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The fluid physics of signal perception by mate-tracking copepods

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Within laboratory-induced swarms of the marine copepod *Temora longicornis*, the male exhibits chemically mediated trail-following behaviour, concluding with fluid mechanical provocation of the mate-capture response. The location and structure of the invisible trail were determined by examining the specific behaviour of the female copepods creating the signal, the response of the male to her signal, and the fluid physics of signal persistence. Using the distance of the mate-tracking male from the ageing trail of the female, we estimated that the molecular diffusion coefficient of the putative pheromonal stimulant was 2.7×10^{-5} cm^2 s^{-1}, or 1000 times slower than the diffusion of momentum. Estimates of signal strength levels, using calculations of diffusive properties of odour trails and attenuation rates of fluid mechanical signals, were compared to the physiological and behavioural threshold detection levels. Males find trails because of strong across-plume chemical gradients; males sometimes go the wrong way because of weak along-plume gradients; males lose the trail when the female hops because of signal dilution; and mate-capture behaviour is elicited by suprathreshold flow signals. The male is stimulated by the female odour to accelerate along the trail to catch up with her, and the boundary layer separating the signal from the chemosensitive receptors along the copepod antennule thins. Diffusion times, and hence reaction times, shorten and behavioural orientation responses can proceed more quickly. While 'perceptive' distance to the odour signal in the trail or the fluid mechanical signal from the female remains within 1–2 body lengths (<5 mm), the 'reactive' distance between males and females was an order of magnitude larger. Therefore, when nearest-neighbour distances are 5 cm or less, as in swarms of 10^4 copepods m^{-3}, mating events are facilitated. The strong similarity in the structure of mating trails and vortex tubes (isotropic, millimetre–centimetre scale, 10:1 aspect ratio, 10 s persistence), indicates that these trails are constrained by the same physical forces that influence water motion in a low Reynolds number fluid regime, where viscosity limits forces to the molecular scale. The exploratory reaches of mating trails appear inscribed within Kolmogorov eddies and may represent a measure of eddy size. Biologically formed mating trails, however, are distinct in their flow velocity and chemical composition from common small-scale turbulent features; and mechanoreceptive and chemoreceptive copepods use their senses to discriminate these differences. Zooplankton are not aimless wanderers in a featureless environment. Their ambit is replete with clues that guide them in their efforts for survival in the ocean.

Keywords: diffusion; pheromone; Kolmogorov; chemoreception; mechanoreception

1. INTRODUCTION

Long-distance and accurate mate-tracking by male *Temora longicornis*, a small (1 mm) coastal marine planktonic calanoid, has been documented by Doall *et al.* (this volume) and Weissburg *et al.* (this volume). To summarize, after randomly crossing the path of the female, the male detects the signals left in the water by the female. The male begins to track females as far as 34 mm away by detecting the more local signal: her trail. He follows her path closely, traversing up to 10 cm (100 body lengths). These trails are on average 5-s old, but males can detect and follow a trail as old as 10 s. This trail-following ability is presumably mediated by receptors that detect water-borne cues and determined by the properties of the cues that allow them to retain their signal strength and coherency in time and space. Fleminger (1967) speculated that mating behaviour in copepods is chemically mediated, and Weissburg *et al.* (this volume) confirm this. By following defined chemical trails within this low Reynolds number fluid environment, copepods do not behave like moths (David *et al.* 1983), lobsters (Moore *et al.* 1991), or crabs (Weissburg & Zimmer-Faust 1994), that cast across odour plumes. Instead, copepods seeking mates display orientation behaviour similar to the trail-following of ants (Hölldobler & Wilson 1991), and snails (Gilly & Swenson 1978; Stirling & Hamilton 1986).

The effectiveness of a particular signal depends on the amount and specificity of information conveyed to the prey, predator, or mate. The value of the information can be derived in different ways.

1. The signals can provide early warning via remote detection. Both mechanical and chemical signals may give cues to an individual, regarding the imminent approach of either food, friend, or foe (Koehl & Strickler 1981; Yen & Fields 1992; Weissburg & Zimmer-Faust 1994; Yen & Strickler 1996).

2. Signals can reveal identity because of their specific properties. Many fluid mechanical signals retain information on the size, velocity and frequency of movements or energy content of the source (Kerfoot *et al*. 1980; Strickler 1984; Kirk 1985; Bleckmann *et al*. 1991; Yen & Strickler 1996). An odour can be a specific pheromone, or a particular metabolite, or a mixture of metabolites that identifies a specific organism (Larsson & Dodson 1993; Lazzaretto *et al*. 1990; Snell & Carmona 1994).
3. Those signals that persist and remain coherent can be traced to their source over greater spans of time and space than non-persistent signals. Persistent and long-lived cues are advantageous for tracking widely separated individuals such as conspecific mates, where long-distance perception is needed.

In addition to signal recognition, copepods separated in the ocean can aggregate to improve their probability of encounter (Gerritsen 1980). Zooplankters are attracted by the scent of algae and can swarm in a phytoplankton patch (Poulet *et al*. 1991; Williamson 1981; Tiselius *et al*. 1993). They can synchronize their vertical migratory pattern and aggregate in a common isolume, at a common location in a temperature gradient, at the pycnocline in a density gradient, or nutricline in a nutrient gradient (Wright *et al*. 1980; Mackas *et al*. 1985; Hamner 1988; Ambler *et al*. 1991). They can accumulate at interfaces such as the benthic boundary layer, the air–sea interface (neuston), or oxycline, between tidal fronts or within windrows (Alldredge *et al*. 1984; Wishner & Winn 1987; Wishner *et al*. 1988; Mackas *et al*. 1993). As a group, zooplankters can also avoid areas of high turbulence (Hwang *et al*. 1994), and aggregate in spaces where they can tolerate the ambient fluid motion, such as behind coral heads in tranquil eddies (Hamner & Carleton 1979; Ueda *et al*. 1983). Some zooplankters avoid areas in which their predators (Bollens & Frost 1989), or odours of their predators (Larsson 1996) are present, and thereby aggregate in areas of relative safety. Within any of these aggregates, they may find prey and can seek mates.

Here, we present further investigations of the biological–physical interactions of mate-tracking copepods within laboratory-induced swarms. We use fluid physics to examine the information content of the water-borne signals accessible to small planktonic animals. These analyses reveal the existence of sensory mechanisms that were not obvious through examination of the behaviour. Our studies show that, in addition to the chemical odour used in trail-following, a fluid mechanical signal helps the male to focus on the trail and orient to the female copepod when in close proximity to her. Our considerations of the fluid physical properties of cues helped to predict the conditions under which signals of various modalities can convey useful information. In our investigation, we consider signals of two modalities—a chemical signal versus a fluid mechanical signal—that alert the male of the presence of the female.

2. METHODS

Sensor sensitivity and signal intensity of the fluid mechanical and the chemical signals that are typically shed by a copepod are considered here. We present general theoretical and empirically derived arguments applicable to many organisms that live in low Reynolds number fluid regimes. Table 1 presents the equations used for the fluid physical analyses of signal type for specific sensory modalities. We presume certain odour structures and trail locations. By adhering to these fluid physical laws, we define certain patterns. Confirmation of these patterns is sought in our empirical studies of copepod sensor sensitivity and copepod behaviour. We briefly outline these equations below, and they are discussed in the following sections.

The rate of decay of energy or chemical concentration will determine the persistence of the signal. In table 1, the diffusion of a solute and of momentum are representative constants for a small chemical molecule at 20 °C and for seawater (34.84%) at 20 °C, respectively. A diffusing Brownian particle has a 68% probability of diffusing as far the the root-mean-square (RMS) displacement away from its source (Lavenda 1985). Following Dusenbery (1992), we use the equation for $\sqrt{2}\times$ RMS displacement, to estimate the characteristic diffusion length (equation (1)). The form of this equation agrees with Einstein's predictions (1910, as cited in Lavenda 1985), that the radial displacement of a particle diffusing in any direction away from a central point 'is not proportional to time but proportional to the square root of time.' We assume an instantaneous emission into still water (Bossert & Wilson 1963; Okubo 1980), and also estimated the consequent characteristic diffusion time (equation (2)). To compare to this instantaneous model, the decay function from a continous odour source, creating a concentration gradient applied to aquatic plumes, is presented (equation (3): from Atema 1988; citing Carslaw & Jaegar 1959). In viscous regimes, diffusion will produce a gradient of chemical intensity that represents the guidance cue for male copepods tracking females using chemoperception, and the rate of diffusion of a solute across a boundary is proportional to the concentration gradient (Fick's law; Lehninger 1970).

To estimate the volume of water into which a plankton-derived odour stimulant is added, we use the volume of the female copepod (equation (4)). The thickness of the boundary layer, representing the diffusive barrier between the signal molecule and the sensillum, was determined by using equations from Ellington (1975; equation (5) in table 1 here) and Dusenbery (1992; equation (6) in table 1 here). The Reynolds number (equation (7)) provides a measure of the dominance of viscous forces at this scale, where diffusive forces influence the small-scale distribution of odorant molecules and momentum within the confines of the trail, while turbulent forces act on larger physical features, such as the entire trajectory of the trail.

