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Reading the copepod personal ads: increasing encounter probability with hydromechanical signals

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Females of the calanoid copepod *Temora longicornis* react to chemical exudates of male conspecifics with little hops, quite distinct from their normal smooth uniform swimming motion. These hops possibly serve to create a hydrodynamical signal in the surrounding water, to increase encounter probability with potential mates. Laser sheet particle image velocimetry was used to investigate the flow fields associated with these hops and to compare them to the flow of the feeding current of an adult female. During, and immediately after a hop, the flow field around the copepod showed a marked difference from that of a foraging animal. During foraging, the highest velocity gradients were located around the feeding appendages of the copepod. During a hop, high velocity gradients are located behind the animal. About 0.5 seconds after the start of swimming leg movement, effects of the hop had virtually dissipated and the flow field resembled that around a foraging animal. The estimated volume of influence (i.e. the volume around the copepod where the animal has a significant influence on the water) increased about 12-fold during the hop compared with the situation around a foraging animal. Furthermore, the rate of viscous energy dissipation within the copepods' volume of influence increased nearly 80-fold. Hops may serve to increase encounter probability, but due to the short duration of the effect and the high energetic costs they would only be adaptive when other cues have indicated that suitable sexual partners are in the vicinity.

Keywords: copepods; *Temora longicornis*; mate seeking; communication; mechanoreception; hydrodynamics

1. INTRODUCTION

One of the first requirements of successful sexual reproduction is the location of a suitable partner. For small planktonic animals such as copepods, living in a dilute three-dimensional environment and possessing limited visual perceptive abilities, this requirement seems extraordinarily difficult to meet. Particularly for non-swarming species, the probability of an adult male and female, both ready to mate, colliding into each other simply by chance is very small indeed, and adaptations to increase encounter probability may be vital to guarantee the continued existence of the species.

Gerritsen & Strickler (1977) developed a theoretical model to evaluate the influence of different parameters on encounter probability in the zooplankton. They found that the following parameters had a significant influence: (i) the number of mates present per unit volume; (ii) the swimming speed of both the copepod and its potential mates; and (iii) the encounter radius of each animal. The encounter radius is the distance over which an organism is able to perceive, or alternatively, the distance over which it can be perceived by another organism. According to this model, the encounter probability shows a linear relationship to the swimming speed and relates to the square of the encounter radius. Therefore, encounter radius has the largest influence on the encounter probability.

The encounter probability is obviously largely dependent on the perceptive ability of the animals involved. Most calanoid copepods lack image-forming eyes. Chemoreception and mechanoreception are their primary means of perceiving signals from the environment (Eloffson 1971; Gill 1986). Chemicals almost certainly play an important role in mate location in copepods (Katona 1973; Friedman & Strickler 1975; Watras 1983). The role of mechanical signals is less clear. Copepods possess a large array of different types of mechanosensory setae on the antennules (e.g. Lenz & Yen 1993; Hartline *et al.* 1996). In the low-to-intermediate Reynolds number regime where these animals operate, water flow is laminar and streamlines do not cross. In this regime a hydromechanical signal gives strongly directional information (Yen & Strickler 1996). Different species of copepod have a different type of motion and, therefore, a different wake. Nauplii react differently to the feeding currents of the cruising predator *Centropages typicus* than to the feeding current of the herbivorous *Centropages hamatus* (Tiselius & Jonsson 1990). In general, whether a male copepod would be able to use the wake of a female conspecific to recognize and locate her, depends on how far the effect of the wake extends and how quickly the wake attenuates.

In *Temora longicornis*, a calanoid copepod very abundant in the coastal zones of the Northern Hemisphere, the males generally swim faster than the females, provided that there is food in abundance (Van Duren & Videler 1995) and no indication of predators in the immediate vicinity (Van Duren & Videler 1996). This difference is

possibly linked to a mate-seeking strategy: the females invest a large part of their energy in the production of eggs, while the males take a greater risk of being perceived by predators and invest a larger part of their energy budget in increasing the chance of finding a female.

When water, conditioned by the presence of females, was mixed with the water in which the males were swimming, their average swimming speed did not increase, nor did it change their turning behaviour (Van Duren & Videler 1996).

