Fluid mechanosensory stimulation of behaviour from a planktonic marine copepod, *Euchaeta rimana* Bradford

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This research provides the first reported thresholds for the behavioural response of an individual planktonic copepod. Using a novel technique to create near-field fluid disturbances, we directed microlitre volumes of water towards the antennulary setae. In response to an increasing strength of this purely mechanical signal, the animal varied its behaviour from a rapid flick to a capture response and finally an escape reaction. This work provides a basis for addressing the criteria copepods use to interpret biologically generated signals to elicit an appropriate behavioural response and offers insight into how these signals are differentiated from the random fluid motion in their environment.

INTRODUCTION

Implicit assumptions of studying the behavioural repertoire of an organism are that it is able to discern different signals and that the uniqueness of each signal is the basis for the animal's distinct behavioural responses. Yet, despite the fact that the behavioural repertoire is how an organism exploits its food resources, escapes predators, and chooses mates, relatively few studies involving small aquatic organisms have been successful in linking the different observed behaviours to specific stimulus parameters. This may be due, in part, to the fact that the methods for controlling and measuring water-borne signals have only recently become sufficiently sophisticated and affordable to permit such rigorous analysis. In this study we used a marine calanoid copepod as a model organism to address the link between fluid signal strength and behaviour. Copepods occupy a crucial position in marine and freshwater food webs by bridging the production of micro-algae and zooplankton with fish and other commercially important organisms. They have been shown to feed selectively (Price, 1988), to actively avoid predators actively (Fields and Yen, 1997; Bollens and Frost, 1989) and to track potential mates (Doall et al., 1998; Weissburg et al., 1998; Yen et al., 1998). Performing these behaviours at an appropriate time (non-randomly) supports the hypothesis that these animals are able to differentiate among numerous signals within their environment.

Copepods possess both mechanosensors and chemosensors on numerous appendages (Friedman, 1980; Weatherby et al., 1994). Compared to other crustaceans (Wiese, 1976), copepod mechanoreceptors are at least an order of magnitude more sensitive, which allows them to detect fluid velocities as small as 20 μm s^{-1} with a sensor displacement of only 10 nm at 1 kHz (Yen et al., 1992) and velocities of 0.5 mm s^{-1} at frequencies of 100 Hz (Fields et al., 2001). At the scale of the individual mechanoreceptor, depolarization of the nerve cell results from the displacement of the associated sensory hair. The rate of displacement and the total distance displaced is likely to provide the animal with information pertaining to the strength of the signal. The number of sensors stimulated may provide the animal with a measure of the size and distance of the disturbance source. Although signal differentiation, in some cases, is likely to be in response to a combination of chemical and mechanical signals, previous work has shown that in the absence of chemical signals, they will alter their behaviour solely in response to a mechanical fluid disturbance (Haury et al., 1980; Fields and Yen, 1996, 1997).

Despite observations that copepods do exhibit distinct behaviours to different natural stimuli, no success has been reported in eliciting behaviours other than the escape reaction to laboratory-generated fluid mechanical signals. In this study we used a novel mechanism to simulate the natural water disturbances of prey and predators.

The goal of this work was to quantify the structure and magnitude of fluid signals involved in eliciting distinct behaviour patterns in *Euchaeta rimana*, a small (2.4 mm prosome length) planktonic marine crustacean.

Previous researchers have presented copepods with hydrodynamic disturbances created by several different mechanisms in an effort to elicit behavioural reactions (Haury *et al.*, 1980; Singarajah, 1969, Drenner *et al.*, 1978; Yen and Fields, 1992, 1994). In this study we used a short duration, pressure-driven water jet to stimulate the mechanosensory hairs on the antennules of *E. rimana*. The use of a water jet was prompted by the observation that *E. rimana*, a carnivorous calanoid copepod, exhibits a capture response only after the prey have initiated an escape reaction. The prey's escape reaction sends a jet-like fluid wake towards the predator (Yen and Strickler, 1996) which is hypothesized to elicit the capture response. Based on the size and speed of the natural wake, we designed an artificial wake that mimics the characteristics of the fluid displacement produced within the natural wake yet could be reproduced accurately, directed precisely towards the copepod and be devoid of any additional chemical information. Thus, we are able to provide quantified hydrodynamic signals at a planktonic scale (< 1–10 mm).