To estimate the fluid mechanical signal strength of water flow, the attenuation of flow emanating from a vibrating dipole signal source was modelled as R^{-3} (R is the radial distance from source, Kalmijn (1988); equation (8)). The decay function of a water jet, with a similar momentum as that within a copepod wake, was derived empirically from small-scale flow visualizations quantifying the shape and velocity of a jet of water emitted from a 200-μm opening, at an initial speed of 175 mm s^{-1} (Yen & Fields 1994). The water flow of this

Table 1. *Fluid physical equations for (a) diffusion phenomenon and (b) flow speed attenuation*

	equation	explanation of variables	equation number
(*a*) (Diffusion coefficient for small molecules: $D=10^{-5}\,\mathrm{cm^2\,s^{-1}}$; kinematic viscosity: $v=10^{-2}\,\mathrm{cm^2\,s^{-1}}$.)			
characteristic diffusion times t_D for diffusion of a chemical from an instantaneous point source	$t_D=r^2/4D$	r is distance from source	(1)[a]
characteristic diffusion lengths r_D for diffusion of a chemical from an instantaneous point source	$r_D=\sqrt{4Dt}$	t is diffusion time	(2)[a]
decay function from a continuous odour source	$C_t/C_0=0.5(\mathrm{erf}(a-x/2\sqrt{Dt})$ $+\mathrm{erf}(a+x/2\sqrt{Dt}))$ $\times\,\mathrm{erf}\,(a/2\sqrt{Dt})$	C_t is concentration at time t after release C_0 is initial concentration x is distance from centre along centre line a is half-width of initial plume D is diffusion coefficient erf is the error function	(3)[b]
copepod volume V	$V=\pi R^2L$	$R=0.025$ cm (1/2 body width) $L=0.1$ cm (body length) $V=2\times10^{-4}\,\mathrm{cm}^3$ $=2\times10^{-4}$ ml	(4)
boundary layer thickness	$\delta_1=L/\sqrt{Re}$ $\delta_2=0.4\sqrt{(L/U)}$	Re is the Reynolds number (equation (7)) L is width of seta U is water flow speed	(5)[c] (6)[a]
(*b*)			
Reynolds number	$Re=UL/v$	U is speed of moving object L is length of object perpendicular to flow v is kinematic viscosity	(7)
decay function of velocity from a dipole source	$U_t=a^3/R^3U_0$	$a=1$ mm (size of signal source) R is distance at an angle of 0° from the signal source, the copepod U_0 is original speed U_t is speed at time t	(8)[d]
decay function of velocity, determined empirically from a jet source	$U_t=1495R^{-3}$ $\mathrm{d}t=1/U(R)\mathrm{d}R$	s.e. of (1495) $=94$; $r^2=0.73$ integrate from R_1 to R_2 to determine time T	(9)[e]
of flow	$T=R_2^4-R_1^4/4\times1495$	R_1 is location of initial flow speed R_2 is location of final flow speed	(10)[f]

[a] Dusenbery (1992).
[b] Carslaw & Jaeger (1959), Atema (1988).
[c] Ellington (1975).
[d] Kalmijn (1988).
[e] Yen & Fields (1992).
[f] Equation (10): to estimate this flow speed, first determine the location R_0 along the jet path on which the female hop speed occurs, replacing the speed, U_t, in equation (9). Next, calculate the speed at the distance that the male is from her hop by adding his distance to R_0 to get R_1. This is the initial signal strength at the point where the male diverges. Then calculate the distance R_2 that the jet travels in the time passed T since the female hop and the male meets the fluid mechanical hop. Replace this distance R_2 back into equation (9) to determine the speed at this distance and after the given time interval when the male crosses where the female hopped.

jet declined rapidly with R^{-3} (equation (9)). However, fluid motion generated within the feeding current can involve a mix of first- and higher-order scanning mechanisms (Childress *et al.* 1987; Yen *et al.* 1991), while at very low Reynolds number *Re*, the velocity field falls off as distance to the -2 power. This second-order model fits the data equally well (equivalent r^2 value of 0.71). However, in the range of low flow speeds closest to natural conditions, the third-order equation best fits the data and is used in our analysis.

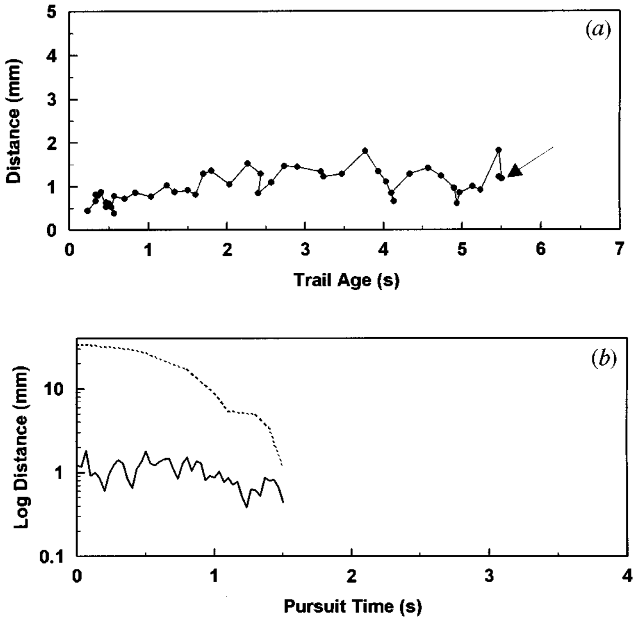

Figure 1. The perceived odour trails of *Temora longicornis*: a male copepod tracking a cruising female. (*a*) The distance of the male from the female trajectory as a function of the age of her trail. The male intersects her trail when it is 5.5-s old (arrow). (*b*) The distance (logarithmic scale) between the male and female copepod mates (dotted line) compared to the distance of the male from her trajectory (solid line) versus pursuit time. The male begins his pursuit of the female copepods at $t=0$ s, and ends when he lunges for his mate.

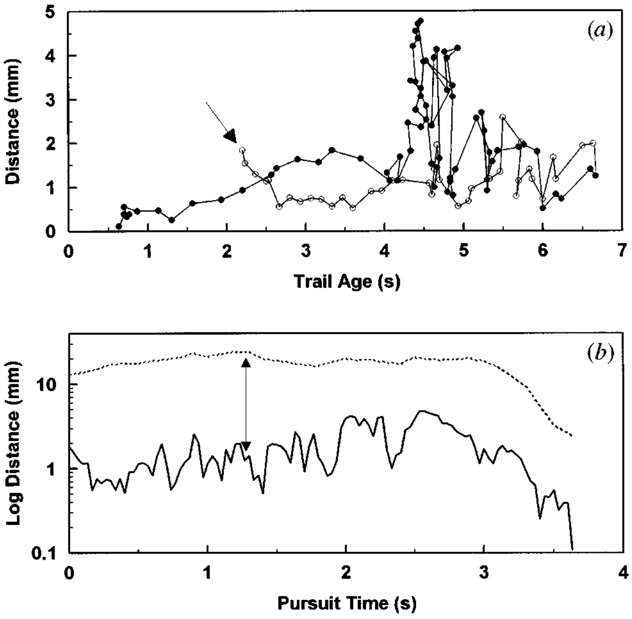

Figure 2. The perceived odour trails of *Temora longicornis*: a male copepod tracking a cruising female. (*a*) The distance of the male from the female trajectory as a function of the age of her trail. The male intersects her trail (arrow) when it is 2.3-s old (open symbols denote when the male goes away from the female), and reverses at 6.7 s (closed symbols denote when the male goes toward the female). (*b*) The distance (logarithmic scale) between the male and female copepod mates (dotted line) compared to the distance of the male from her trajectory (solid line) versus pursuit time. The male begins his pursuit of the female copepods at $t = 0$ s, and ends when he lunges for his mate. Here the male initially went the wrong way and reversed at $t=1.27$ s (arrow).

3. RESULTS AND DISCUSSION

(a) *Mate-tracking by* Temora longicornis

An analysis of signal perception by mate-tracking copepods requires specific details of the temporal and spatial aspects of the behaviour. To provide these details, we represent the observations of Doall *et al.* (this volume) as a function of the following time–space variables: (i) age of trail; (ii) pursuit time of male; (iii) distance between male and female trajectory; and (iv) distance between male and female copepods. We discuss three typical responses exhibited by the copepod *T. longicornis* when mate-tracking: that of a male copepod tracking a cruising female and correctly going toward her (figure 1), that of a male copepod tracking a cruising female where he initially went away from the female (figure 2), and that of a male copepod tracking a hovering female where he again initially went the wrong way (figure 3).

In the first example, the male copepod finds the trail of the female when it is 5.5-s old (figure 1*a*). At this point, the female is 34.2 mm from him (figure 1*b*; Doall *et al.*, this volume). When the male pursues the cruising female, the male maintains a consistent distance of 1 mm from the female trajectory (figure 1*b*). When the male is less than 1 s from apprehending the female, the variability in the track distance decreases as he homes in on the female trajectory and the female herself (figure 1*b*). The distance from the female steadily decreases as the male copepod catches up with the cruising female (figure 1*b*).

In the second example, the male intersects the female trail when it is 2.3-s old (figure 2*a*), at a distance of 1.8 mm from the female trajectory and 13 mm from the female (figure 2*b*). Initially, he goes in the incorrect direction and the variability in his track distance increases. After moving away from the female for 1.27 s, he turns around when the female trail is 6.7-s old (figure 2*a*). When the male corrects his heading, he retraces the trail accurately yet deviates at the point where his intrusion first disrupted the trail. The variability in this track increases and the male's distance from the trail oscillates wildly between 0.5 mm and 5 mm. When he is within 1.5 s from catching up with his mate, the variability in the track distance decreases and the distance between the male and female decreases. When the female is 2 mm from the male, he successfully executes his capture lunge to form the mating pair.

In the third example, the male intersects a 2.1-s-old trail of a hovering female (figure 3*a*). He is only 0.2 mm from the female trajectory and 5 mm from her and yet he goes the wrong way or away from the female (figure 3*b*). For the 2.3 s he goes the wrong way, the variability in his track distance and distance from the female herself increase. He reverses his course when the female trail is 3.9-s old, then locks onto her trail, reducing the deviation in his distance from her trajectory, and closes in rapidly on the female copepod. When he is 1.5 mm from the female copepod, he lunges for her.

Figures 1, 2 and 3 illustrate that as the trail ages, the tracking distance of the male increases to a relatively constant value. For times less than 1.5 s, the distance of

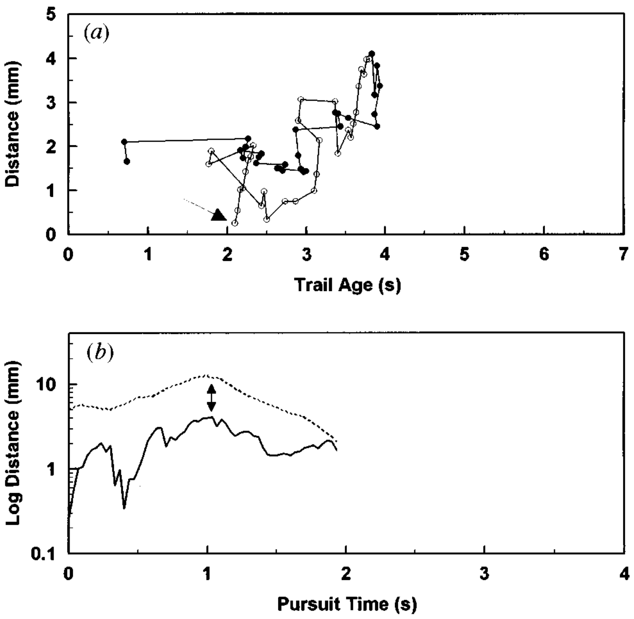

Figure 3. The perceived odour trails of *Temora longicornis*: a male copepod tracking a hovering female. (*a*) The distance of the male from the female trajectory as a function of the age of her trail. The male intersects her trail (arrow) when it is 2.1-s old (open symbols denote when the male goes away from the female), and reverses at 3.9 s (closed symbols denote when the male goes toward the female). (*b*) The distance (logarithmic scale) between the male and female copepod mates (dotted line) compared to the distance the male is from her trajectory (solid line) versus pursuit time. The male begins his pursuit of the female copepods at $t = 0$ s, and ends when he lunges for his mate. Here the male initially went the wrong way and reversed at $t = 1.0$ s (arrow).

the male from the female trajectory decreases rapidly until the final capture lunge at approximately one body length from the female herself.