On the other hand, the females did show a reaction to water conditioned by the presence of males. They increased the frequency of little 'hops'. These hops are normally shown by both sexes at a rate of about 2–4 min^{-1}. Hops are distinct from their normal smooth, gliding, swimming motion, and they are also very different from an escape movement. A hop typically lasts about 0.06–0.08 s and the displacement of the animal amounts to not more than 3–4 body lengths, whereas an escape response lasts for more than 0.15 s and results in a much larger displacement, up to several centimetres.

It is, of course, tempting to hypothesize that these hops serve to increase encounter probability by creating hydrodynamical signals. Copepods perceive disturbances in the water when changes in the relative velocity between animals and water cause mechanoreceptive setae to bend. Consequently, the properties of a hydrodynamical signal depend more on the velocity gradients in the water, such as shear and strain, than on absolute flow velocities (Strickler & Bal 1973; Strickler 1975; Haury *et al.* 1980; Fields & Yen 1993, 1997).

We have applied particle image velocimetry (PIV) to investigate the hydrodynamical properties of the disturbance caused by a hop of a copepod, and compared this to the disturbance created by a foraging animal. The volume of water around the copepod, where significant velocity gradients occur, has been measured, as well as the change in these gradients over time. This has allowed us to assess the benefits of hops in terms of enlarging the encounter radius, and to evaluate the additional cost in terms of energy expenditure.

2. MATERIAL AND METHODS

(a) *Animals*

Adult female *Temora longicornis* from a laboratory culture were used. Culture conditions were similar to those described in Klein Breteler *et al.* (1986). The animals were kept on a diet of small flagellate algae (*Rhodomonas* sp. and *Isochrisis galbana*) from continuous cultures. The heterotrophic flagellate *Oxyrrhis marina* was also present in the culture tanks and provided the main food source for the larger copepod stages. The temperature of the culture was maintained at 15 °C.

(b) *Tethering*

Animals were tethered to the tip of a very thinly drawn glass pipette using a suction restraint technique (Gill 1987). The tip of the pipette was polished until smooth to prevent damage to the animals and to create a tight seal between the pipette and the carapace. Thickness of the pipette was adjusted according to the width of the carapace of the experimental animal. Prior to tethering the animals were anaesthetized in a solution of 0.02% MS 222 (Sandoz) in seawater. The pipette with the tethered animal was mounted on a micromanipulator for precise positioning.

(c) *Particle image velocimetry (PIV)*

PIV is a technique based on analysing the movement of particles in one plane. This is achieved by illuminating an experimental vessel, filled with seawater and seeded with particles of an appropriate size (we used nylon beads, TSI inc., diameter 4 μm), with a laser light sheet (Stamhuis & Videler 1995). A tethered female copepod was positioned in the light sheet, with its side towards the camera and the light sheet through the centre of the copepod along the rostral-caudal axis, perpendicular to the antennules. Particle movement around the feeding and hopping animal was recorded with a video camera (I2S) operating at 25 frames s^{-1}, fitted with a 35 mm macro lens and a 30 mm extension ring. Shutter speed was set at 1/125 s. The resulting image covered a field of view of 8.1 × 5.9 mm. The camera was connected to a Sony U-Matic video recorder.

The image analysis system allowed analysis of individual video fields resulting in a maximum temporal resolution of 0.02 s between images.

(i) *Image analysis*

The analysis technique derives velocity vectors from the displacement of particles between two subsequent images with a known time-interval. The video images were analysed using a combination of subimage cross-correlation PIV (SCPIV) and particle tracking velocimetry (PTV) (Stamhuis & Videler 1995). SCPIV is based on the recognition of particle patterns in corresponding subimages. A cross-correlation is performed between pairs of subimages in two subsequent frames from the same location in each frame. The result of this routine is a peak with an offset from the subimage centre corresponding to the average displacement of the particles between the two frames. This procedure is then repeated with the next pair of subimages with an overlap of 50% until the whole frame has been scanned. The size of the subimage (and therefore the spacing of the resulting velocity vectors) is based on the seeding density. This method has the advantage of being fully automated, but does not work very well in areas with low seeding density or very close to the surface of an object or an animal. In these areas PTV was applied, which is based on manually identifying individual particles in subsequent frames.