METHOD

Ideally experiments would be performed on free-swimming animals. However, to introduce a controlled fluid stimulus to animals positioned in a repeatable manner requires that the animals are tethered and positioned in a manner that allows observations from multiple directions. Animals were tethered to a 0.1 mm diameter tin electrical wire (with a small droplet of cyanoacrylate) and suspended in the centre of a 10 cm^3 vessel filled with 0.45 μm-filtered sea water at 21°C. Filming used a single, low-powered helium-neon laser (5 mW-632 nm, Newport Corp). The 0.8 mm beam was split, expanded to 20 mm, and then used to illuminate two perpendicularly mounted video cameras. Filming optics were arranged in a modified Schlieren pathway for maximum contrast and depth of field (Strickler *et al.*, 1995).

The prey mimic and the copepod's response

To create a fluid disturbance, we forced water through a 1 mm capillary tube pulled to an outer mouth diameter of 100, 150, or 200 μm. We varied the pressure and the duration of the applied pressure (Table I) using a solenoid valve and timer package created by General Valve Corp. The motion of the water jet was visualized using the Schlieren optical pathway described above. To measure the characteristics of the expelled fluid, we loaded the pipette with 28 ppt salt water and ejected it into our experimental

vessel, which was filled with 34 ppt salt water. Although there is only a slight difference in fluid density (0.6%), the different fluids provided enough optical difference to be detected using our Schlieren pathway (Fields and Yen, 1997). Fluid motion was filmed digitally at 2000 Hz and an equivalent shutter speed of 1/40 000 s [Motion Scope PCI 2000s—Redlake Imaging; (Fields *et al.*, 2001)]. Changes in the displacement of the head of the water jet over time were quantified from sequential video images using NIH IMAGE software (Figure 1). The data used were to calculate fluid displacement and speed and then were fitted to a Weibull Peak equation (four-parameter) to estimate the fluid velocity at the specific distance of the seta for each experiment. During the actual experiments with *E. rimana*, however, the wakes were created using the same water as the surrounding fluid. The tip of the pipette was positioned at distances ranging from 3 to 5 mm anterior to the antennae of a tethered female *E. rimana* (Figure 2). At these distances, the speed and width of the fluid disturbance, calculated from a polynomial fit to the data, bracket the natural wake generated by copepod prey (Yen and Strickler, 1996). By varying the size of the pipette and the duration of the stimulus, we were able to create unique mechanical signals that uncoupled the size of the wake from the speed at which the wake travelled (Figure 3). As a result, the copepod's response to the speed of the wake could be ascertained independently from the wake size.

Based on the behavioural observations of free-swimming animals (Doall *et al.*, 2001; Fields and Yen, 1997), we scored our observations as one of four possibilities (no response, antennule flick, capture, or escape) distinguished on the basis of different appendage motion. An antennule flick was noted when either one or both antennules were retracted partially or fully against the body with no change in the movement of the cephalic or abdominal appendages. A capture response involved the full extension of the maxillipeds (capture appendages) and a single cycle of the pereiopods (thoracic legs). An escape reaction consisted of the full retraction of both antennules and numerous cycles of the pereiopods with no extension

Table I: Experimental set-up used for each pipette

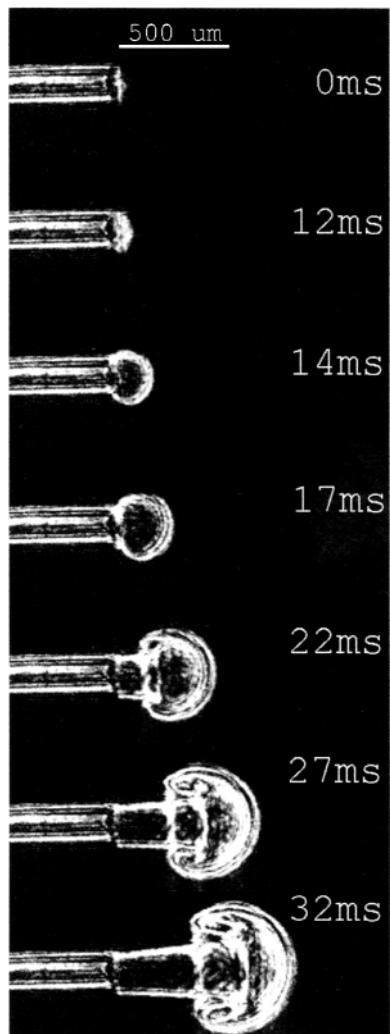| Pipette size (OD) (μm)	Pressure (psi)	Solenoid duration (ms)	Distance from animal (mm)
100	20	3–8	3.8
150	5	3–10	5.2
200	5	2–6	5.1

Fig. 1. A time series of the released water jet from a 150 µm pipette. The pressure behind the solenoid was 5 psi and the solenoid remained open for 7 ms. The movement of the expelled water was filmed at 2000 Hz using a Schlieren optical pathway. Note that the water is only beginning to exit the mouth of the pipette 12 ms after the solenoid was opened.

of the maxillipeds. No effect was scored when the animal continued with its previous behaviour after the introduction of the stimulus.