Given these quantified observations, we now present an analysis of the fluid physics that mediate the transmission of signals, to assess the varying roles of different cues in guiding the male copepod to his mate. By comparing the persistence of odours and of flow within an invisible trail created by the female and detected by the male, we examine the validity of the following hypothesis: the chemical signal mediates trail-following behaviour, whereas the mechanical signal mediates the final approach and mate-capture response.

(b) *Diffusion coefficients*

Our first argument in this analysis of copepod signalling considers diffusion rates. In the low Reynolds number world of copepods, odours often retain their spatial integrity. Viscous forces restrict the advective disruption of odours in algal phycospheres or in the wake of a swimming copepod. Molecular diffusion acts to smear the edges slowly, so that odours appear as discrete trails and not diffuse plumes. In contrast, a fluid mechanical signal is short-lived. The diffusion of momentum is $10^{-2}\,\mathrm{cm}^2\,\mathrm{s}^{-1}$ (Mann & Lazier 1991), whereas the diffusion coefficient for small molecules is $10^{-5}\,\mathrm{cm}^2\,\mathrm{s}^{-1}$ (Jackson 1980). Hence, momentum diffuses 1000 times faster than a chemical signal.

As the male encounters the female trail after 5 s or more (Doall *et al.*, this volume), it is unlikely to be a fluid mechanical signal that provides the initial cue. Analysis of the velocity field of a natural wake shed by a jumping copepod (Yen & Fields 1994) shows a rapid decline in velocity within a few millimetres from the copepod. Furthermore, Van Duren *et al.* (this volume) examined the energy content of a copepod hop and found the energy to dissipate within 0.5 s. Therefore, a velocity gradient will not remain distinct in the fluid at distances in excess of a few millimetres from the passing copepods, or over periods of more than 1–2 s since path creation. In addition, one component of fluid flow, the pressure wave, transmits from a point source radially and linearly (Harris & van Bergeijk 1962; Tautz 1979). The path of the male to the female, however, was highly convoluted. Even when the female was very close to the male, he did not swim directly towards her. Instead, the male faithfully follows the path that she took and eventually finds his mate. These considerations suggest a trail of a chemical nature.

(c) *Long-lived chemical signals*

For a chemical signal derived from an instantaneous point source emitted into still water, we can examine the time needed to diffuse a certain distance as a function of the molecular diffusivity of the chemical molecule (table 1; equations (1) and (2)). Doall *et al.* (this volume) found that the male copepod responded to females that were separated from them by distances of 2.34–34.20 mm (see figures 1–3). If the odour diffused over these distances, it could take between 24.6 min and 81.2 h for the odour molecule to diffuse from the source (the female copepod) to the receiver (the male)! The male cannot be detecting the female as the immediate signal source. He must be detecting something closer, namely the female's trail.

Initially, we assume the trail is liberated around the coordinates of the female (figure 4*a*). At the moment that the male spins to initiate mate-seeking behaviour, the distance of the tracking male from the trajectory of the female ranges between 0.2 mm and 3.5 mm, and this track distance increases to an asymptote with trail age. The offset could be caused by diffusion of the odour from the ageing path of the female. The time needed for a chemical molecule to diffuse to the male ranges between 10 s and *ca.* 1 h (see equation (1) and table 2). As the male finds the female trail within less than 10 s of its formation, it is unlikely that the trail edge has spread only by diffusion. In fact, for the range of times between 0.2 s and 10.3 s when the male found the trail, the estimated distance travelled in these time intervals by a diffusing molecule ranges between 44.7 μm and 203 μm. Thus, the edges of the plume barely change in the 10-s interval. Hence, we conclude that the trail is not exactly coincident with the female's trajectory.

(i) *The invisible trail*

So where is the invisible trail? Qualitatively, observations of the male show he remains below her trajectory. This suggests that her hydrodynamic wake, containing the odour, is formed of water advected and pushed down by her feeding currents and swimming movements (see figure 4*b*). Quantified differences in the z-coordinates,

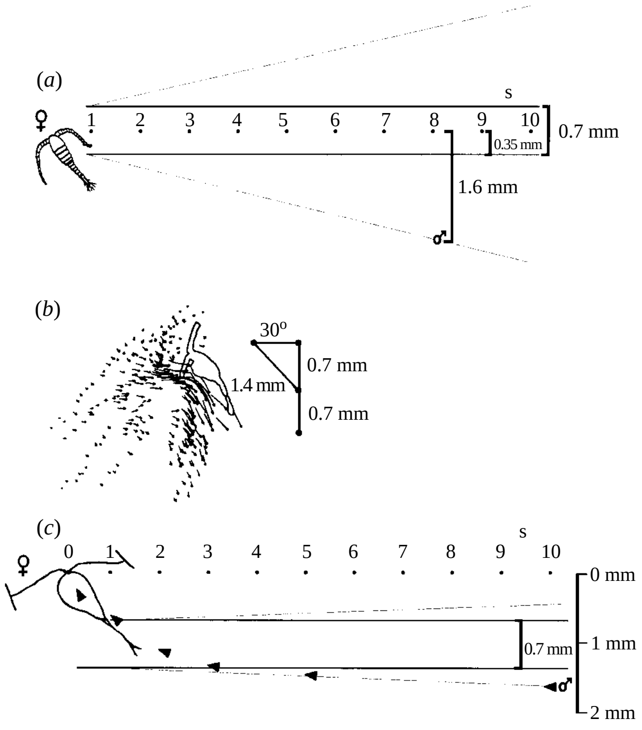

Figure 4. Hypothetical location of the invisible trail of a female *Temora longicornis*. (*a*) Odour trail as the exact trajectory of the female path (filled symbols are the digitized location of the copepod rostrum; copepod drawing from Katona (1973)). The width of the trail is approximated as one body length (0.7 mm) and the edge of trail without diffusion (solid line) is 0.35 mm off the axis of the female trajectory. The location of a mate-tracking male copepod averages 1.6 mm off-axis after 3 s (Weissburg *et al*., this volume). (*b*) Posture and hydrodynamic structure for a swimming copepod. Postural angle is 30° with respect to the path. Location of the copepod urosome, at 0.7 mm below the trajectory, is the presumed upper edge of the odour trail. The influence of the feeding current (upside-down flow field of *Eucalanus*; from Strickler 1982) can be noted at least one body length below the female, and is used to define the lower edge of the odour trail. (*c*) Hypothetical location of trail and observed location of the male tracking the trail. The trajectory of the female represented by the digitized point (filled symbol) on the rostrum of the female. The trail (solid lines) is 0.7 mm wide and is placed one body length below the female trajectory. After 10 s, the lower edge of the trail diffuses 0.2 mm (dotted line). The male's location (triangles) is shown with respect to the diffusing edge.

along with visual examination on the computer, of the rotated full three-dimensional trajectories of the male with respect to the female trail, show that he is almost always below the female (J. Yen, M. J. Weissburg and M. H. Doall, unpublished observations). To proceed with our physical analysis, we estimate the most likely physical location of the trail (figure 4*c*). By comparing the location of this trail to the location defined by the mate-tracking male's distance from the female, we can test the validity of the hypothesized structure and location of the trail.

Trail edges

Profiles of copepod feeding-currents (Strickler 1982; Tiselius & Jonsson 1990; Yen *et al*. 1991; Fields & Yen 1993; Bundy & Paffenhöfer 1996; Yen & Strickler 1996), show that the flow follows the dorsal surface closely, shedding entrained water off the urosome. This water may gather secretions from glands located over the surface of the body (e.g. Strickler 1975), as well as excretions from the anus located at the end of the urosome. To define the upper edge of the trail, we determine the location of the urosome. Many copepods swim with their body axis orientated at an angle with respect to their paths, and Weissburg *et al*. (this volume) found that the hovering females of *T. longicornis* were orientated at 37°, while the fast swimming, cruising copepods were orientated at 9°. If the trail-making copepod is orientated at 30° with respect to the trail direction, the urosome would be 0.7 mm below the location of the tip of the rostrum, the digitized point defining the female trajectory (figure 4*b*). On the ventral surface, much of the flow from the feeding current can be wider, influencing water up to an additional body length below the copepod. We can approximate the width of the trail to be one body length, delineated by the outer limit of the flow field of *T. longicornis* near the distal tip of the paired antennules (Yen & Fields 1992; Tiselius & Jonsson 1990). This limit is similar to the width of the hydrodynamic wake of a cruising copepod denoted by the steep velocity-gradient (Strickler 1982).

Trail location

Let us assume that the original trail is 0.7 mm wide, with the upper edge being 0.7 mm below the female's digitized trajectory. If the lower edge of the trail is 1.4 mm at $t=0$, it will diffuse outwards by 0.2 mm in 10 s (figure 4*c*; table 2). Therefore, if the edge-detecting male copepod was following the odour trail, at 10 s it could be approximately 1.6 mm from the trail. This is indeed the average observed distance (1.57 ± 0.18 mm (95% confidence interval; $n=426$); Weissburg *et al*., this volume) of males from female trails older than 5 s. For trails older than 2 s, the male maintains an average distance from the female trajectory that approximates the location of the diffusing edge. For trails less than 2-s old, the location of the male is close to the central axis of the trail or within the plume. At trails less than 1-s old, he is less than 0.2 mm from the female trajectory or within the spatial resolution of the digitized video-image. For fresh trails, the male no longer follows the diffusing chemical trail and instead follows the female herself.

