape velocity, reaction distance and initial ϵ_{attack} angle. Furthermore, mean escape velocity (V_s in m s^{-1}) of *Crangon crangon* is size-dependent and is estimated (at 13°C) using the relationship:

$$V_s = 0.0415L - 0.0004L^2 - 0.008 \quad (9)$$

when L is expressed in millimetres (taken from Table 1 of Arnott et al., 1998).

The initial ϵ_{attack} angle that maximises $Y_{rel,i}$ represents an 'optimal' angle because it results in the biggest potential miss by the predator during an actual strike. This optimum angle can be resolved when the differential of equation 8 equals zero which, in its simplest form, reduces to:

$$\cos\theta = -V_s/V_p. \quad (10)$$

From equation 8, it is possible to determine, for a specific set of circumstances, the range of initial ϵ_{attack} angles that enables a shrimp to evade capture. Angles that do not allow the shrimp to escape define a situation-specific exclusion envelope that will result in capture. These calculations have been performed for shrimps ranging between 10 and 65 mm in length under the following situations: case 1, $V_p=1.2 \text{ m s}^{-1}$, $D=2 \text{ cm}$; case 2, $V_p=1.0 \text{ m s}^{-1}$, $D=2 \text{ cm}$; case 3, $V_p=1.2 \text{ m s}^{-1}$, $D=4 \text{ cm}$.

In all three cases, the predator's gape, G , has been set at 2 cm. Fig. 9B shows an example of the output from equation 8 for a 20 mm shrimp in case 2. In this situation, the shrimp is able to escape with a certainty $P=0$ only when the shrimp's initial ϵ_{attack} angle lies between 116° and 144° (from equation 10, the optimum angle is found to be 131°). Between the ranges $70\text{--}116^\circ$ and $144\text{--}164^\circ$, $0 < P < 1$, and when $\theta < 70^\circ$ or $\theta > 164^\circ$, $P=1$.

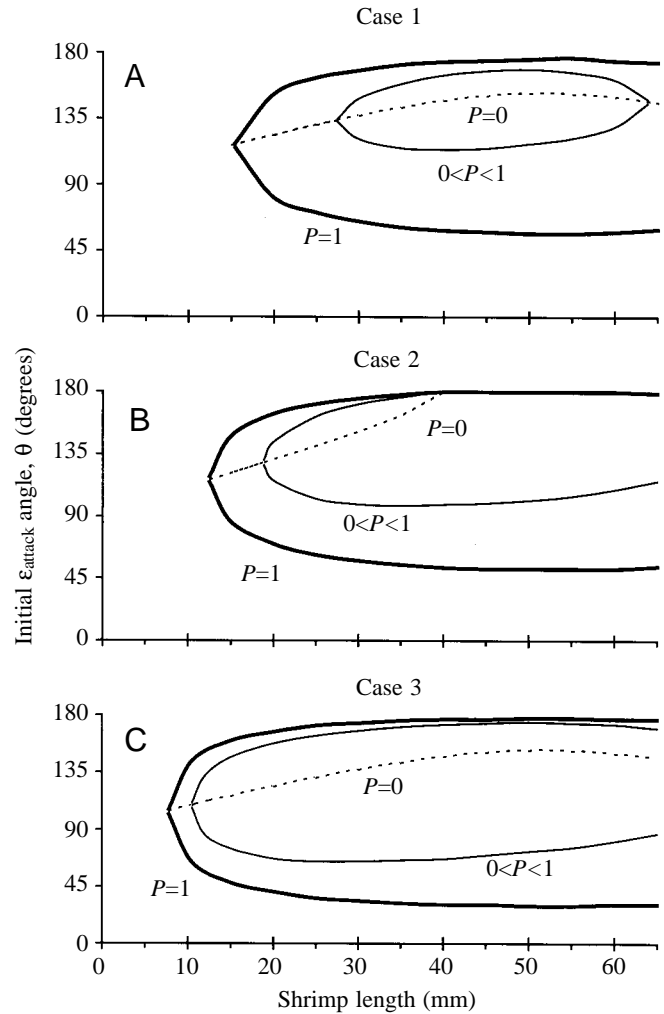


Fig. 10. An example of modelled data showing theoretical relationships between shrimp length, initial ϵ_{attack} angle (initial escape angle relative to attack angle) and the boundaries (solid lines) separating regions of different capture probability, P . The dashed line represents the optimal initial ϵ_{attack} angle (equation 10), for a given length of shrimp, that maximises $Y_{rel,i}$ (the distance of the shrimp's centre of mass above the x -axis at time $t=i$). The gape of the predator has been set at 2 cm in all cases, whilst the attack velocity (V_p) and reaction distance (D) have been varied as follows: (A) case 1, $V_p=1.2 \text{ m s}^{-1}$, $D=2 \text{ cm}$; (B) case 2, $V_p=1.0 \text{ m s}^{-1}$, $D=2 \text{ cm}$; (C) case 3, $V_p=1.2 \text{ m s}^{-1}$, $D=4 \text{ cm}$.