RESULTS

In general, the activity of the animal increased with increasing speed and width (the two quantified descriptors) of the fluid stimulus. Fluid speeds below ~ 5 mm s^{-1} rarely gave rise to any behaviour in *E. rimana* while a greater number of responses were noted when fluid wakes were wider than 0.8 mm across. (Figure 4A,B). We observed three distinct behaviours in response to our

stimuli differing in both the appendages used and the duration of the behaviour. The flick (Figure 5A) lasted only 17–33 ms and, as defined above, involved only movement of the antennules. The capture (Figure 5B) with its characteristic extension of the maxillipeds and single cycle of the pereiopods lasted between 17 and 67 ms, with typical responses occurring in 33 ms or less. The escape reaction (Figure 5C,D) took the most time of the three behavioural responses, typically lasting over 100 ms with several responses lasting as long as 1 s. Each of these behaviours is important to the survival of *E. rimana* and can be interpreted with respect to *E. rimana*'s general ecology. *Euchaeta* are obligate predators (Bamstedt and Holt, 1978; Yen, 1982) and dominate the biomass in many oceanic regimes (McGowan and Walker, 1979, Yen et al., 1992). They have been shown to be a selective feeder discriminating, in part, on the basis of movement (attacking only live moving prey) as well as prey size (Yen, 1985). *Euchaeta rimana*'s capture region is a cubic volume of 8 mm^3 anterior to its head (Doall *et al.*, 2002). This volume is large compared to other similar organisms: i.e. *Acartia tonsa*, 0.35 mm^3 (Jonsson and Tiselius, 1990); *Eucalanus pileatus*, 0.13 mm^3 (Paffenhofer and Lewis, 1990); *Leptodora*, 0.0 mm^3 requiring physical contact (Browman *et al.*, 1989). Based on escape speeds (S_{max}) of typical prey items [~ 250 mm s^{-1}; (Trager *et al.*, 1984; Fields, 1996)] and assuming that speed of the wake decays at a rate proportional to the inverse of distance (D) cubed, as does the near field displacement created by a dipole (Kalmijn, 1988), the signals we used then can be discussed in terms of the natural fluid speeds (S) to which *E. rimana* would be exposed.