According to our fluid physical calculations, this asymptotic distance represents the diffusing edge of the trail. Therefore, the male copepod appears to be sensing the chemical trail. It is possible that the location or structure of the trail may be different from that described here, or that the source could be a secretory gland on the head (but see text explaining figure 4*a*) and not on the urosome. However, if the origin of the trail is placed on the head or at a very different location than one body length below the female trajectory, it would require higher levels of turbulent diffusion to explain the transport of the odour molecule to the location in which the male detects it. Such rates of diffusive mixing could eliminate the gradient and preclude trail-following. The evident close tracking of the trail by the male indicates a clear lack of disturbance of the trail, which therefore conserves the information in the female signal.

Table 2. *Calculations of characteristic diffusion times t_D and lengths r_D affecting the size and odorant concentration of copepod excretory patches and plumes*

(t_D: from equation (1); r_D: from equation (2); R is the width of odour patch, initially estimated as width of copepod; L is the length of odour patch, initially estimated as length of copepod; V is the volume of odour patch from equation (4); volume of hop from Van Duren *et al.* (this volume); $\langle C \rangle$ is the concentration of an amino acid, a possible chemical stimulant; % is the per cent of original chemical concentration in: * a copepod-size patch; and ** a 100 μm odour plume (Atema 1988).)

t_D(s)	r_D(μm)	R(cm)	L(cm)	V(cm^3=ml)	$\langle C \rangle$ (M)	%*	%**
0	—	0.0250	0.100	2.0×10^{-4}	1×10^{-5}	—	—
1	63	0.0313	0.126	3.5×10^{-4}	5.7×10^{-6}	57%	90%
2	89	0.0339	0.118	4.3×10^{-4}	4.7×10^{-6}	47%	—
3	110	—	—	—	—	—	—
5	140	0.0390	0.128	6.1×10^{-4}	3.3×10^{-6}	33%	—
10	200	0.0450	0.140	8.9×10^{-4}	2.2×10^{-6}	22%	10%
15	245	0.0500	0.149	1.2×10^{-3}	1.7×10^{-6}	17%	—
140	750	—	—	—	—	—	—
250	1000	—	—	—	—	—	—
1000	2000	0.2250	0.300	4.8×10^{-2}	4.2×10^{-8}	0.4%	0.1%
		hop		76.9	2.6×10^{-11}	10^{-5}%	—

(ii) *Trail diffusion*

Bossert & Wilson (1963) use the behaviour of ants to define the location and presence of odour molecules that mediate ant behaviour. In their table 1, they derive the value of D for the ant pheromone diffusing and volatilizing into air, thus presenting the case for instantaneous emission in still air. Here, we have used the behaviour of copepods to define the location of the odour trail. The distance of the male from the female trajectory represents the diffusing edge of the female's odour trail. By monitoring how the trail expands over time, we obtain an estimate of D, the diffusivity coefficient of the chemical in the trail. As the movement of the trail-makers and trackers result in $Re < 10$, the consequences of eddy diffusivity (Okubo 1971; Csanady 1973) is considered absent in our still-water observation vessels; laminar flow is assumed (i.e. the ambient fluid is at rest). Therefore, the time change in the location of the trail, delineated by the location of the male with respect to the female trajectory, should represent a diffusion phenomenon. If figure 5 is modelled by equation (2), we obtain a value of $D = 1.45 \times 10^{-3}$ cm^2 s^{-1}, that is higher than the molecular diffusion coefficient of small molecules (10^{-5} cm^2 s^{-1}). The value of D suggests, as Bossert & Wilson (1963) offered for the ant trails, that this coefficient does not describe diffusion in a perfectly still fluid medium, but includes transport mechanisms distributing odorants resulting from turbulent diffusion. When the male retraces his route along the path he has previously disrupted (figures 2 and 3), we do see wider casts than when he is on an undisturbed trail.

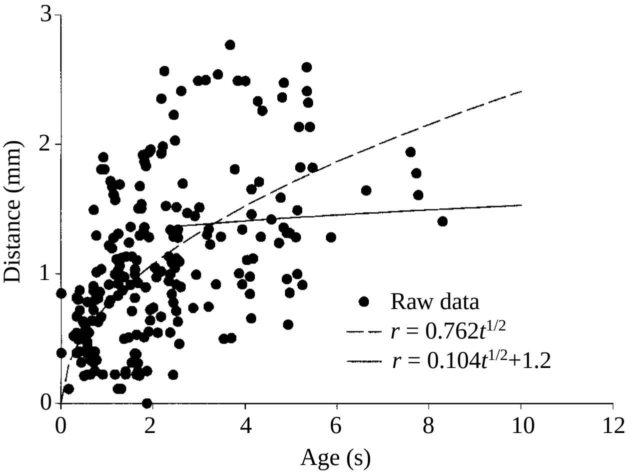

Figure 5. Theoretical model of diffusion of the odour trail edge of *Temora longicornis* where r is the distance (mm) and t is the age (s). The diffusion coefficient D is derived from the distance of the male from the exact path of the female at different trail ages. The model shows that when all the data were included, the diffusion coefficient $D = 1.45 \times 10^{-3}$ cm^2 s^{-1} (equation $r_D = \sqrt{[4Dt]}$, $\sqrt{(4D)} = 0.762$, s.e. $= 0.032$, $r = 0.71$, significant below the 0.001% level for $n = 221$; raw data from Weissburg *et al.*, this volume). For times greater that 1.5 s, we adjust the y-intercept to $r_0 = 1.2$ mm which approximates the location of the trail's diffusing edge at 1.3 mm at 1.5 s. The diffusion coefficient D is 2.7×10^{-5} cm^2 s^{-1} (equation $r_D = \sqrt{[4Dt]} + r_0$; $\sqrt{(4D)} = 0.104$ for $t > 1.5$ s, s.e. $= 0.003$, $r = 0.167$; significant at the 5% level for $n = 137$).

We propose that in this situation, the graph of the relation between male track distance and trail age (figure 5) represents two phenomena: that of molecular diffusion for trail ages greater than 1.5 s and that influenced by a different signal for young trails. For trail ages greater than or equal to 1.5 s, the value of D is 2.7×10^{-5} cm^2 s^{-1}. The shallow slope of the upper line more closely represents the slow process of molecular diffusion of the edge of the chemical plume. By using the distance of a copepod from the trail as the radius of the sphere describing the physiological–behavioural threshold surrounding the source, we can estimate D, and such values of the diffusion coefficient may provide a measure of the molecular weight of the chemicals signalling trail-following.

(d) *Short-lived fluid mechanical signals*

For trails less than 1–2-s old, the relation between track distance and trail age (figure 5) has a much steeper slope, and intersects zero when the male captures the female to form the mating pair. It appears that when the trail is fresh, another signal influences male behaviour. When the male copepod follows trails younger than 1–2-s old, decreases are noted both in the distance he is from the trail

Table 3. *Evaluation of the signal strength of a fluid mechanical signal of the female copepod*

(Using the theoretical dipole equation (8) and the equation (9) fit to empirical data for the attenuation of flow speed from a small water jet designed to mimic the hydrodynamic wake shed by a moving copepod. Swimming speeds of hovering and cruising copepods are used to represent water flow speeds. U_0, flow speed of source is swimming speed of female copepod (from Weissburg *et al.*, this volume); R, distance from source that a certain flow speed occurs, from equation (8); t, time since flow initiation that a certain flow speed occurs, from equation (10); B, behavioral threshold ($2\ \mathrm{mm\,s^{-1}}$) (Yen & Fields 1994); N, neurophysiological threshold $= 20\ \mu\mathrm{m\,s^{-1}}$ (Yen *et al.* 1992).)

female behaviour	cruise	hover
U_0 (mm s^{-1})	6.56 ± 1.77	3.73 ± 1.01
R_B (mm)	1.4	1.2
R_N (mm)	6.9	5.7
t_B (ms)	915	645
t_N (min)	8.7	8.7

and the variability in this distance. For young trails, the standard errors track distances of males following fast-swimming females are half those of males following slow-swimming females (table 1 in Doall *et al.*, this volume), suggesting an effect of female swimming speed. For older trails, there is no correlation of the male's initial distance from the trail with female swimming speed, which is further support of initial detection of the trail being chemically mediated. On fresh trails, the male appears sure of where the trail is. When he is within one body length of the female, he appears sure of where she is. The successful capture indicates that the male copepod was able to locate the female accurately in three-dimensional space.

(i) *Theoretical model of flow signal: dipole source*

Why does the male home in on the exact female trajectory when the trail is less than 1-s old? We hypothesize that an additional cue is now detected by the copepod. This is the fluid mechanical cue that persists because the female, when swimming, advects a mass of water nearly equivalent to her own mass and at a speed similar to her own. In order for the fluid mechanical cue to be detected, the speed of water flow must be above the threshold of mechanosensory setae, which can be estimated from behavioural responses (table 3). The behavioural threshold for prey capture requires at least 2 mm s^{-1} of flow speed (Yen & Fields 1994). The threshold for subtle movements involved in the orientation response may be smaller. The neurophysiological threshold at 20 μm s^{-1} (Yen *et al.* 1992) is much lower than the behavioural threshold, as has been documented for mechanoreceptive responses of crayfish (Ebina & Wiese 1984).

To determine if females swim at speeds sufficient to produce a signal detectable to the male, we examine their original swimming speeds which is presumed to be the speed of the consequent water flow. The female copepod swims at an average speed of 5 mm s^{-1} (3.73 mm s^{-1} and 6.56 mm s^{-1} are the speeds of cruising and hovering copepods shown in table 3). If the flow attenuates as distance to the −3 power (equation (8), Kalmijn 1988), the neurophysiological threshold is found 6.3 mm from the female. At this location, the male is within 1–2 s of apprehending the female, and as her flow becomes perceptible he may be alerted to her presence. At distances of less than 1.4 mm, flow velocities due to the motion of the female swimming are greater than the behavioural threshold of 2 mm s^{-1} (table 3). The rapidly increasing strength of the intensity of the fluid mechanical signal provokes the obvious behavioural response of the male to leap and capture his mate.