The boundaries between the different regions of capture probability for shrimps of 10–65 mm in cases 1, 2 and 3 are shown in Fig. 10. The results demonstrate that, in many situations, not only is there a lower limit to the shrimp's initial ϵ_{attack} angle that allows it to escape, but also that there is an upper limit. Thus, if the shrimp escapes at too shallow an angle, either towards or away from the predator, it will be captured (although in the latter situation, if the shrimp is fast enough, it may have sufficient time to finish its first tail-flip and then change direction before an encounter occurs). Second, as shrimps increase in length, their escape velocity increases (except in the very largest shrimps), and this broadens the

range of initial ϵ_{attack} angles that result in a successful escape. However, whilst absolute escape velocity generally increases, escape velocity in terms of body lengths per second actually decreases with shrimp length (Arnott et al., 1998). This causes the range of successful escape angles (i.e. those that give $P=0$) to decline again in larger shrimps as a result of an increasing chance of being caught by a body part trailing behind their centre of mass.

The effects of altering the attack velocity or reaction distance can be seen by comparing the curves in Fig. 10. As expected, decreasing the attack velocity (case 2; Fig. 10B) or increasing the reaction distance (case 3; Fig. 10C) allows shrimps of a smaller size to escape and increases the range of initial ϵ_{attack} angles that can be used for a given size of shrimp. Low attack velocities also result in large optimal initial ϵ_{attack} angles, whilst increasingly faster attacks result in smaller optimal initial ϵ_{attack} angles (although the optimum will always be greater than 90° since, in equation 10, $\cos\theta$ tends towards zero as V_p increases).

During an escape, the principal concern of the shrimp is that its initial ϵ_{attack} angle does not fall within the exclusion envelope (especially the region where $P=1$). The experimental data suggest that *C. crangon* adhere to this general rule, but also indicate that shrimps fail to select the theoretical 'optimum' initial ϵ_{attack} angle within this range. Were shrimps

to do so, initial ϵ_{attack} angles would remain unaltered as the attack direction changed, and yet the results in Table 1 indicate that this is not the case. One reason for this might be that (apparently) non-optimal escape angles that lie within the safe zone ($P=0$) offer better manoeuvring options to the shrimp once the first tail-flip of an escape has been completed. Alternatively, shrimps may escape along non-optimal escape angles simply because they lack the ability to detect and process the sensory information available to them with sufficient accuracy within such a short period. Therefore, as the conditions become more restrictive (i.e. faster attacks or shorter reaction distances), an error is more likely to occur as the safe zone ($P=0$) narrows.

In Fig. 10, the regions lying outside $P=0$ represent the exclusion envelope, as defined in the previous section. By considering the interaction of the calculated exclusion envelopes with the shrimp's escape envelopes, it is possible to determine, under a specific set of circumstances, whether a shrimp will be capable of escaping to its ipsilateral or contralateral side without being caught (i.e. whether it falls within the region $P=0$). The escape envelopes represent morphological limits of the shrimp and were defined above as lying between 75° and 156° to the shrimp's left or right (irrespective of the attack angle). In reality, it is possible that these values may differ between shrimps of different sizes (see

Table 2. Analysis of initial escape directions (ipsilateral or contralateral) that enable 15–65 mm shrimps to escape from a strike (i.e. capture probability $P=0$) when they are attacked from different angles by a predator (gape 2 cm) under varying conditions (cases 1–3 in the model described in the text)