$$S = (S_{max})(D^{-3}) \qquad (1)$$

THRESHOLDS

Flick response

The threshold speed for the antennule flick response was 14 mm s^{-1} (Table II), well above the physiological threshold (Yen *et al.*, 1992). This response was exhibited with all of the pipettes a maximum of 40% of the time (Figure 6A). To create a fluid velocity of 14 mm s^{-1}, a prey item that escapes at a typical speed of 250 mm s^{-1}, would need to be 2.6 mm from *E. rimana* (from equation 1). Although this distance is well outside the capture region of *E. rimana*, the fluid motion is well within the neurophysiological detection limits of the copepod (Yen *et al.*, 1992). Upon detection, the elicited motor response of an antennule flick may serve as a mechanism for repositioning or reorienting the predator in such a way that it allows for a more accurate interpretation of subsequent signals. Thus the
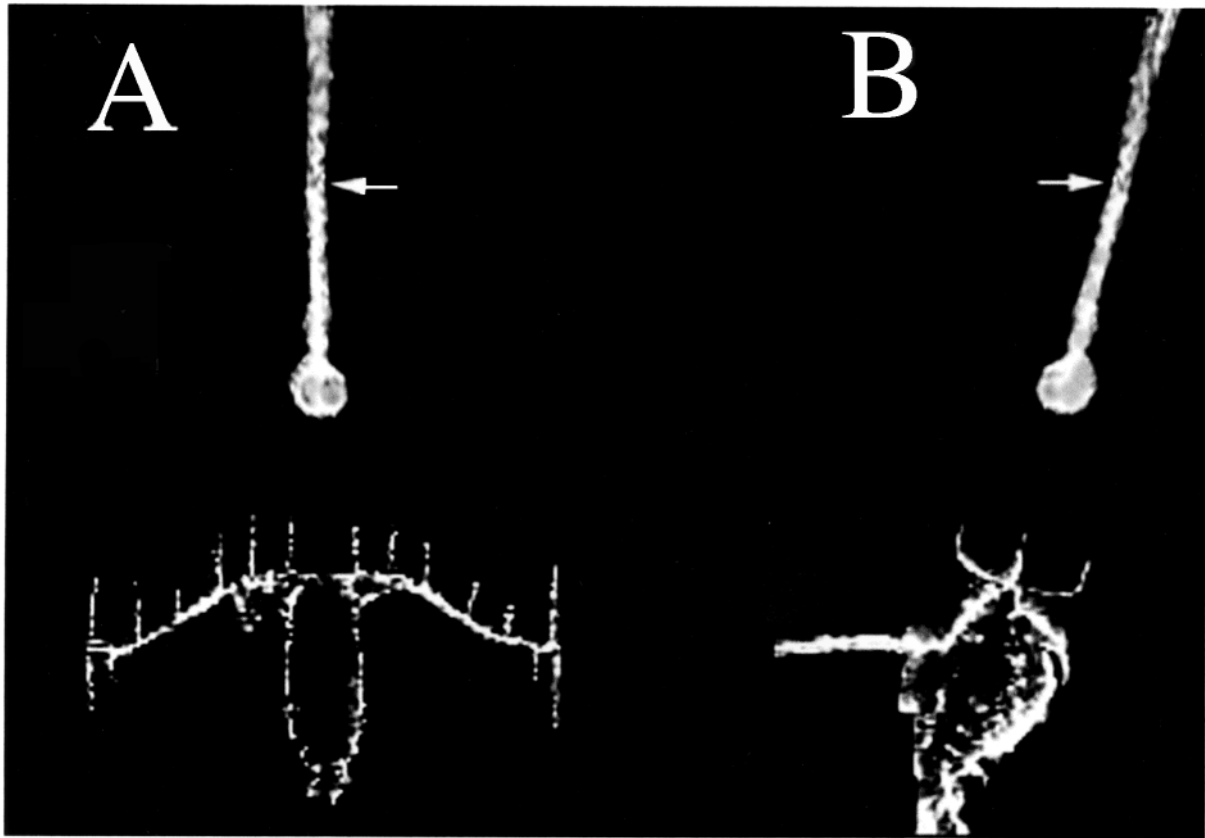
Fig. 2. The relative orientation between the tip of the pipette and the tethered *Euchaeta rimana* is shown in the dorsal (**A**) and lateral (**B**) view. In (**B**), the ventral region of the animal is to the right. The arrows mark the location of the pipette tip.
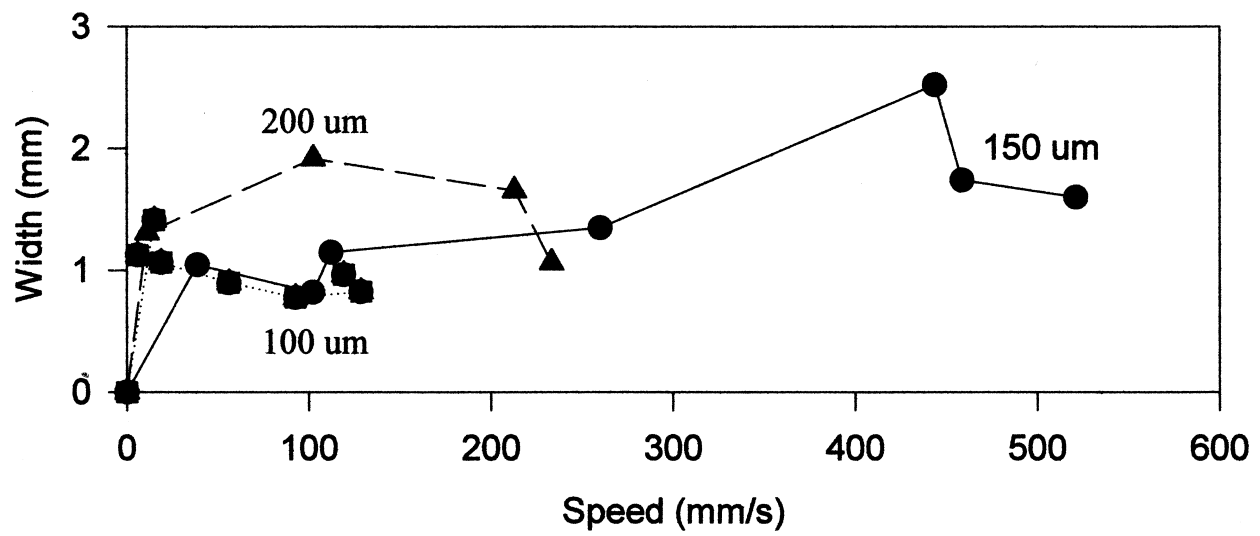