The choice of the temporal resolution was based on the flow velocities. During, and immediately after swimming leg movement, a time-interval of 0.02 s was taken, but around the foraging animal and more than 0.04 s after swimming leg movement had ceased, a time-step of 0.04 s was taken to ensure sufficient particle displacement between the two images.

(ii) *Flow field analysis*

Flow fields were calculated from the particle displacements measured in the subsequent images (Stamhuis & Videler 1995). These flow fields were expressed in fields of regularly spaced velocity vectors. The resolution of the flow field (i.e. the size of the grid cells) is chosen on the

basis of the subimage size of the SCPIV analysis. For the flow fields of these experiments, each grid cell represents a surface area of 0.048 mm^2.

Gradient parameters, such as vorticity, shear and spatial acceleration rates, were calculated for each cell from the partial derivatives of the x and y components of the velocity vectors ($\boldsymbol{u}$ and $\boldsymbol{v}$). Another descriptive parameter calculated from these partial derivatives is the discriminant of complex Eigen values (d), which is a mathematical tool to calculate the exact location of the centre of a vortex.

$$d = \left(\frac{\partial \boldsymbol{u}}{\partial x} + \frac{\partial \boldsymbol{v}}{\partial y}\right)^2 - 4 \times \left[\left(\frac{\partial \boldsymbol{u}}{\partial x} \times \frac{\partial \boldsymbol{v}}{\partial y}\right) - \left(\frac{\partial \boldsymbol{u}}{\partial y} \times \frac{\partial \boldsymbol{v}}{\partial x}\right)\right]. \quad (1)$$

This is an extremely useful parameter because a vortex is often masked by translational flow and cannot be accurately located by simply looking at the flow vectors, as is illustrated in figure 1*a*,*b*. Figure 1*a* shows a vector plot of the flow behind a hopping copepod. A jet of water can be seen behind the animal, but a vortex is difficult to recognize. The vortex can be visually emphasized by subtracting the average velocity of all the vectors in the flow field from each individual vector and graphically scaling up all vectors with the same factor (figure 1*b*). Note that this does not affect any of the velocity gradients in the flow field, as the same value is subtracted from each vector. It simply removes the masking effect of the translational flow, making the vortex ring more visible.

(d) *Post processing*

The volume of influence around a copepod was defined as the volume of water around the animal where the shear rate was more than 0.7 s^{-1}. This value was chosen on the basis of experiments in water without animals present, where we measured values of up to 0.5 s^{-1} and on the observation of Yen & Fields (1992). They observed that *Acartia tonsa* nauplii escaped from the flow field of *T. longicornis* at shear rates of 0.8 s^{-1}.

By its nature, laser sheet PIV yields two-dimensional results. Flow around copepods is known to be symmetrical when viewed dorsally, but viewed laterally, there are significant differences between the dorsal and the ventral flows (Fields & Yen 1993; L. A. van Duren, unpublished results). Our images show the lateral view. To estimate the volume of influence, we rotated the velocity vectors around an imaginary axis, similar to Yen *et al.* (1991). We therefore had to make the following assumptions: (i) that in the plane where measurements were taken there was no out-of-plane flow component and (ii) that the axis is located in and parallel to the plane of focus (i.e. the position of the light sheet).

When a vortex ring was present behind the animal, we calculated a line straight through the centre of this vortex. This was achieved by calculating a line between the position of the minima of d, and assumed the rotation axis to run through the centre of this line, perpendicular to it (see figure 1*c*). When no vortex ring was present (e.g. when the animal was foraging), the rotation axis was assumed to run through the feeding appendages of the animal, parallel to the body axis.