L (mm)	Case 1 ($V_p=1.2\text{ m s}^{-1}$; $D=2\text{ cm}$) Attack angle (degrees)					Case 2 ($V_p=1.0\text{ m s}^{-1}$; $D=2\text{ cm}$) Attack angle (degrees)					Case 3 ($V_p=1.2\text{ m s}^{-1}$; $D=4\text{ cm}$) Attack angle (degrees)				
	0	45	90	135	180	0	45	90	135	180	0	45	90	135	180
15	X	X	X	X	X	X	X	X	X	X	I/C	I/C	C	C	I/C
20	X	X	X	X	X	I/C	C	C	C	X	I/C	I/C	C	C	I/C
25	X	X	X	X	X	I/C	I/C	C	C	I/C	I/C	I/C	I/C	C	I/C
30	I/C	C	C	C	X	I/C	I/C	C	C	I/C	I/C	I/C	I/C	C	I/C
35	I/C	C	C	C	X	I/C	I/C	C	C	I/C	I/C	I/C	I/C	C	I/C
40	I/C	C	C	C	X	I/C	I/C	C	C	I/C	I/C	I/C	C	C	I/C
45	I/C	C	C	C	X	I/C	I/C	C	C	I/C	I/C	I/C	C	C	I/C
50	I/C	C	C	C	X	I/C	I/C	C	C	I/C	I/C	I/C	C	C	I/C
55	I/C	C	C	C	X	I/C	I/C	C	C	I/C	I/C	I/C	C	C	I/C
60	I/C	C	C	C	X	I/C	I/C	C	C	X	I/C	I/C	C	C	I/C
65	X	X	X	X	X	I/C	C	C	C	X	I/C	I/C	C	C	I/C

I/C indicates that a shrimp has the option of escaping successfully to either its ipsilateral or contralateral side, whereas C indicates that it can only escape successfully to its contralateral side.

X represents situations when a shrimp is unable to escape successfully, regardless of its initial escape direction (i.e. it is too slow under the given conditions).

L, shrimp body length; V_p , attack velocity; D, reaction distance.

Daniel and Meyhöfer, 1989; Arnott et al., 1998), but here they are considered to be fixed. Table 2 shows, for cases 1–3, whether shrimps of different lengths are able to escape to their ipsilateral or contralateral side, whilst still escaping successfully ($P=0$). The analysis reveals that the choice of using an ipsilateral or contralateral escape is strongly dependent upon the conditions of the interaction. Under case 1, only shrimps of between 30 and 60 mm are able to escape successfully (regardless of their escape angle), and only when attacked from between 0° and 135° . Furthermore, shrimps are confined to contralateral escapes, except when they are attacked from 0° . The conditions of the escape can be modified if the shrimp reacts sooner to the approaching predator. This is represented by case 3, in which the reaction distance has increased from 2 to 4 cm, and enables shrimps of all lengths to escape successfully when attacked from all angles. In most cases, ipsilateral escapes can only occur when attacks are from 0° , 45° and 180° , a result that closely reflects the escape pattern observed in our laboratory investigation. Similarly, in case 2, where the reaction distance remains set at 2 cm but the attack velocity has been decreased from 1.2 to 1.0 m s^{-1} , the range of shrimp sizes that can escape successfully increases in comparison with case 1, and ipsilateral escapes are confined to 0° , 45° and 180° attacks.

Final escape events (subsequent tail-flips)

Escape strategies

When an animal has a specific point-source refuge that it uses to shelter from predators, escapes are normally directed towards the refuge when a threat occurs (e.g. Woodbury, 1986; Nalbach, 1990; Land and Layne, 1995; Kramer and Bonenfant, 1997). No specific point-source refuge was provided for shrimps in the experiments described here, which is representative of the natural open-substratum habitat of *Crangon crangon*. Shrimps use sediment as a refuge (they are cryptic against it and bury within it; Pinn and Ansell, 1993), and it is generally available to them in all horizontal directions. The potential effects of natural obstructions (e.g. boulders or the influence of land when very close to the shore) are not considered here.

Tail-flip responses by *Crangon crangon* were directed predominantly in the horizontal plane. The probable advantage of this strategy is that it keeps the shrimp close to the refuge provided by the substratum. It also avoids silhouetting the shrimp against the water surface, thereby minimising the attacker's (or other potential predators) ability to track it visually (Thetmeyer and Kils, 1995).