Fig. 3. The combination of speed and width of the wakes created by the three micropipettes used in this experiment.
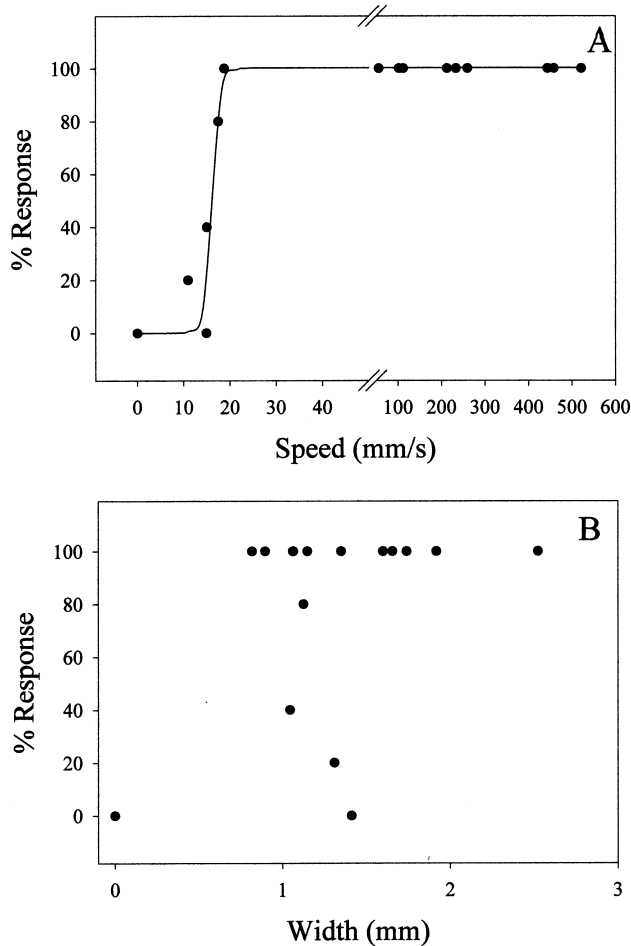
Fig. 4. The frequency of a behavioural response to the wake with respect to the speed (**A**) and the width of the fluid disturbance (**B**). Behaviour was noted when a change in the activity of the animal was observed. No distinction was made between each of the different behaviours. The ordinate in (**A**) has been expanded between the speeds of 0 and 40 mm s^{-1} to elucidate the speed at which the activity of the animal increased.

Table II: The three behavioural responses were fitted to a Gaussian peak curve of the form $R = ae^{\left[-0.5\left(\frac{x - x_0}{b}\right)^2\right]}$

Behaviour	a	b	x_0	r^2
Flick	24.5	4.3	14.5	0.51
Capture	72.4	66.7	132.8	0.51
Escape	100	195.3	430.9	0.75

The value of x_0 represents the speed of the fluid coinciding with the peak frequency of the Gaussian curve. The parameter a is the calculated maximum frequency of the response. Parameter b represents the speed of the fluid at the inflection point were the slope of the curve becomes undefined. All values were solved by numerical iterations until residual sum of squares was no longer significantly decreased. The r^2 value is the coefficient of determination.

Peak capture responses (> 70%) occurred at speeds of 132 mm s^{-1}, mimicking the water speed created by an escaping prey 1.2 mm from *E. rimana*. This is well within the capture region of the animal and suggests that an attack based on such a stimulus would result in a successful capture.

Escape response

The transition from a capture response to an escape response was marked by high variability in the percentage response at the transition speed (Figure 6C). The transition occurred in all three pipettes at a speed of 180–220 mm s^{-1} and with wakes ranging in size from 1.1 mm to 1.7 mm. When exposed to wake speeds above 250 mm s^{-1} the behavioural response of *E. rimana* was dominated by escape reactions. The speed of the wake was determined to be a significant factor affecting both the capture ($P < 0.03$) and the escape ($P < 0.001$) reaction of *E. rimana*. In contrast, the wake width was found to be insignificant for both reactions. Based on these results the response can be described as a function of stimulus speed (Figure 7). However, for the escape reaction, the interaction term was statistically suspicious ($P = 0.07$). This appears to be related to *E. rimana* failing to respond to wakes within the 1.0–1.5 mm size range which travelled at speeds less than 40 mm s^{-1}. Thus a single wake with these characteristics may not provide sufficient evidence as to the identity or the distance of signal source and therefore does not warrant behaviour. It will be interesting to examine the behavioural responses of *E. rimana* to very large (5–10 mm) and relatively slow (50 mm s^{-1}) moving fluid disturbances, such as those produced by a swimming fish.

flick response appears to be elicited when potential prey are too distant for *E. rimana* to launch a successful attack or when the source of a fluid disturbance is oriented in such a way that its wake does not intersect the antennule hairs directly, making its interpretation ambiguous.