To estimate the volume of influence, the flow field is rotated over +90° and −90°, around the calculated axis (figure 1*d*). In other words, we assume the part of the flow field above the rotation axis to be representative of the flow dorsal to the animal and the part of the flow field below

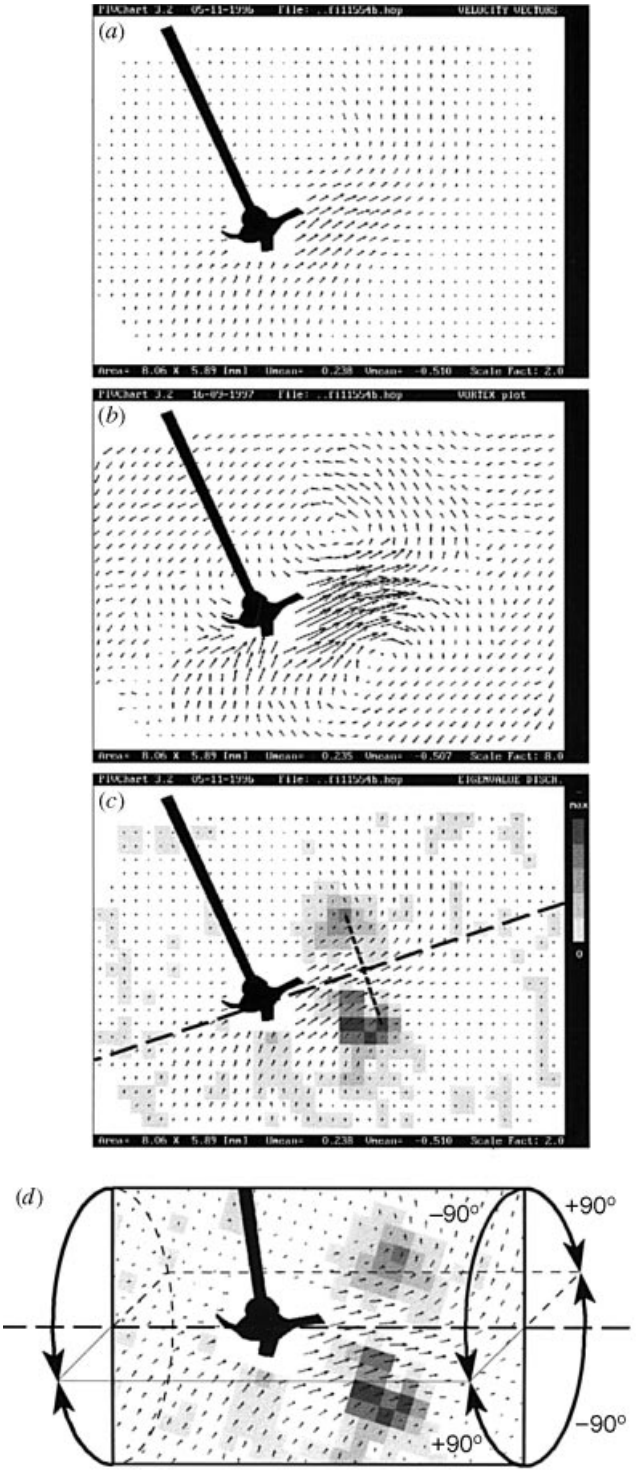

Figure 1. (*a*) Vector plot of the flow field around a copepod seen from the lateral side. The head of the copepod points to the left, the tether is attached to the dorsal side of the carapace, the swimming legs are visible on the ventral side. (*b*) Same as (*a*). The average velocity of all the vectors in this plot has been subtracted from each individual vector, and the vectors have been scaled up to unmask the vortex behind the animal. (*c*) Calculation of the rotation axis through the centre of the vortex behind the animal. (*d*) Rotation of the flow field over a total of 180° around the rotation axis.