The final escape trajectories of all pooled data in response to the artificial stimulus were non-randomly distributed. The majority of escapes (81%) were final-away responses, as indicated by the mean final ϵ_{attack} angle of $+161^\circ$ and the mode of $\pm 180^\circ$. This strategy appears to be similar to the predictions arising from the theoretical evasion model devised by Weihs and Webb (1984) in which the prey attempts to maximise the distance between itself and a predator once a pursuit has begun. In doing so, the prey maximises the duration of the pursuit and

the energetic costs of capturing it, thereby increasing the likelihood that the predator will abort the chase. The main prediction of the model of Weihs and Webb (1984) is that the optimal escape trajectory will always lie at an angle greater than 159° away from the predator's concurrent position during a chase, irrespective of the relative escape and pursuit velocities. However, they also point out that their model does not apply during a 'final end-game' situation, when the predator is close enough to launch an actual strike. At this point, the predator and prey cannot be treated as point masses, response latencies are of the order of interaction times and morphological characteristics (such as mouth gape) become important (these points are addressed in the initial escape trajectory model described in the previous section). Once *C. crangon* escapes an initial strike, the predator will be located at the approximate starting position of the shrimp owing to the typically small reaction distances involved, and the predator will need to reorientate itself towards the shrimp before engaging in a chase. If the shrimp is escaping along a straight line by this time, it will in effect automatically be travelling directly away from the predator when the chase begins, regardless of the initial and final ϵ_{attack} angles of the escape (which refer only to the original direction of attack). Turning manoeuvres by the shrimp early on in the response may be beneficial if they result in the predator having to turn through a greater angle before it can chase, but the effectiveness of this decreases as the distance between the predator and the shrimp increases. Therefore, with *C. crangon*, a more appropriate interpretation of the evasion model of Weihs and Webb (1984) might be: after the initial phase of an escape, continue to travel along an approximately straight line unless the predator approaches too close (in which case, a 'final end-game' situation will again ensue). This appears to be the strategy that shrimps adopted in the laboratory experiments: although large manoeuvres sometimes occurred early on during an escape, thereafter trajectories were approximately linear.

In their natural habitat, *Crangon crangon* escape a relatively short distance when they are disturbed and then land back on the sediment, where they remain motionless (or bury). If a predator tracks the shrimp to its new position and strikes again, the shrimp will attempt another escape. As a result, several tail-flip swimming bouts may occur during an encounter until the predator aborts the chase, loses the shrimp or captures it (Tallmark and Evans, 1986; Arnott, 1996). With this strategy, maximising the shrimp-to-predator distance during a swimming bout makes it more difficult for the predator to observe precisely where the shrimp has landed and enhances the shrimp's crypsis against the sediment. Furthermore, if visibility is restricted (e.g. if the water is turbid), maximising the distance may remove the shrimp from the visual range of the predator altogether. These considerations are important because (i) escape swimming itself may increase the risk of encountering other predators, and (ii) the predator's burst swimming endurance may exceed that of the shrimp's. For example, fish have been reported to perform burst swimming bouts lasting as long as 20 s (Satchell, 1991). In contrast, *C.*

crangon become fatigued after approximately 50 tail-flip cycles (Onnen and Zebe, 1983; Kamp, 1989), which corresponds to less than 6 s on the basis of the duration of single tail-flips (Arnott et al., 1998).

Not all the escapes were final-away responses. An appreciable proportion had final-toward trajectories, and the probability of this occurring increased if the initial ϵ_{attack} angle was small (usually when attacked from head-on or tail-on). The advantage of a final-toward response is that it steers the shrimp into the predator's blind zone, a sector that, in fish, typically spans 40–60° to their rear (Wardle, 1993). This will either remove the shrimp from the predator's visual field, thereby enabling the shrimp to land undetected on the sediment, or induce an aborted attack because fish are less likely to pursue items behind than in front of them (Luecke and O'Brien, 1981; Schmidt and O'Brien, 1982). Even if a pursuit does occur, final-toward responses should increase the time required by the predator to realign itself with the shrimp before chasing it.

Attacks from 45–135° committed most shrimps to an initial ϵ_{attack} angle directed away from rather than towards the side of the attack (except in ipsilateral escapes from 45°). Such escapes only rarely produced a final-toward response, possibly because they require a larger turning manoeuvre to steer behind the attacker, which increases the risk of capture (Howland, 1974).

Unpredictable elements of escape responses

Fish have been shown to improve their capture and handling ability of prey with experience (e.g. Werner et al., 1981; Wainwright, 1986; Croy and Hughes, 1991; Huntingford, 1993; Mackney and Hughes, 1996). Therefore, a shrimp may be at a disadvantage if it encounters a predatory fish with recent experience of capturing other shrimps. One means of counteracting this is to incorporate protean behaviour (i.e. unpredictability) into escapes to prevent predators from learning a single pattern of response and compensating for it (Driver and Humphries, 1988). However, these unpredictable elements must operate within certain limits, since a completely random set of trajectories will include suboptimal responses that increase the risk of capture (e.g. escapes into the exclusion envelope).