Capture response

Increasing the wake speed to 20 mm s^{-1} gave rise to a transition in the behavioural response from the flick to the capture response (Figure 6B). All three pipettes, when fired at speeds ranging from 20 mm s^{-1} to 260 mm s^{-1}, elicited the capture response for part of the time. At the lowest speeds required to elicit a capture response, the moving prey would need to be 2.3 mm from *E. rimana*.
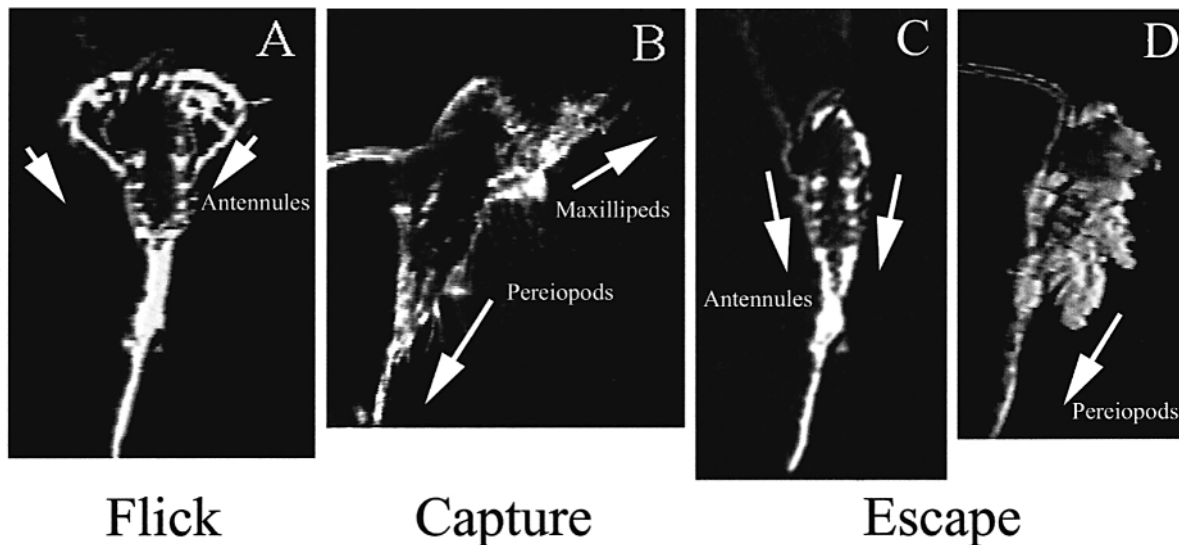
Fig. 5. The behavioural responses of *Euchaeta rimana* (2.4 mm) elicited by well-controlled, laboratory-generated wakes. An antennule flick (**A**), shown from the dorsal view, involved the partial or full retraction of one or both antennules against the body with no change in the movement of the cephalic or abdominal appendages. A capture response (**B**), shown here in the lateral view, involves the full retraction of one or both antennules against the body, the full extension of the maxillipeds (capture appendages) and a single cycle of the pereiopods (thoracic legs). The duration of the capture response was typically less than 67 ms. An escape reaction (**C,D**) consists of the full retraction of the antennules (similar to the capture response). Differing from the capture response however, the escape response involves numerous cycles of the pereiopods and no extension of the maxillipeds (**D**). The duration of the escape reaction was often greater than 100 ms.

DISCUSSION

The performance of this copepod in response to our defined stimuli corroborates our present knowledge of the behavioural ecology of this animal. The sequence of events: flick, capture and escape, represent motor activities requiring an ever-increasing expenditure of metabolic energy, quantifiable by the increase in the speed of movement and the number of appendages deployed and the duration of the activity. When the stimulus strength is small or the direction of the source is unclear, the data suggest that the copepods reorient in order to position directionally the complex array of sensitive sensors along the paired antennules (Boxshall *et al.*, 1997) in a more favourable manner. When the signal is of greater intensity and has the characteristics of a prey's wake, the results suggest that *E. rimana* elicit the capture response. However, this appears to occur primarily when the prey is within the capture range of *E. rimana*. The high efficiency of capture (73%, [(Doall *et al.*, 2002)]) suggests that the attack response is a costly reaction and only performed when success is likely. Similarly, the energetically expensive high-speed escape (Morris *et al.*, 1985; Alcaraz and Strickler, 1988) is a critical survival decision, yet it requires a much larger signal strength and is exhibited only during the final stages of a predator's attack. Thus in an effort to minimize the superfluous expenditure of energy, the intensity of the

signal needed to elicit the escape is greater than that generated by small prey and up to an order of magnitude greater than that generated by background small-scale turbulence (Fields and Yen, 1997).