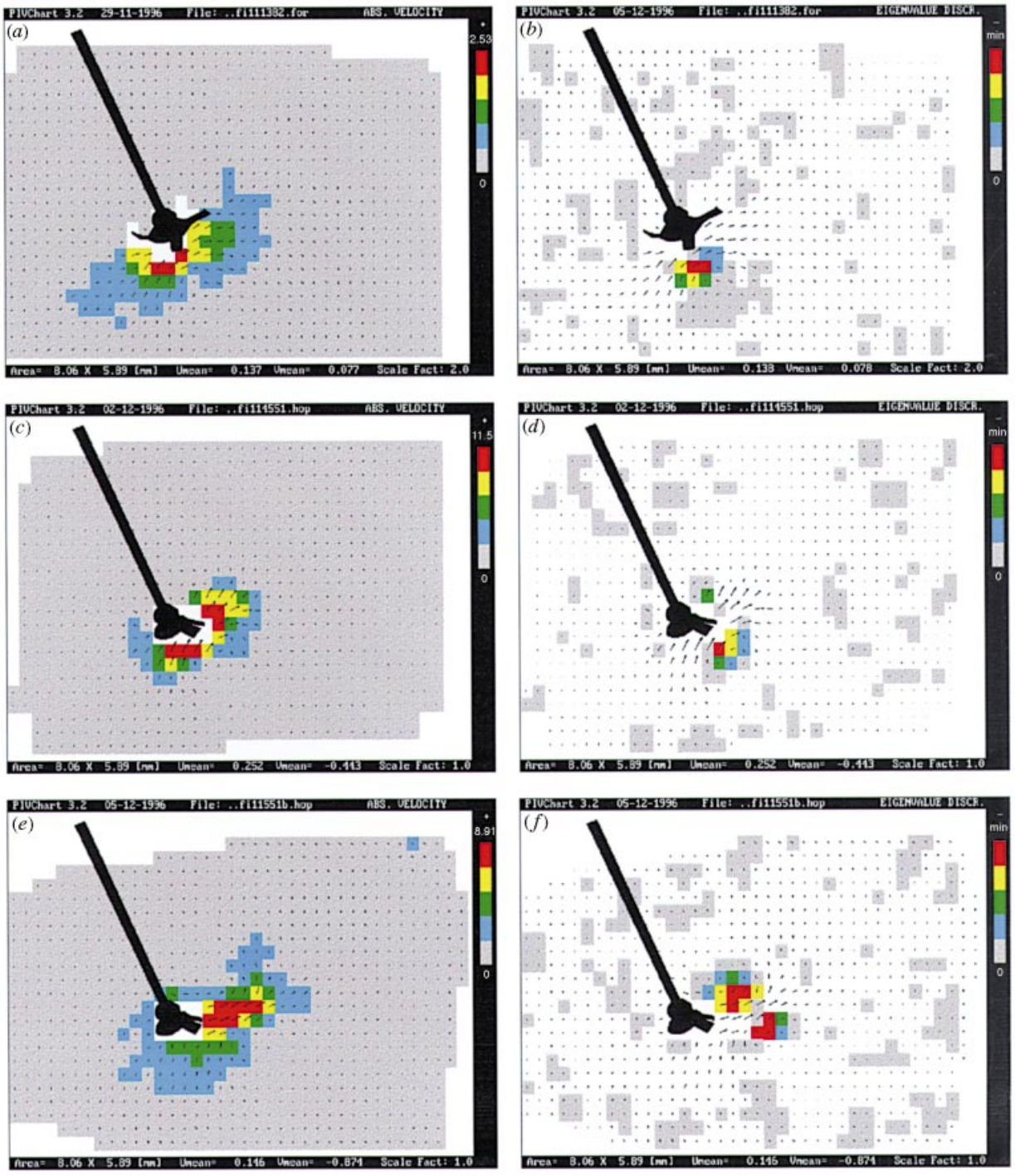

Figure 2. Description of the history of the flow morphology of a hop. The start of swimming leg movement is taken as the start of the hop ($t=0$).Note that scaling of colours is relative for every flow field. The orientation of the animal is as in figure 1. (*a*) Colour-coded plot of velocity distribution around the animal prior to the hop. Red colour indicates the highest velocity. (*b*) Colour-coded plot of *d* around a foraging animal. (*c*) As in (*a*) at $t=0.02$ s. The swimming legs of the animal are moving. (*d*) As in (*b*), at $t=0.02$ s. (*e*) As in (*a*) at $t=0.04$ s. (*f*) As in (*b*) at $t=0.04$ s. (*g*) As in (*a*) at $t=0.10$ s, swimming leg movements have ceased. (*h*) As in (*b*) at $t=0.10$ s. (*i*) As in (*a*) at $t=0.26$ s. (*j*) As in (*b*) at $t=0.26$ s. (*k*) As in (*a*) at $t=0.50$ s. (*l*) As in (*b*) at $t=0.50$ s.

this axis to represent the flow dorsal to the animal. The total volume of the volume of influence then corresponds to:

$$V_{tot} = \pi \sum (A_i r_i), \tag{2}$$

where A_i is the surface area of a cell with a shear rate $>0.7\,s^{-1}$ and r_i is the distance of the centre of this cell to the rotation axis.