Tail-flip escape responses by *Crangon crangon* contain unpredictable elements during both the initial and final stages of escape. During the first tail-flip, escapes occur randomly to the left or right of the shrimp when attacks are from 0° and 180°, but become confined towards the contralateral side when attacks are from a lateral position. Similar escape patterns in response to head-on and/or tail-on attacks also occur in other animal groups such as cockroaches (Camhi and Tom, 1978), toad larvae (Boothby and Roberts, 1995) and fish (Domenici and Blake, 1993), although differences between their discrimination zones do exist. In a study by Dill (1977), it was found that, when the Pacific tree frog *Hyla regilla* was approached by an artificial stimulus from head-on, frogs escaped to their left or right in an unpredictable manner. Repeated measurements on individual frogs suggested that,

whilst most showed no preference for left or right escapes, a few were 'left-handed'. Whether this occurs in *C. crangon* could not be determined from our data, but individual bias seems more likely to arise from recent experience prior to an attack (such as the prior stimulus) than from any long-term preference.

At the end of the first tail-flip of an escape by *Crangon crangon*, a second element of unpredictability occurs that determines whether the escape will have a final-away or final-towards trajectory. Within the first 100–200 ms of an escape, the shrimp may suddenly change direction by as much as 70° and escape along a new trajectory. Therefore, if a fish fails to catch a shrimp on its first strike, it not only has to react to whether the escape occurs towards the left or right side, but it may also have to make a further readjustment immediately afterwards. Video recordings of cod–shrimp pursuits indicate that this sudden turn can introduce a delay of more than 200 ms as the cod first reacts to the shrimp's initial escape trajectory and then has to realign itself with the final escape trajectory (Arnott, 1996).

Domenici and Blake (1993) found that attacks from within the discrimination zone of the angelfish *Pterophyllum eimekei* produced a bimodal distribution of final ϵ_{attack} angles with peaks at 180° and –130°. The bimodal distribution differed significantly from a unimodal von Mises function fitted to the data, indicating the occurrence of two different preferred trajectories. They also reanalysed escape trajectories of the soldier crab *Mictyris longicarpus* (data from Nalbach, 1990) and the cockroach *Periplaneta americana* (from Camhi and Tom, 1978; Comer and Dowd, 1987) and found that their distributions were bimodal and multimodal respectively. In *Crangon crangon*, the final ϵ_{attack} angles of contralateral responses to 45–135° attacks had circular distributions that differed significantly from one another. Pooling the data produced a circular distribution with peaks at 180° and +130°, but these did not differ significantly from a unimodal von Mises function. The same was true when all the final ϵ_{attack} data were pooled. Therefore, although *C. crangon* do express variability in their final-away responses, this may occur more evenly across a range of final escape trajectories compared with angelfish, soldier crabs and cockroaches.

For a predator with a well-developed learning ability, a logical response to protean behaviour would be to modify its direction of attack so as to induce an escape that is as predictable as possible. This factor was not investigated in detail and could potentially be compounded by other factors (e.g. preference of certain prey orientations for swallowing). Nevertheless, when attacking *Crangon crangon*, one would expect attacks from the side of the shrimp to produce responses that are more predictable because shrimps would then escape to the contralateral side and follow a final-away trajectory. However, *in situ*, *C. crangon* tend to remain buried beneath the sediment surface unless light levels are low (Al-Adhub and Naylor, 1975; Hagerman, 1970; Burrows et al., 1994), so predators are probably unable to determine the shrimp's pre-escape orientation in most encounters. This is especially true

if senses other than vision (e.g. chemosensory cues) are predominant in locating prey. A further defence against lateral attacks may be provided by the shrimps' ability to pre-set its escape direction, as revealed by their contralateral side-leaning behaviour. In this situation, a trade-off occurs. If the shrimp is confined to escaping contralaterally by a lateral attack, the escape path will be reasonably predictable to an experienced predator and, therefore, broadcasting the shrimp's intention may not matter if an alternative advantage is gained that increases the effectiveness of the initial phase of the escape. A preparatory response to asymmetrical stimuli has also been reported in the spiny lobster *Jasus lalandii* (Cattaert et al., 1988; Newland et al., 1992) and may serve to reduce the latency of the response. In *C. crangon* for instance, although insignificant, there was a trend for reaction distances to be greater in response to attack angles that only produced contralateral escapes (posterior attacks by cod and 90–135° attacks by the artificial stimulus). The leaning may also communicate a visible signal to the predator, since recognition of a prey's readiness to respond can lead a predator aborting its attack (Webb, 1982).