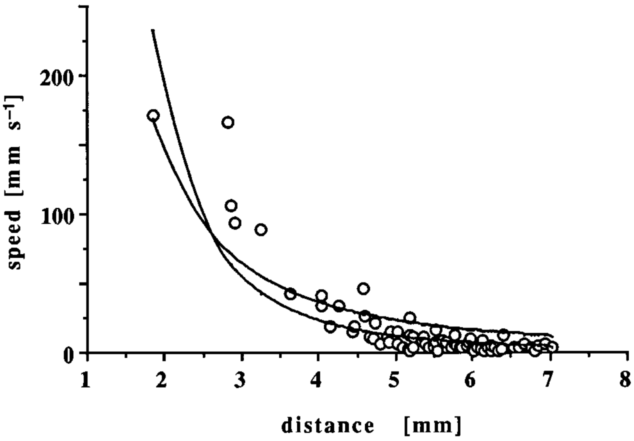

Figure 6. The decline in the speed of a water jet emanating from a pipette with a 200 μm mouth opening created by a pressure of 5 psi and a pulse duration of 4 ms (J. Yen and D. Fields, unpublished data). The data were fit to two models: $U_t = 1495\,r^{-3}$; s.e. = 94; $r^2 = 0.712$ (upper curve at 2 mm) and $U_t = 584\,r^{-2}$; s.e. = 36; $r^2 = 0.715$ (lower curve at 2 mm). The third-order equation was used to estimate the distance travelled by the water jet. By multiplying by the speed, the time it took for the flow speed to attenuate was estimated. This water jet was selected to mimic the wake shed by a small copepod. The flow speeds analysed were that part of the curve showing similar magnitudes to those observed in nature (*ca.* 5 mm s^{-1}).

(ii) *Empirical measurements of flow attenuation*

Empirical measurements were taken of the reduction in flow speed of a fine microjet of water, designed to mimic the speed and structure of a natural wake shed by a copepod (figure 6, from Yen & Fields 1994). Here, the flow also slowed as a function of R^{-3} (equation (9)). It takes 810 ms for a 5 mm s^{-1} flow, shed by the female copepod swimming at this speed, to decay to 2 mm s^{-1} (equation (10), table 3). This flow speed is the behavioural threshold for the capture response. The orientation response may have a lower threshold, such as 1 mm s^{-1}, which would be detectable after more than 1 s. These physical considerations show that for times of less than 1 s, the intensity of the fluid mechanical signal increases rapidly with decreasing distance from the source: the female copepod. The response to this strong fluid mechanical signal as well as the intense odour signal is observed in the male copepod's ability to continue swimming down the trail, taking precisely the same trajectory as the female. The linearity of the transmitted component of water flow can influence the final straight-line directed leap the male takes to capture his mate. Information about both direction and proximity was obtained by using both sensory modalities.

(iii) *Reactive and perceptive distances*

The reactive distance is defined here as the distance between the receiver (the male copepod), and the signal source (the female). This distance varies in the selected mating events, from 2.3 to 34.2 mm (figures 1, 2 and 3; Doall *et al.*, this volume). It is not the same as the perceptive distance, defined here as the distance to the signal. Signal perception still occurs within 1–2 body lengths (BL): the female trail is 1–2 BL from the male upon perception for subsequent mate-tracking behaviour; the female is 1–2 BL from the male upon perception for subsequent mate-capture behaviour. This is similar to the perceptive distances in prey–predator interactions (Yen 1988; M. H. Doall and J. Yen, personal observations).

(d) *Chemically mediated behaviour in trail-following copepods*

In the following sections, we examine the hypothesis that chemical gradients mediate specific responses within the trail-following behaviour of the copepod *T. longicornis*. These responses include: trail discovery and trail loss, directionality of trail-following, and detection of the edges and end of the trail.

(i) *Trail location: across-plume gradient*

When the male finds the trail, he spins and exhibits rapid casting behaviour. What aspect of the trail allows him to detect its presence? One explanation involves the response to sharp gradients. When a male crosses a trail, the concentration goes from the background level to possibly 10^4 times the background level. An amino acid concentration change of this magnitude is detectable by aquatic crustaceans (Carr & Derby 1986; Carr 1988; Derby & Atema 1988; Zimmer-Faust 1989). As most animals respond to large changes in signal intensity, a loss of this signal can also elicit a response. We notice that when the male loses the trail, he again spins and exhibits increased casting behaviour. Fryer (1957) noted the spirals of cyclopoid predators when their prey was lost. A circular swimming pattern in a concentration gradient of a stimulant would result in a sinusoidal variation in the signal intensity (Kittredge *et al.* 1974). They observed that the swimming behaviour of *Labidocera* described a curtate cycloid with the ratio of the major to the minor radius being a function of the intensity of the gradient, and suggested that this behaviour indicated some power of spatial orientation and short-term memory in this copepod.

In addition to copepods, other planktonic organisms show spinning behaviour when contacting or losing contact with an odour, either in the trail or directly on the object of desire. Rotifers spin when contacting the female (Snell *et al.* 1995). Shrimps spin when losing the food trail (Hamner & Hamner 1977). Frequent changes of direction are displayed by krill (Price 1989), copepods (Buskey 1984), and larval crabs (Weissburg & Zimmer-Faust 1991), when entering a patch of odour. According to Benhamou (1992), variations in sinuosity and speed can improve the efficiency of area-concentrated searching behaviour in a patchy environment. Dusenbery (1989) calls the behaviour of frequent turns 'fixed action patterns'. The interaction of the male copepod with the female path, and ultimately with the female copepod herself, has defined one of these patterns in zooplankton.

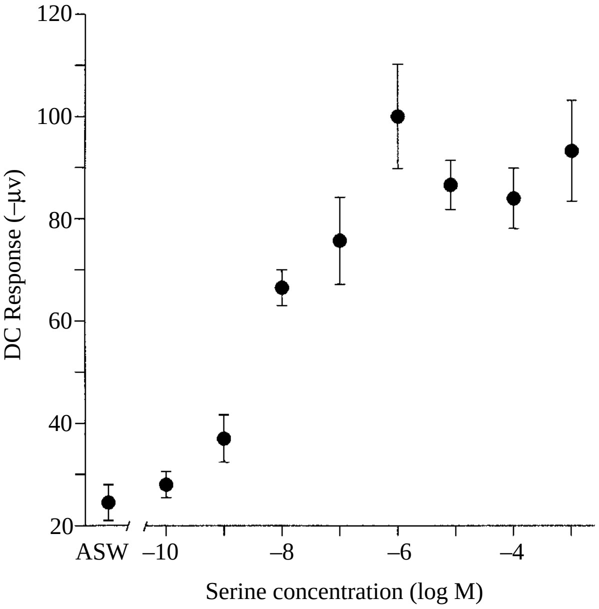

Figure 7. Dose response functions of *Undinula* sp. to serine, an amino acid. Represented are the values for the magnitude of shift in the DC recordings as a function of serine concentration, with standard errors of 5–10 replicates, taken from electroantennagrams of copepods, using a technique developed for insects by White (1991) and Schneider (1963), and modified for aquatic copepods by M. J. Weissburg and J. Yen (unpublished data). The linear portion of this curve denotes the range in odorant concentrations (between 10^{-9} and 10^{-6} M) that can be most finely discriminated. In this region of the curve, small changes in odorant concentrations elicit strong variations in evoked neural reponse.

(ii) *Trail direction and backtracking: along-plume gradients*

When a male copepod intersects the female trail, he detects it quickly. Yet 40% of the time, he goes down the trail the wrong way (Doall *et al.*, this volume). Further consideration of odorant gradients provides plausible mechanisms for this behaviour. Along the trail, patches of odours are adjacent to patches of similar concentrations of female odorant. This results in an along-plume gradient that is much weaker than the across-plume gradient and consequently, it can be difficult to determine the gradient direction.

When a male makes a wrong turn, he swims away from the female until the trail is 4–5-s older (figures 3 and 4), and then corrects his heading. Within 4–5 s, the patch volume increases by three times, thus diluting the concentration (table 2). A concentration change of this magnitude can be perceptible, particularly if the concentration range falls within the linear region of the dose–response curve (figure 7) of a population of chemosensors (Derby & Atema 1988). Further selective degradation or bacterial uptake also may alter the blend of compounds (if the signal is a mixture), rendering the chemical signal less active and resulting in an amplified decrease in its stimulating capacity (Tamaki 1985). Thus, the sensitive chemoreceptors on the copepod may be able to detect this change in odorant concentration and he may thereby correct his mistaken heading. This reversal and back-tracking behaviour strongly suggests that copepods determine polarity from the odour gradient. When the copepod swims in the incorrect direction, the swimming behaviour widens and becomes more like pre-tracking behaviour.

Other organisms also find and follow chemical gradients, displaying different movement patterns. Bacteria exhibit up-gradient swimming, with less frequent turning, that is clearly different from down-gradient swimming, which is indistinguishable from swimming in isotropic solutions (Berg & Brown 1972). By moving in two modes—run and tumble—bacteria transform the problem of sensing spatial gradients to one of sensing temporal concentration changes (Jackson 1989). As Edelstein-Keshet (1994) described for the moving ant, the pheromone is a volatile substance painted on the path which diffuses and creates a corridor of scent, and can be sensed by paired antennae for which there is a keen but finite sensitivity of the pheromone receptors; thus, errors such as losing a trail, or turning towards the direction of decreasing pheromone strength, occur. Holldöbler & Wilson (1991) comment on how order is created from disorder when ants repeatedly follow the trail and thus amplify the directional signal.

Animals following odour signals may employ solely chemical cues, or use chemical cues in conjunction with signals derived from other sources. For snails, direction is determined in part from the macro-gradient of the chemical (Gilly & Swenson 1978). Shrimps only use the chemical to tell them there is a trail, with a consequent simple response of swimming down trails as long as 20 m (Hamner & Hamner 1977). These organisms rely heavily on chemical information, while other organisms also rely on cues that collimate the stimulus (Dusenbery 1991). For example, when blue crabs detect odour plumes, the presence of flow acts to polarize olfactory-guided locomotion in the up-current direction (Weissburg & Zimmer-Faust 1994). Snakes detect polarity from the placement of remnant odours asymmetrically on stones in the path (Schwenk 1994). Physical chevrons in the mucus trail of snails provide a collimating directional cue (Raftery 1983; Stirling & Hamilton 1986). Thus, we see again that trail-following in the copepod is similar to terrestrial (two-dimensional) systems, where chemical signal intensity alone is the definitive cue, but different from other (predominantly marine) systems that rely on odour in conjunction with other types of signals.