Within this volume of influence the rate of energy dissipation through viscous friction can be estimated as

$$E = \mu \sum V_i \Phi_i \tag{3}$$

where dissipation function Φ is expressed in s^{-2} (Budó 1980; Yen *et al.* 1991):

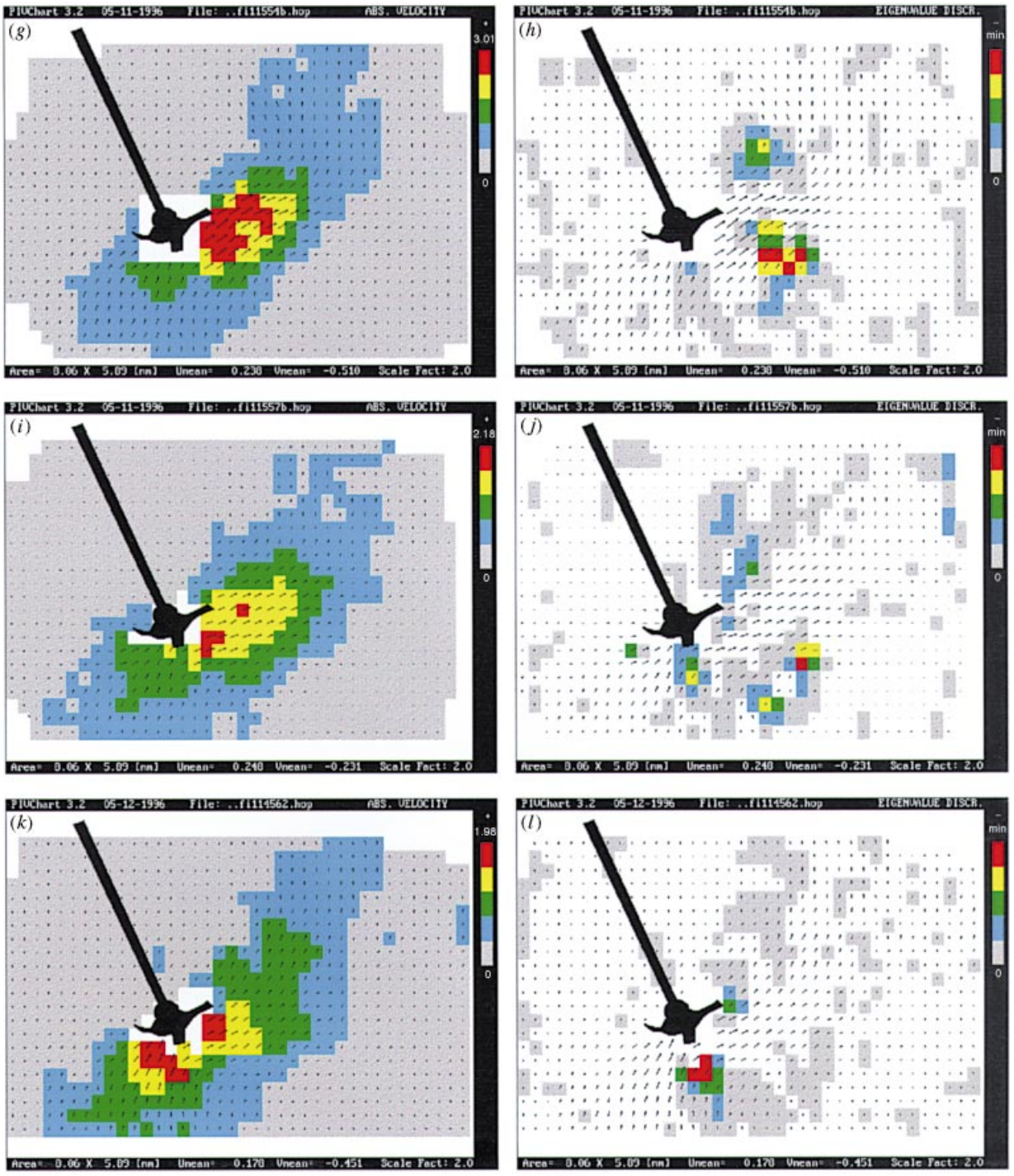

Figure 2. (*Cont.*)