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References

- Al-Adhub, A. H. Y. and Naylor, E.** (1975). Emergence rhythms and tidal migrations of the brown shrimp, *Crangon crangon* (L.). *J. Mar. Biol. Ass. U.K.* **55**, 801–810.
- Alexander, R. McN.** (1970). Mechanics of the feeding action of various teleost fishes. *J. Zool., Lond.* **162**, 145–156.
- Arnott, S. A.** (1996). The tail-flip escape response of the brown shrimp *Crangon crangon* (L.) in the context of predator–prey interactions. PhD thesis, University of Glasgow, Scotland, UK.
- Arnott, S. A., Neil, D. M. and Ansell, A. D.** (1995). Escape trajectories of the brown shrimp, *Crangon crangon*, in response to visual stimuli presented by natural and artificial predators. In *Nervous Systems and Behaviour: Proceedings of the 4th International Congress of Neuroethology* (ed. M. Burrows, T. Matheson, P. L. Newland and H. Schuppe), p. 466. Stuttgart: Thieme Medical Publishers Inc.
- Arnott, S. A., Neil, D. M. and Ansell, A. D.** (1998). Tail-flip mechanism and size-dependent kinematics of escape swimming in the brown shrimp *Crangon crangon*. *J. Exp. Biol.* **201**, 1771–1784.
- Atema, J.** (1988). Distribution of chemical stimuli. In *The Biology of Crustacea: Structure and Function*, vol. 3 (ed. D. C. Sandeman and H. L. Atwood), pp. 369–398. New York: Academic Press.
- Batschelet, E.** (1981). *Circular Statistics in Biology*. London: Academic Press Inc.
- Berghahn, R.** (1996). Episodic mass invasions of juvenile gadoids into the Wadden Sea and their consequences for the population dynamics of brown shrimp (*Crangon crangon*). *Mar. Ecol.* **17**, 251–260.
- Berghahn, R., Wiese, K. and Lüdemann, K.** (1995). Physical and physiological-aspects of gear efficiency in North Sea brown shrimp fisheries. *Helgolander Wiss. Meererunters. Mar. Invest.* **49**, 507–518.
- Boothby, K. M. and Roberts, A.** (1995). Effects of site of tactile stimulation on the escape swimming responses of hatching *Xenopus laevis* embryos. *J. Zool., Lond.* **235**, 113–125.
- Breithaupt, T., Schmitz, B. and Tautz, J.** (1995). Hydrodynamic orientation of crayfish (*Procambarus clarkii*) to swimming fish prey. *J. Comp. Physiol. A* **177**, 481–491.
- Burrows, M. T., Gibson, R. N., Robb, L. and Comely, C. A.** (1994). Temporal patterns of movement in juvenile flatfishes and their predators – underwater television observations. *J. Exp. Mar. Biol. Ecol.* **177**, 251–268.
- Camhi, J. F. and Tom, W.** (1978). Escape behaviour of the cockroach *Periplaneta americana*. I. Turning response to wind puffs. *J. Comp. Physiol. A* **128**, 193–201.
- Cattaert, D., Clarac, F. and Neil, D. M.** (1988). Anatomical and physiological organisation of the swimmeret system of the spiny lobster *Jasus lalandii* as adaptive components of the tail flick. *J. Comp. Physiol. A* **162**, 187–200.
- Chance, M. R. A. and Russell, W. M. S.** (1959). Protean displays: a form of allaesthetic behaviour. *Proc. Zool. Soc. Lond.* **132**, 65–70.
- Comer, C. M. and Dowd, J. P.** (1987). Escape turning behaviour of the cockroach. Changes in directionality induced by unilateral lesions of the abdominal nervous system. *J. Comp. Physiol. A* **160**, 571–583.
- Croy, M. I. and Hughes, R. N.** (1991). The influence of hunger on feeding behaviour and the acquisition of learned foraging skills by the fifteen-spined stickleback, *Spinachia spinachia* L. *Anim. Behav.* **41**, 161–170.
- Daniel, T. L. and Meyhöfer, E.** (1989). Size limits in escape locomotion of caridean shrimp. *J. Exp. Biol.* **143**, 245–265.
- del Norte-Campos, A. G. C. and Temming, A.** (1994). Daily activity, feeding and rations in gobies and brown shrimp in the northern Wadden Sea. *Mar. Ecol. Prog. Ser.* **115**, 41–53.
- Dill, L. M.** (1977). 'Handedness' in the Pacific tree frog (*Hyla regilla*). *Can. J. Zool.* **55**, 1926–1929.
- Domenici, P. and Blake, R. W.** (1993). Escape trajectories in angelfish (*Pterophyllum eimekei*). *J. Exp. Biol.* **177**, 253–272.
- Driver, P. M. and Humphries, D. A.** (1988). *Protean Behaviour: The Biology of Unpredictability*. Oxford: Oxford University Press.
- Edmunds, M.** (1974). *Defence in Animals*. Harlow: Longman Press.
- Ellis, T., Howell, B. R. and Hughes, R. N.** (1997). The cryptic responses of hatchery-reared sole to a natural sand substratum. *J. Fish Biol.* **51**, 389–401.
- Hagerman, L.** (1970). Locomotory activity patterns of *Crangon vulgaris* (Fabricius) (Crustacea: Natantia). *Ophelia* **8**, 255–266.
- Hart, P. J. B. and Hamrin, S. F.** (1990). The role of behaviour and morphology in the selection of prey by pike. In *Behavioural Mechanisms of Food Selection*, NATO ASI series, vol. G 20 (ed. R. N. Hughes), pp. 235–254. Berlin: Springer-Verlag.
- Heatwole, H.** (1968). Relationship of escape behaviour and camouflage in anoline lizards. *Copeia* **1968**, 109–113.