(iii) *Edge detection*

The ability to detect edges may employ orientation behaviour to place sensors into two different concentrations. By increasing the span of the sensor, the copepod can compare a spatially wider gradient, and also possibly a weaker one. Sandeman *et al*. (1993) have suggested that long chemosensory or mechanosensory appendages (and corresponding increases in the size of particular regions in the brain), may be associated with processing odour (and/or mechanosensory) information in spatially complex habitats. Hence, sensors with large spans may permit increased spatial resolution of chemical signals, as has been postulated for the forked tongue of snakes (Schwenk 1994). Schwenk found that snakes which have deeply forked tongues use this sensor to detect trails left by wide-ranging prey, whereas snakes with blunt tongues do not follow trails and tend to be more 'sit-and-wait' predators. Similarly, the long, paired antennules of the calanoid copepod *Temora* can detect trails, allowing the copepod to remotely detect wide-ranging mates in a three-dimensional ocean. Harpacticoids, with their stubby antennules, may rely more on contact pheromones (Frey *et al*., this volume), and their movements are restricted more or less to the two-dimensional world of meiofauna. Upon contact, perhaps these body-bound pheromones are aphrodisiacs, as found for salamanders (Arnold 1977; Arnold & Houck 1982), persuading the organisms to engage in sex.

When a trail is fresh, the edge is sharp and the steep gradient can be perceived easily. Over 10 s, the edge diffuses 200 µm. The weaker chemical gradient may not be as easily detected for a limited sensor span. In many male copepods, the proximal quarter sector of the antennule is crowded with chemosensors (see Boxshall & Huys, this volume), and odours produced by female copepods collect on proximal antennulary aesthetascs for *Calanus pacificus* (Griffiths & Frost 1976). The span of *T. longicornis*' antennules is approximately 1 mm. Chemosensors may cover 10% of the proximal sectors of the antennules over a span of 100 µm (Fleminger 1967, 1985; Griffiths & Frost 1975; Huys & Boxshall 1991; Boxshall *et al*. 1998), which is less than the width of the diffused edge. If detection relies on the arrays of sensors sensing one concentration different from the other, the edge may not be detected immediately by the copepod, because the sensors cannot compare concentration in and out of the plume at the same time. This approach takes the edge as a defined separate entity, requiring simultaneous signal detection. In reality, the edge of a chemical patch is a gradient and can be detected by moving the sensors through the gradient.

(iv) *Trail's end: threshold detection levels*

In our behavioural analyses (Doall *et al*., this volume; Weissburg *et al*., this volume), trails older than 10 s were rarely followed. By using physical analyses, we can determine how the signal changes in this 10-s interval. If we consider the signal as a patch released at a moment in time along the path and left there to diffuse by molecular forces, a copepod-size odour patch would increase in size by 4.5 times in 10 s, from a volume of 2×10^{-4} ml to 8.9×10^{-4} ml (table 2). This would dilute the odorant signal to 22% of its original level.

The signal shed by a swimming copepod can also be defined as a trail, rather than a patch. Models employing a more continuously emitted plume from a source, yield the following results based on relations determined for heat flow (equation (3) from Atema 1988; citing Carslaw & Jaegar 1959). Considering a 100 µm plume left by a copepod, after 10 s, the concentration would be 10% of the original. Taking the neurophysiological detection threshold for the amino acid, serine, determined with electroantennograms to be around 10^{-9} M (figure 7), the original concentration could be back-calculated to 4.5×10^{-9} for the patch or 10^{-8} M for the plume. However, as behavioural thresholds are most commonly 1–3 orders of magnitude greater than physiological thresholds (Derby & Atema 1988), a more conservative approach would be to assume that the lower limits of detection are in the order of 10^{-7} M so that the concentration released by the female can be at a level of 10^{-6} M. In either case, these concentrations are still well within estimates for concentrations released by zooplankton or around swarms, or found to stimulate swarming behaviour (10^{-3} to 10^{-8} M: Williams & Muir 1981; Poulet & Ouellet 1982; Wheeler 1983; Poulet *et al.* 1991). Thus, production of an amino acid odour trail may be possible, although we cannot rule out the existence of more specific signal molecules from other chemical classes.

(v) *Hops*

When a female hops, the volume of the wake increases to 76.9 ml (Van Duren *et al.*, this volume). This is 10^5 times the volume in the cruising copepod's trail (table 2). The resulting extreme dilution of the chemical signal may explain, in part, the loss of the trail by the male at this point. Van Duren *et al.* note that the hop dissipates within 0.5 s. Therefore, a fluid mechanical signal and its directionality would only be registered if the male crossed her path soon after the hop. From our observations (Doall *et al.*, this volume; Weissburg *et al.*, this volume), we know when and where the male loses the trail because he begins showing the wide, fast casts of sharp turns. At this point he is 2.2–3.2 mm from the place where the female hopped. Her hops, occurring 1–3.5 s prior to his arrival, were at speeds of 30–50 mm s^{-1}. The flow from her hop will attenuate to 4.6–10 mm s^{-1} at the location where the male hops off the trail (equation (9)). Over time (equation (10)), the flow will decay further to 0.8–2 mm s^{-1} in the interval between hop occurrence and the male arriving at the hop location. These flow speeds are close to the behavioural threshold found for eliciting the antennular flick to turn and reorient the copepod (Yen & Fields 1994). The female's motion causes a change in the intensity of signals of the two modalities: the hop dilutes the odour signal beyond recognition, while the flow speed of the hop evokes a fluid-mechanically mediated reflex of the male to reorient. The male loses the trail because of these changes in signal properties.

(e) *Trail structure and odour response*

In the following sections, we examine the hypothesis that the intensity of the female odour signal elicits a graded response, expressed behaviourally as increases in the male's swimming speed.

(i) *Wake volume and trail structure: velocity and odour gradients*

When an animal swims through the water at different speeds, particular hydrodynamic patterns are formed in its wake (Yen & Strickler 1996). These patterns carry signals and convey information to those that cross the trail and who are equipped with sensors to detect the fluid mechanical and chemical cues. To understand the consequence of swimming behaviour on signal structure, we first provide a description of the swimming behaviour.

The swimming patterns of copepods could be defined in a manner similar to the gaits of a horse: walk, trot, canter, and gallop. The analogous sequence of movement patterns of a copepod: hovering, cruising, hops, and escapes result in faster forward motion with each successive gait. During mate-tracking, we saw two distinct gaits of the female copepod: hovering (upright posture, slow swim speed), and cruising (body axis parallel to the direction of motion, faster swim speed). These swimming styles can create wakes of different volumes. With Schlieren optics, we see that the hovering wake has a much larger volume than the slim, trim wake following the cruisers (Yen & Strickler 1996). The cruiser's wake more closely resembles the laminar flow around a cylinder at an *Re* of approximately 1. The volume in a cruiser's wake is estimated to be approximately its body volume. The volume in the hoverer's feeding current can be 175 times larger, as found for *Pleuromamma* (Fields & Yen 1993), or about two orders of magnitude larger. That gives an estimate of the volume of water into which the female excretes a certain amount of odorant. As Strickler & Hwang (1998) summarized, the hydrodynamic disturbances mix the chemicals, but as the disturbances are short-lived, the turbulence cannot diffuse chemicals further than the animal's linear dimensions. Perhaps the feeding current serves in a limited fashion to disperse the pheromone, as noted for the ventilation currents of Asian moths (Wunderer *et al.* 1986).

If a fixed amount of chemical is released by the copepod, we can estimate odorant concentrations. As we do not know the identity of the odorant, we could not measure its concentration. Instead, we used literature values for the concentration of amino acids, a possible stimulant (Poulet & Martin-Jezequel 1983; Poulet & Ouellet 1982; Poulet *et al.* 1986). The background concentration of amino acids in seawater is 10^{-10} M, a concentration of 10^{-6} M has been found to elicit swarming behaviour in copepods, and an intracelluar concentration can be 10^{-3} M (McCarthy & Goldman 1979; Wheeler 1983; Carlucci *et al.* 1986; Poulet & Ouellet 1982; Poulet *et al.* 1991). We suggest that the concentration in the thin trail of a single copepod's wake is 10^{-5} M. The concentration in the thick wake of a slowly swimming, hovering copepod can be two orders of magnitude less or 5×10^{-8} M. Because a hovering copepod swims at half the speed of a cruising copepod, the concentration of amino acids accumulating over the same period may be doubled. The male responds to these odorant levels with a graded behavioural response. Fast pursuit speeds are elicited at the high odour concentration and slow pursuit speeds at the low odour concentrations (table 4).

As Gill & Poulet (1988) documented, the addition of mixtures of amino acids can cause an average of a 1.2-fold increase in the beat frequency of the antennae, the locomotory appendages largely responsible for the resultant translation of the copepod while swimming. Hamner & Hamner (1977) found that a shrimp increased its speed by a factor of three when following a food trail. This suggests that when the stimulus concentration increases, more sensors are activated and/or each sensor is firing more intensely. The increased neural response triggers a larger motor response, here manifested as higher swimming speed. Such relations have been observed in blue crabs (Weissburg & Zimmer-Faust 1994), and measured for larval crabs (Weissburg & Zimmer-Faust 1991). If this relation holds, it may be possible to use copepod swimming speed as a quick indicator of the concentration of certain odorants in the sea that exist at levels below those detectable by conventional man-made probes, or that occur in patches much smaller in volume than those normally sampled by

Table 4. *Effects of behaviour and swimming speed on odour concentration, boundary layer thickness, δ, surrounding a setal chemosensory fibre on a copepod antennule, and the diffusion time, t, of a small chemical molecule through this layer*

behaviour of male	non-tracking	hover-tracker	cruiser-tracker
male swim speed (mm s^{-1})[a]	9.5	16.69 ± 4.16	27.55 ± 7.77
behavior of female	absent	hovering	cruising
female swim speed (mm s^{-1})[a]	5.9	3.73 ± 1.01	6.56 ± 1.77
odour patch size	eddy size *ca.* 1 cm[b]	175 × copepod vol.[c]	copepod vol.[d]
odour concentration	10^{-10} M[e]	5×10^{-8} M[f]	10^{-5} M[g]
Re (seta)[h]	1.9×10^{-2}	3.3×10^{-2}	5.5×10^{-2}
δ_1 (μm)[i]	14.5	10.9	8.5
δ_2 (μm)[j]	5.8	4.4	3.4
t_1 (ms)[k]	52.6	29.7	18.1
t_2 (ms)	8.4	4.8	2.9
male speed/female speed	1.61	4.5	4.2
male speed/normal speed	—	1.76	2.91
factor increase in δ	—	1.33	1.7
factor decrease in t	—	1.8	2.9

[a] Average copepod swim speeds taken from table 1 in Weissburg *et al.*, this volume.
[b] Mann & Lazier 1991.
[c] Fields & Yen 1993.
[d] Initial odour patch size.
[e] Background concentration.
[f] 1/175 of [g], or approximately two orders of magnitude less.
[g] Excreted concentration: range (10^{-3}, 10^{-6}) M.
[h] Reynolds number from equation (7) for a copepod seta is *ca.* 2.5 μm wide.
[i] Thickness of boundary layer according to equation (5).
[j] Thickness of boundary layer according to equation (6).
[k] Characteristic diffusion time from equation (1).

such probes. The copepod may be useful as a biosensor of the small-scale spatial distributions of chemical odours.