$$\Phi_{xy} = \left(\frac{\partial \boldsymbol{u}}{\partial x}\right)^2 + \left(\frac{\partial \boldsymbol{v}}{\partial y}\right)^2 + \left(\frac{\partial \boldsymbol{u}}{\partial y} + \frac{\partial \boldsymbol{v}}{\partial x}\right)^2 \qquad (4)$$

and E is expressed in W (kg m^2 s^{-3}), μ is the dynamic viscosity (kg m^{-1} s^{-1}) and $V_i = \pi A_i r_i$ (m^3).

3. RESULTS

A time-series of 11 flow fields was calculated during and after the hop of one female *T. longicornis*. One flow field was calculated prior to the start of the hop when the animal was displaying a steady feeding current.

Figure 2*a*,*b* shows a lateral view of the flow field around the foraging female copepod. The highest velocities (2.53 mm s^{-1}) were measured around the feeding appendages (red colour, figure 2*a*). Water was drawn into the region of the feeding appendages from the anterioventral side of the animal and was pushed away in the posterioventral direction, resulting in an asymmetrical vortex system on the ventral side of the animal with its centre close to the feeding appendages (figure 2*b*).

At the start of a hop the feeding appendages stopped moving and the highest velocities of up to 11.51 mm s^{-1} were measured around the tips of the moving swimming

legs (figure 2*c*,*d*). At 0.04 s after the start of swimming leg movement, a jet formed behind the animal resulting in the formation of a vortex ring, the centre of which was initially located just behind the furthest position of the swimming legs (figure 2*e*,*f*). Swimming leg movement ceased after 0.06 s, at which point water velocities had reached 13.67 mm s^{-1}. At this stage the vortex ring was fully formed and was moving backwards. The ring subsequently became wider and the jet velocity started to decrease (figure 2*g*,*h*). About 0.24 s after the start of the hop, the animal resumed movements of the feeding appendages. At this point the vortex resulting from the hop was still clearly visible, though it had clearly diminished in intensity while, simultaneously, the feeding vortex system had started to form again (figure 2*i*,*j*). At 0.5 s the feeding vortex had fully developed and the vortex ring behind the animal had completely disappeared (figure 2*l*). The maximum velocities measured at this point were of the same order of magnitude as those measured around a feeding animal and located similarly around the feeding appendages (figure 2*k*). However, when figure 2*a* is compared to figure 2*k*, there is clearly still some effect visible in the velocity distribution 0.44 s after swimming leg movement ceased.

While the animal was foraging, the highest shear rates ($\pm 3.5\ s^{-1}$) were located around the feeding appendages (figure 3*a*). The area where the shear rate exceeds the defined threshold for the volume of influence extends about 1.5 mm in front of the copepod and for around 1 mm behind the animal. While the swimming legs were moving, peak shear rates of up to 25.3 s^{-1} occurred around and immediately behind the moving appendages. After swimming leg movement ceased, the shear peaks behind the animal reduced immediately to 6.6 s^{-1} (figure 3*b*). Shear rates exceeding 0.7 s^{-1} were measured up to 2 mm to the anterioventral side of the animal and in a wide area fanning out behind the animal. The maximum extent of the range of influence measures about 4.5 mm. Within 0.5 s the shear rate values and the distribution had completely returned to the foraging situation (figure 3*c*).

The wake behind a hopping animal shows strong directional components. Figure 4*a* shows the shear distribution across the vortex ring, along the line indicated in the insert. The sign of the value of the shear rate indicates the direction of the gradient. The copepod in this figure is drawn to the same scale as the *x*-axis, giving an indication of the range of shear rates a male copepod would experience over the length of its antennules when it approaches a hopping female from behind. Behind a foraging copepod very little variation and directional structure can be observed in the shear rate (figure 4*b*).