- Heinisch, P. and Wiese, K.** (1987). Sensitivity to movement and vibration of water in the North Sea shrimp *Crangon crangon*. *J. Crust. Biol.* **7**, 401–413.
- Henderson, P. A. and Holmes, R. H. A.** (1989). Whiting migration in the Bristol Channel: a predator–prey relationship. *J. Fish Biol.* **34**, 409–416.
- Howland, H. C.** (1974). Optimal strategies for predator avoidance: the relative importance of speed and manoeuvrability. *J. Theor. Biol.* **47**, 333–350.
- Huntingford, F. A.** (1993). Development of behaviour in fish. In *Behaviour of Teleost Fishes*, 2nd edition (ed. T. J. Pitcher), pp. 609–644. London: Chapman & Hall.
- Johnson, G. E.** (1924). Giant nerve fibres in crustaceans, with special reference to *Cambarus* and *Palaemonetes*. *J. Comp. Neurol.* **36**, 323–373.
- Kamp, G.** (1989). Glycogenolysis during recovery from muscular work. *Biol. Chem. Hoppe-Seyler* **370**, 565–573.
- Kovach, W. L.** (1994). *Oriana for Windows, ver. 1.0*. Pentraeth, Wales, UK: Kovach Computing Services.
- Kramer, D. L. and Bonenfant, M.** (1997). Direction of predator approach and the decision to flee to a refuge. *Anim. Behav.* **54**, 289–295.
- Land, M. and Layne, J.** (1995). The visual control of behaviour in fiddler crabs. II. Tracking control systems in courtship and defence. *J. Comp. Physiol. A* **177**, 91–103.
- Luecke, C. and O'Brien, W. J.** (1981). Prey location volume of a planktivorous fish: a new measure of prey vulnerability. *Can. J. Fish. Aquat. Sci.* **38**, 1264–1270.
- Mackney, P. A. and Hughes, R. N.** (1996). Foraging behaviour and memory window in sticklebacks. *Behaviour* **132**, 1241–1253.
- Nalbach, H.-O.** (1990). Visually elicited escapes in crabs. In *Frontiers in Crustacean Neurobiology* (ed. K. Wiese, W.-D. Krenz, J. Tautz, H. Reichert and B. Mulloney), pp. 165–172. Basel: Birkhäuser Verlag.
- Neil, D. M. and Ansell, A. D.** (1995). The orientation of tail-flip escape swimming in decapod and mysid crustaceans. *J. Mar. Biol. Ass. U.K.* **75**, 55–70.
- Nemeth, D. H.** (1998a). Modulation of buccal pressure during prey capture in *Hexagrammos decagrammus* (Teleostei: Hexagrammidae). *J. Exp. Biol.* **200**, 2145–2154.
- Nemeth, D. H.** (1998b). Modulation of attack behavior and its effects on feeding performance in a trophic generalist fish, *Hexagrammos decagrammus*. *J. Exp. Biol.* **200**, 2155–2164.
- Newland, P. L. and Neil, D. M.** (1990). The tail flip of the Norway lobster, *Nephrops norvegicus*. I. Giant fibre activation in relation to swimming trajectories. *J. Comp. Physiol. A* **166**, 517–527.
- Newland, P. L., Neil, D. M. and Chapman, C. J.** (1992). Escape swimming in the Norway lobster, *Nephrops norvegicus*. *J. Crust. Biol.* **12**, 342–353.
- Norton, S. F.** (1991). Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics. *Ecology* **72**, 1807–1819.
- Norton, S. F.** (1995). A functional approach to ecomorphological patterns of feeding in cottid fishes. *Env. Biol. Fish.* **44**, 61–78.
- Onnen, T. and Zebe, E.** (1983). Energy metabolism in the tail muscles of the shrimp, *Crangon crangon*, during work and subsequent recovery. *Comp. Biochem. Physiol. A* **74**, 833–838.