(ii) *Boundary layer thickness and reaction times*

When the male increases his swimming speed in response to odours, the boundary layer surrounding his sensors thins. Therefore, it will take less time for the signal molecule to diffuse to the surface of the aesthetascs housing the receptors. Unsheathed chemoreceptors communicate with the external environment through pores in the protective chitinous wall of the aesthetasc (Friedman & Strickler 1975). Diffusion through the viscous sublayers or boundary layer to the receptor is sometimes the rate-limiting step in stimulus transport (Dusenbery 1992). With a neural conduction velocity of 1 m s^{-1} or a reaction time for a 1 mm copepod of 1 ms, the diffusion time provides a good measure of reaction time. Here, we make estimates of the width of the viscous boundary layer that surrounds the receptors of the male copepod, not the thinner concentration boundary layer which would describe the solute distribution around the female.

In pre-tracking sequences, the male normally swims 9.5 mm s^{-1}, which is faster than the female. When he intersects the female trail, he accelerates to 16.7 mm s^{-1} and 27.6 mm s^{-1}, which are 4.2 and 4.5 times the speeds of the female hoverer and cruiser, respectively. When the male accelerates to 1.8 times his speed to follow a hoverer, his boundary layer thickness decreases by a factor of 1.33, from 14.5 μm to 10.9 μm, and the diffusion time decreases by a factor of 1.8, from 52.6 ms to 29.7 ms. When the male accelerates to 2.9 times his speed to follow a cruising copepod, his boundary layer thickness decreases to 8.5 μm and the diffusion time decreases to 18.1 ms. By doubling his speed to follow hovering females, the diffusion time is cut in half. By tripling the speed to follow the cruisers, the diffusion time is one-third the time for normal non-tracking male copepods. The shortened reaction times appear to improve the male's ability to adjust his orientation more quickly over shorter reaches when following the fast female, as confirmed in kinematic analyses (Weissburg *et al.*, this volume). When following a slower female, the broader reaches he takes may reflect the longer times needed to react at these swimming speeds. Thus, by expending the energy to accelerate to speeds faster than the female's, not only is the male able to catch up to the female, but his sensory capability is improved. The male copepod gains an advantage of a significant reduction in the time needed for the pheromone to diffuse to the receptor, thus shortening his reaction time.

The boundary layer may be especially thin around the proximal chemosensors located within the high velocity region of the feeding current (Boxshall *et al.* 1997), promoting a good exchange of fluid adjacent to the sensor. Furthermore, as the boundary layer thins to 3.4–10.9 μm (table 4), the flow may pass between some of the 30–50 μm long fibre-like sensory hairs, that are 2–3 μm thick with gaps of 10–50 μm. Considerations according to Koehl (1993) show that the fence of sensory fibres can be 'leaky' in some sectors of the antennule. (At $Re = 10^{-2}$ for a gap–setal width ratio of 5 : 25, leakiness changes from 10% to 30%; Koehl 1993.) The flow passing between the sensors then carries water-borne cues closer to the sensor's surface. In moths, flow passing through the filter can improve signal perception (Kaissling 1971). In copepods, the characteristic spin may function like the flick of a lobster antenna, sampling a new odour-laden parcel of fluid (Schmidt & Ache 1979).

4. A NEW MODEL OF MATE LOCATION IN *TEMORA*

Our detailed studies of copepod behaviour and the fluid physics of signal transmission, type and structure, have revealed an interplay of forces that sculpt copepod behaviour, and the adaptations that sharpen a copepod's ability to find mates in a low *Re* fluid environment. There are two main conclusions drawn from this study which address (i) sensory modalities; and (ii) the role of fluid physics. We consider how these factors influence the timing and spatial location of mating events in the vast sea.

(a) *Two sensory modalities*

In our laboratory-induced swarms, we observed mate-seeking behaviour of the marine planktonic copepod, *Temora longicornis*. Our behavioural and fluid physical analyses support the following events: (i) a 'cruising' female emits a stream of odorant, which is mixed over a width of one body length, and forms a chemical trail in the fluid, in which the concentration remains detectable (by the male) for up to 10 s; (ii) a male randomly searches the fluid until he intersects the trail; (iii) he follows the trail, though he cannot always tell which direction to go along it until he has sensed whether the ambient chemical concentration is rising or falling, if the latter he turns around; (iv) when he arrives within about 2 mm of the female he starts to feel the fluid motions caused by the female's swimming (these decay much more rapidly than the chemical signal because the diffusivity of momentum is at least 10^3 times that of solute) and aims directly for her; (v) when following a female that swims in a different style e.g. 'hovering'—where she is nearly at rest relative to the fluid far away but generating a feeding current that mixes the fluid and her odorant over a volume of diameter approximately 5 mm—the male has to detect the stationary but slowly translating cloud before homing in on the female.

In these mate-tracking events, chemical mediation dominates the capability of male copepods to track the scent trails of females, especially those trails older than 1–2 s. The high velocity spirals scan a volume containing the trail, thinning the boundary layer adjacent to sensors along the body to allow faster identification of the odour and faster detection of the across-plume and along-plume odour gradients. The precision with which the male follows the trail of the female, and even tracks the diffusing edge of the trail, reveals the remarkable persistence of the chemical signal within the confines of this viscous low *Re* fluid environment.

Fluid mechanical mediation helps focus tracking on newly prepared trails within 1–2 body lengths of the female and within 1 s of her passage, which is less than 10% of the full trail. The swimming speed of the female provides a measure of the intensity of the fluid mechanical signal. When the male intersects the trail, there is no correlation between female speed and distance of the male from the trail, supporting the lack of a fluid mechanical signal as an initial orientation cue. Males following fresh trails are found a defined distance from the female trajectory with lower variability in this distance. The male's precise approach and final leap are in response to the rapidly increasing intensity of the fluid mechanical signal of the female in close proximity. The copepod pounce is triggered by female flow speed. The female's fluid mechanical wake provides both direction and proximity cues as additional information along with the odour signal to guide the male.

Hence, two cues of different modalities from the female elicit different responses from the male: the long-lived chemical signals of the female mediate the response of trail-following, whereas the short-lived fluid mechanical signals mediate the final fast track-and-pounce response of the male for his mate. From analyses of many varied behavioural responses of copepods, we surmise that chemical odours mediate slower responses acting over longer distance-like aggregations, orientation and mate-seeking, whereas fluid mechanical signals mediate fast responses like turns, captures and escapes. This seems to be a common pattern displayed by a variety of other crustaceans (Breithaupt *et al*. 1995; Weissburg 1998).

What other signals can the copepod use? The study by Tsuda & Miller (this volume) suggests that *Calanus* males detect a signal and use gravity as the proximate cue to descend to the sinking female without having to ascertain a gradient. Using gravity as an accessory cue would not be very useful where there is a lot of horizontal mixing, displacing the patch from the female below. Here we have demonstrated that *Temora longicornis* exhibits chemically mediated trail-following behaviour which concludes with a fluid mechanical signal eliciting the final formation of the mating pair. Swimming gait and trail formation strongly influenced the kinematic patterns and may provide some species-specific cues. Mating success can be enhanced by leaving cues in the calm stratified layers of the ocean, where the signal-to-noise ratio is high and where turbulent diffusion is low so trails are not erased. These studies reveal the potential variety of mating behaviours of copepods as a reflection of the ocean environment.

(b) *Spatiotemporal coordination of mating events*

As swarms appear necessary to have reasonable probabilities of encountering a trail, we predict that animals using chemoperception have corresponding adaptations to promote aggregations in areas where the fluid dynamical regime is conducive to successful chemosensory guidance. This suggests that there are spatial, in addition to temporal, constraints on copepod mating practices. Copepods must time their sexual development and maturation to coincide with the occurrence of regions of fluid stability in the ocean. Stable waters can occur at certain times of the year, such as in summer when vertical mixing is low or, for example, at the pycnocline where the density gradient is strong, thus limiting mixing and adding to the persistence of hydrodynamic signalling. Gallager *et al*. (1996) found that the strong swimmer *Calanus* aggregated where static stability of the water is high (high Richardson number *Ri*).

Mackas *et al.* (1993) found different species associated with layers of different turbulent energy. A consideration of biological–physical interactions and environmental conditions will help us explain the particular temporal–spatial coordination that separate mating events for different copepods species in the sea.

Haury & Yamazaki (1995) examined the nearest-neighbour distances (NNDs) within copepod patches and found them to be much greater than the perceptive distances of 1–4 mm for copepod interactions. Even if copepods aggregate, these authors could not see how the copepods would interact. Our study documents a reactive distance an order of magnitude higher than previously reported results. Although the male is still perceiving the local odour signal, he is reacting to females up to 5 cm away. All the swarms reported in Haury & Yamazaki (1995) had NNDs at least as close as this, representing an abundance of $10^4\,\mathrm{m}^{-3}$. Within these patches, NNDs do match the reactive distances of mating interactions, strongly supporting the hypothesis that patches are necessary for improving the probability of finding a mate. Indeed mating can and probably does occur in these swarms, as hypothesized by Hebert *et al.* (1980). Swarming in midges may fulfil a similar function in these terrestrial insects. Midges, which rely on visual cues, swarm at an eocrepuscular time on a particular visually recognized marker (Downes 1969). These swarms are useful for gathering dispersed wide-ranging or short-lived species and facilitate mating interactions between conspecifics (Chiang *et al.* 1978).