The success of copepods in planktonic communities is contingent on the sensitivity of their detection system and their ability for rapid response. Our results have demonstrated that this copepod species can respond to fluid displacements without any additional chemical signals. Similar responses to directed fluid motion have been shown for the much larger crustaceans such as crayfish, in which stimulation of the mechanoreceptors in the absence of chemical signals gives rise to sweeps by the antennae and chelae and to directed body movements, presumably aimed at increasing its success during predator–prey interactions (Tautz, 1987). Furthermore, some marine decapods have been shown to orient to prevailing flows to locate food (Weissburg and Zimmer-Faust, 1993) and lobsters appear to use the direction of wave surges to locate their shelter (Hernkind and McLean, 1971). Yet clearly in copepods, as in most animals, the primary survival tactics of feeding, mating and avoiding predators are powerful agents for natural selection and are not likely to be controlled solely by one sensory modality. Indeed, chemical signals have been shown to cause or modify behavioural responses in other crustaceans. For example, *Daphnia* have been shown to decrease their thresholds for escape
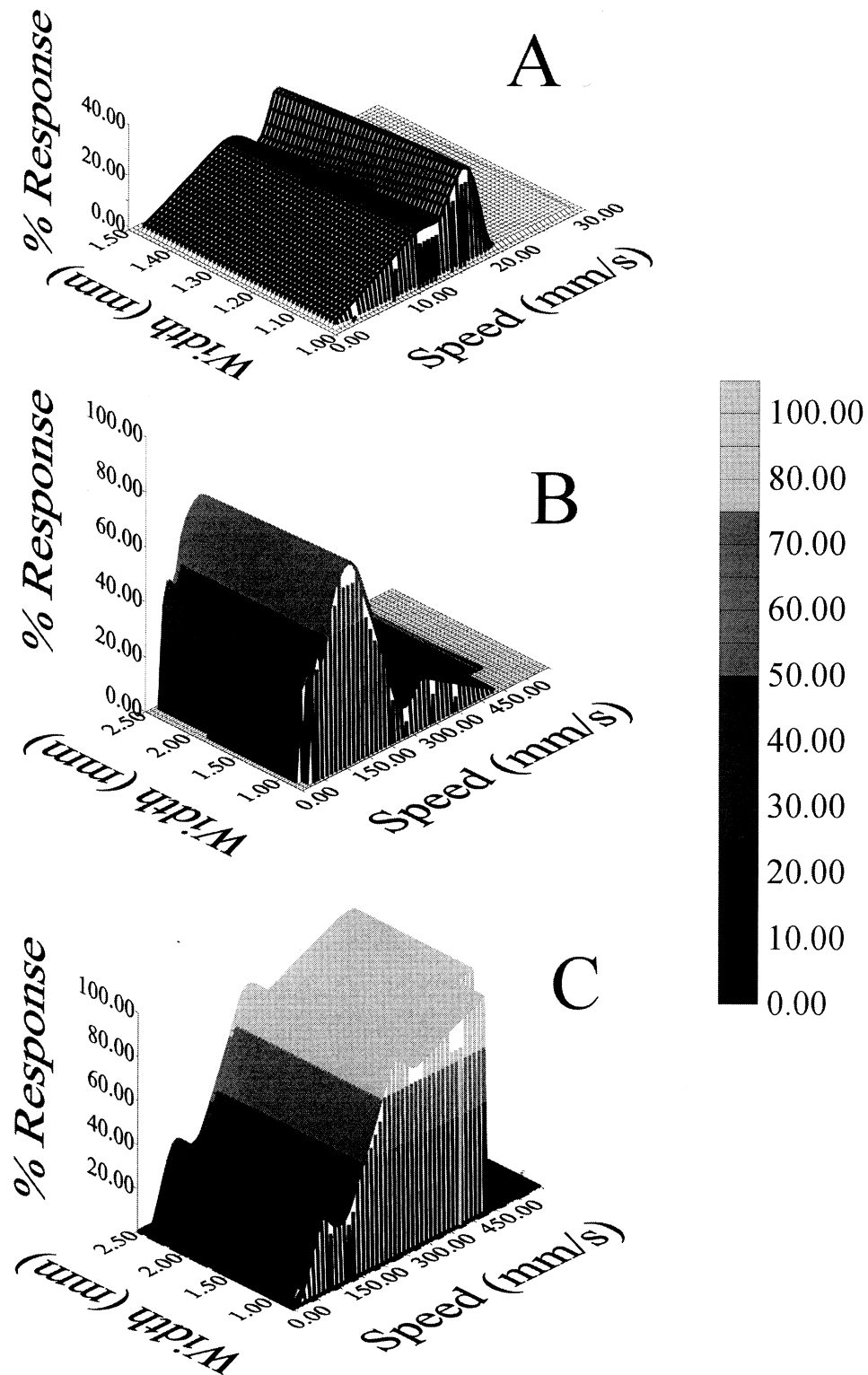
Fig. 6. A surface plot of the behavioural response of *Euchaeta rimana* to the generated wake. The independent variables are the speed and width of the wake with the frequency of the behavioural reaction as the abscissa. The colour bands represent the frequency of the response. The threshold for the flick response (**A**) occurred at speeds of 14 mm s^{-1}. The threshold speed for the capture response (**B**) occurred at 20 mm s^{-1} with maximum response occurring at speeds of 132 mm s^{-1}. At speeds greater than 250 mm s^{-1} the capture response was elicited at a frequency of 20%, forming the dome-shaped capture–response curve. The escape reaction (**C**) was elicited 50% of the time at speeds in excess of 200 mm s^{-1}. At speeds greater than 250 mm s^{-1} the escape reaction was observed in excess of 75% of the time.
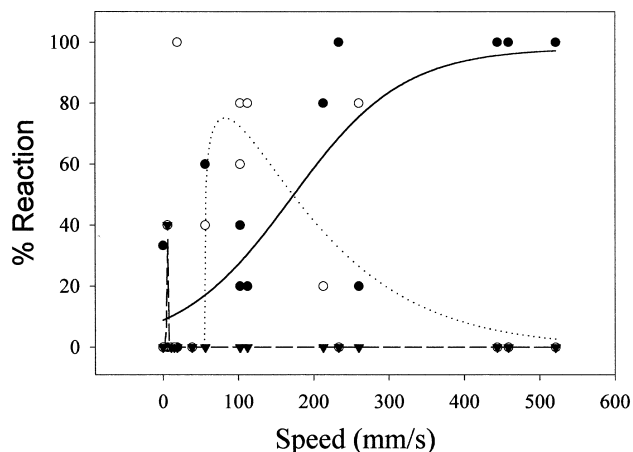
Fig. 7. The behaviour of the *Euchaeta rimana* in response to the speed of an artificial wake. The percentage response for each behaviour is fitted to a Gaussian curve (see Table II for parameters). Maximum flick response occurred at 14 mm s^{-1}. The capture response was elicited with fluid speeds as low as 20 mm s^{-1}, with peak response occurring at 132 mm s^{-1}. No capture responses were elicited to fluid speeds exceeding 300 mm s^{-1}. The escape reaction occurred at all fluid speeds with the majority of escape reaction occurring in response to fluid speeds in excess of 200 mm s^{-1}.