- Pinn, E. H. and Ansell, A. D.** (1993). The effect of particle size on the burying behaviour of the brown shrimp, *Crangon crangon*. *J. Mar. Biol. Ass. U.K.* **73**, 365–377.
- Satchell, G. H.** (1991). *Physiology and Form of Fish Circulation*. Cambridge: Cambridge University Press.
- Schmidt, D. and O'Brien, W. J.** (1982). Planktivorous feeding ecology of Arctic grayling (*Thymallus arcticus*). *Can. J. Fish. Aquat. Sci.* **39**, 475–482.
- Tallmark, B. and Evans, S.** (1986). Substrate related differences in antipredator behaviour of two gobiid fishes and the brown shrimp and their adaptive value. *Mar. Ecol. Prog. Ser.* **29**, 217–222.
- Thetmeyer, H. and Kils, U.** (1995). To see and not be seen: the visibility of predator and prey with respect to feeding behaviour. *Mar. Ecol. Prog. Ser.* **126**, 1–8.
- Tiews, K.** (1970). Synopsis of biological data on the common shrimp *Crangon crangon* (Linnaeus, 1758). *FAO Fisheries Report*. **57**, 1167–1224.
- Wainwright, P. C.** (1986). Motor correlates of learning behaviour: feeding on novel prey by pumpkinseed sunfish (*Lepomis gibbosus*). *J. Exp. Biol.* **126**, 237–247.
- Wardle, C. S.** (1993). Fish behaviour and fishing gear. In *Behaviour of Teleost Fishes*, 2nd edition (ed. T. J. Pitcher), pp. 609–644. London: Chapman & Hall.
- Webb, P. W.** (1976). The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri* and a consideration of piscivorous predator–prey interactions. *J. Exp. Biol.* **65**, 157–177.
- Webb, P. W.** (1979). Mechanics of escape responses in crayfish (*Orconectes virilis*). *J. Exp. Biol.* **79**, 245–263.
- Webb, P. W.** (1982). Responses of northern anchovy, *Engraulis mordax*, larvae to predation by a biting planktivore, *Amphiprion percula*. *Fishery Bull.* **79**, 727–735.
- Webb, P. W.** (1984). Chase response latencies of some teleostean piscivores. *Comp. Biochem. Physiol.* **79A**, 45–48.
- Webb, P. W. and Skadsen, J. M.** (1980). Strike tactics in *Esox*. *Can. J. Zool.* **58**, 1462–1469.
- Weihls, D. and Webb, P. W.** (1984). Optimal avoidance tactics in predator–prey interactions. *J. Theor. Biol.* **106**, 189–206.
- Werner, E. E., Mittlebach, G. G. and Hall, D. J.** (1981). The role of foraging profitability and experience in habitat use by the bluegill sun fish. *Ecology* **62**, 116–125.
- Wiese, K.** (1976). Mechanoreceptors for near field water displacement in crayfish. *J. Neurophysiol.* **39**, 816–833.
- Wine, J. J. and Krasne, F. B.** (1972). The organisation of escape behaviour in the crayfish. *J. Exp. Biol.* **56**, 1–18.
- Wine, J. J. and Krasne, F. B.** (1982). The cellular organization of crayfish escape behaviour. In *The Biology of Crustacea: Neural Integration and Behaviour*, vol. 4 (ed. D. C. Sandeman and H. L. Atwood), pp. 241–292. New York: Academic Press.
- Woodbury, P. B.** (1986). The geometry of predator avoidance by the blue crab, *Callinectes sapidus* Rathbun. *Anim. Behav.* **34**, 28–37.
- Ydenberg, R. C. and Dill, L. M.** (1986). The economics of fleeing from predators. *Adv. Study Behav.* **16**, 229–249.
- Zar, J. H.** (1996). *Biostatistical Analysis*. New Jersey: Prentice Hall International Inc.