(c) *Small-scale turbulence and diffusion*

Over evolutionary time, we can presume that the copepod has evolved to be efficient and to search only that volume that requires searching. At the scale of plankton, small-scale turbulence creates eddies that may convolute the trail in the order of 1 cm (Mann & Lazier 1991; Yamazaki 1993; Yen *et al.* 1991). Therefore, when a female trail is intersected by a male, the male should only search that volume within which the trail could be convoluted. To quantify that volume, we can look down the trail of the tracking male, relying on the precision of the optical innovations designed by Strickler (this volume; Strickler *et al.* 1995; Strickler & Hwang 1998). If we examine the three-dimensional volume the male searches (figure 8), we see that the average length-scale of the reach of exploratory casting trajectories, across the volume searched for the lost hop-trail, is in the centimetre-range, possibly inscribed within small-scale eddies. The reach across the cross-sectional area of the volume scanned by the hover-trackers is 5 mm, whereas the reach across the volume examined by cruise-trackers is 1 mm. When the male tracks the cruising female, he explores only her thin trail, which is 1 mm wide. These views show that as signal strength increases, the volume explored condenses. The male copepod focuses more precisely on the trail. The millimetre-to-centimetre scale of these search paths may reflect a true measure of Kolmogorov eddy size, as predicted for such viscosity-dominated fluid regimes.

Furthermore, unlike moths that cast perpendicular to air flow, the isotropic casting of the male in search of the trail indicates that within the low Reynolds number regime of the copepod, flow is essentially absent and no longer provides directional information. Again, the copepod behaviour confirms the fluid physical predictions that viscosity attenuates flow at these small scales.

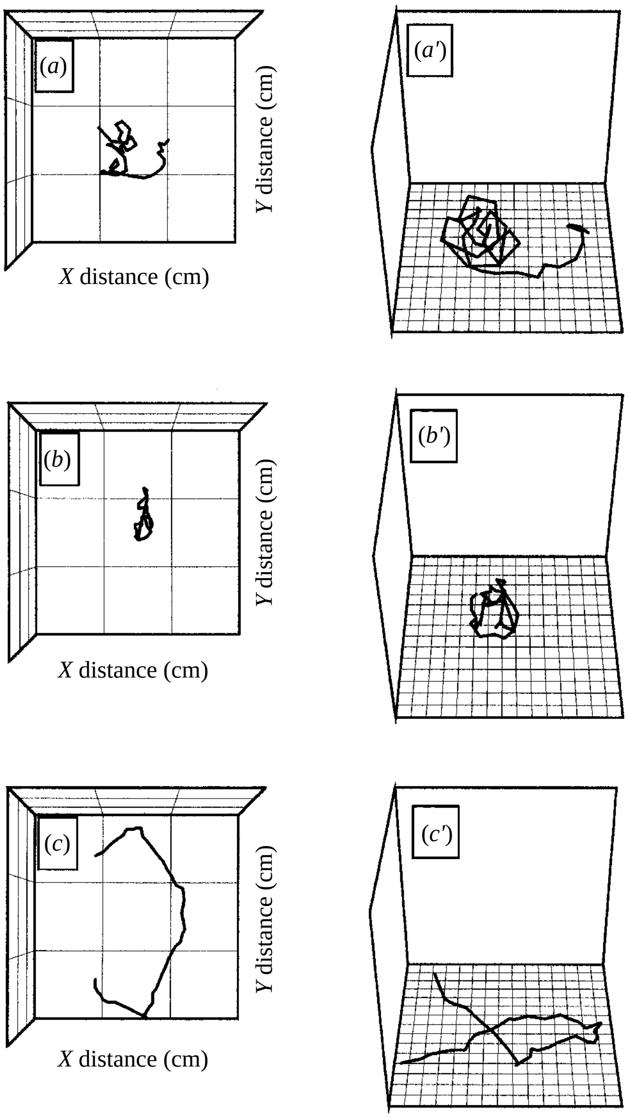

Figure 8. The structure and diameter of the volume explored by males at different steps in the mating sequence for the copepod, *Temora longicornis*. Two views (plain, primed) are presented: looking onto the trail (*x–y* view), and looking down the trail itself (various perspectives). Divisions (*a*, *b*, *c*) represent 1 mm distances. A 1.5 s portion of the male copepod's trajectory is represented. (*a*) A male that lost the trail shows sharp turns covering a 10 mm-diameter volume. (*b*) The male following a hovering female (as in figure 4) shows smooth turns covering a 5 mm-diameter volume. (*c*) The male following a cruising female (as in figure 2) shows turns just like the female's path, diverging within the volume of her path or within a 1 mm-diameter volume. As the signal gets stronger, the volume explored condenses.

At the molecular scale, diffusion and swimming gaits define the 'tunnel of love' that the male copepod follows. The female rearranges the water, aligning the velocity gradients as the local fluid motion to conform to her flow field. The walls of the tunnel—defined by the location of maximum shear in the hydrodynamic flow field—are ephemeral, whereas odour molecules diffuse away slowly, allowing the chemical trail to persist. The hydrodynamic shape and odour intensity are strongly influenced by the female's behaviour: hoverers leave wide diluted trails, cruisers leave narrow concentrated trails, hops erase the trail by diluting the chemical well below the sensitivity of the copepod receptors and by scattering the flow so that no directional cues remain to help guide the male in his search. Diffusive forces influence reaction times and consequently fine-scale copepod orientation response. The large turning angles of the male, oscillating within a hoverer's trail, and the small turning angles of the male, with little deviation within a cruiser's trail, are also isotropic with reaches limited to about 1 mm (Weissburg *et al.*, this volume), lending further support to the three-dimensionality of the tunnel created by the female.

Over the 10-s time-scale of the male's search, the trail edges are barely smeared by diffusion. In fact, the role of diffusion as depicted by Katona (1973) cannot mediate mate-finding behaviour. His illustration shows a female creating a broad diffusive plume. The diffusion of a chemical molecule originating at the female, to a male located initially 4 mm distant from the source, would require that female to remain at that spot for 1 h without swimming away (as Katona did note that females remained immmobile for about 45 min). We now know that the primary role of diffusive forces is not translating the pheromone from the female to the male, but instead, translating the odour molecule through the thin viscous boundary layer to the receptor.

As Murlis *et al.* (1992) outlined, the two processes influencing the odour structure also occur on different scales of time and space: (i) vigorous turbulent diffusion with wide temporal–spatial scales; and (ii) slow molecular diffusion on smaller scales. Atema (1988) further contrasts the turbulent plumes followed by lobsters which have very different temporal lives and spatial structures from the odours entrained in the viscous copepod feeding current (Andrews 1983; Strickler 1985). Moore *et al.* (1994) empirically showed how the copepod feeding current pulls the diffuse algal phycosphere into its laminar flow field where the odour becomes streamlined and more localized within a sheared filament. Weissburg (1998) and Weissburg & Zimmer-Faust (1994) state how these different scales translate into differences in sensory mechanisms, where strict chemotaxis cannot work when turbulent diffusion eliminates the gradients needed for this guidance mechanism. The copepod mating behaviour that we have studied also conforms to effects that differ according to these scales.

Our data indicate the importance of trail coherence for successful mate location. However, natural conditions may impose constraints on the degree to which chemosensory guidance is an effective mate-finding strategy. If the water contains large turbulent features, the odour trail may get convoluted, although gentle twists or turns in the path do not generally result in unsuccessful tracking. Males can clearly follow the wavey trails formed by hovering females. However, turbulence that stretches the trail can make the chemical signal too dilute, rendering it below the detection threshold. Small-scale turbulence can have more directly negative effects. Turbulence elicits escapes (Hwang *et al.* 1994), and when a female jumps, the chemical signal becomes intermittent and the male loses her trail.

Perhaps, as suggested by Hamner & Hamner (1977), the deep sea, with its low turbulence, is laced with a complex array of attractive or repellant chemical trails, dispersed slowly and over short distances. Yet even in the thermocline where the dissipation rate is larger than in the deep sea, the organized flow structures of small-scale turbulence remain coherent for 10 s with dimensions 10–100 times their width (Yamazaki 1993). Here we find that the biologically formed structures of mating trails appear to be controlled by the same forces that influence the longevity of turbulent features. The trails display aspect ratios close to those of vorticity tubes, 0.7 mm wide and 7–70 mm long, and they remain recognizable to the copepods for 5–10 s, which is similar to the lifetime of Kolmogorov-scale flow features. The maximum length of the detectable copepod mating trail already reveals the action of turbulent diffusion, as the lifetimes of the trails correspond to those found undergoing small-scale turbulence. A. Okubo (personal communication) also calculated that trails in the order of 10 cm persist for about 10 s before they are disrupted by turbulent diffusive forces.

However, several features of biologically formed signals enable the copepod to distinguish the trail from common small-scale turbulence features. Copepod feeding currents have shear that is comparable within a smaller length-scale than small-scale turbulence (Yen *et al.* 1991), and copepods swim slightly faster than velocity fluctuations in the seasonal thermocline (Yamazaki & Squires 1996). To help the copepod further discriminate between trails and vorticity tubes, the presence of odorant molecules labels these paths for mates.

5. CONCLUSIONS

The trail-following ability of copepods has changed our view of plankton behaviour in the aquatic environment. Instead of living in a shear-disturbed and turbulent diffusion-mixed realm devoid of water-borne signals, the low Reynolds number regime of zooplankton conserves distinct species-specific cues that direct their behaviour. Within small Kolmogorov eddies, where viscosity limits forces to the molecular scale, these trails persist and their signals are not ephemeral. The kinetic energy of the physical shearing forces has been reduced so that the fluid motion is no longer effective in taking apart these biologically created signals. Zooplankton are not aimless wanderers in a featureless environment, an image suggested by the Greek word 'planktos'. Their ambit is replete with clues that guide them in their search for food or mates and in their other efforts for survival in the ocean.

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