behaviour from fluid disturbances in the presence of fish kairomones, thus improving their escape success (Dodson, 1988). Chemical signals have also been shown recently to mediate the mate tracking response in copepods; trail-following by mating pairs of *Temora longicornis* has recently been described (Doall *et al.*, 1998; Weissburg *et al.*, 1998; Yen *et al.*, 1998). Parker suggested that copepod males were chemically attracted to females (Parker, 1902) while Katona described a mate-seeking behaviour mediated by pheromones (Katona, 1973), as did Griffiths and Frost for male *Calanus* and *Pseudocalanus* (Griffiths and Frost, 1976). Yet the final mate-capture response is triggered by the fluid mechanical signal in the female's wake (Yen *et al.*, 1998). If the fluid disturbance created by males (which are of similar size to the females) elicits an escape reaction in the females, the chance of successful mating decreases. Since both male and female antennules are equally sensitive to fluid mechanical signals (Yen and Fields, unpublished results), we hypothesize that there may be a chemical emitted by the male or created by the female that inhibits the fluid-mechanically triggered escape response of the female. Inhibition may also be controlled internally when she becomes reproductively viable. The opposite effect of repressing the escape reaction may occur in response to species-specific chemical signals, thus facilitating mating. Hence, the modulation of mechanosensory thresholds through chemical signals offers a potentially important mechanism to regulate mating success and provides testable hypotheses aimed at understanding the specific behavioural patterns of calanoid copepods.

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