During foraging the volume of influence measured 6.54 mm^3. Figure 5 shows the development in time of the volume of influence during and after the hop, $t=0$ being the start of swimming leg movement. After a very sharp increase to a maximum volume of 79.4 mm^3, the volume of influence started to decrease as soon as the swimming legs stopped moving. The maximum size of the volume of influence reached during the hop is about 12 times the size of the volume of influence of the feeding current.

Figure 6 shows the rate of energy dissipation due to viscous friction within the volume of influence over time.

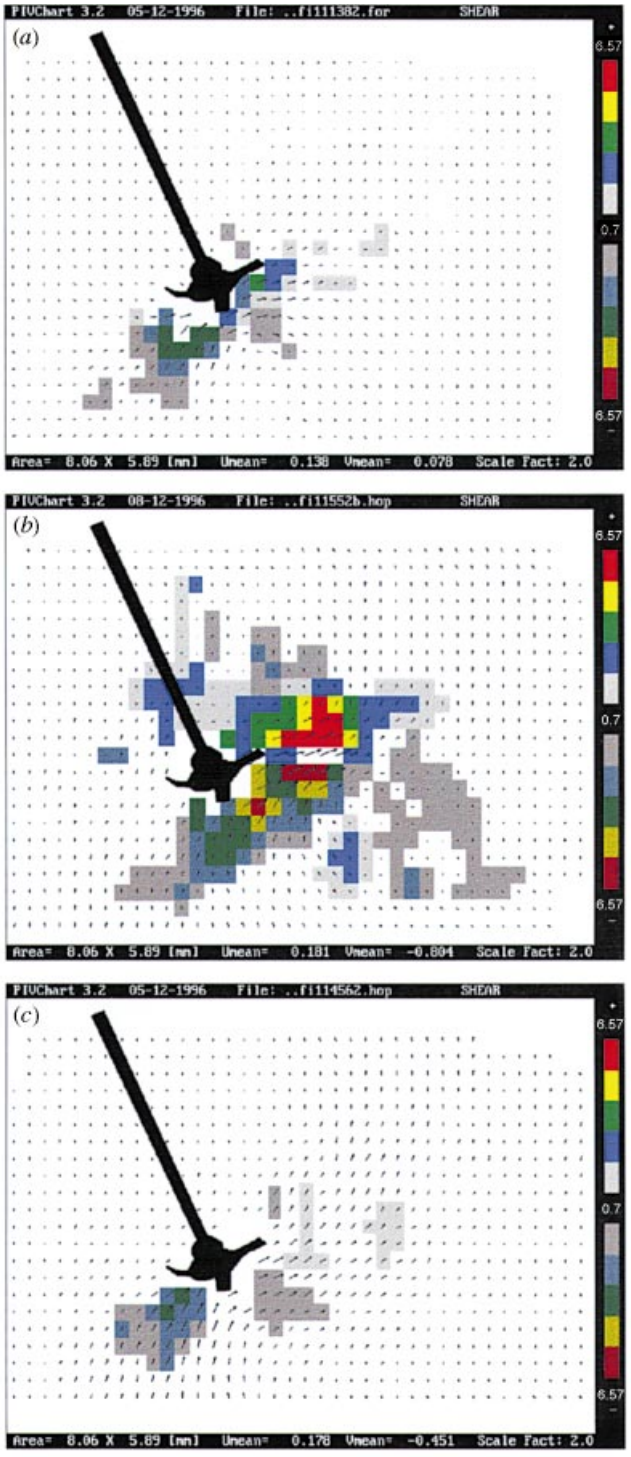

Figure 3. (*a*) Shear distribution around the copepod prior to the hop, showing only the cells where the shear rate is higher than 0.7 s^{-1}, the threshold level for the range of influence. (*b*) Shear distribution immediately after cessation of swimming leg movement ($t=0.08$ s). (*c*) Shear distribution 0.5 s after start of swimming leg movement. Note that in this plot, the colour coding is absolute, i.e. it is the same for all three plots.

The dissipation rate during foraging ranges around 1.1×10^{-11} W, while the highest value measured during the hop was 8.3×10^{-10} W. The very high velocity gradients during swimming leg movement thus result in an energy dissipation rate 80 times higher than that which occurs during foraging.

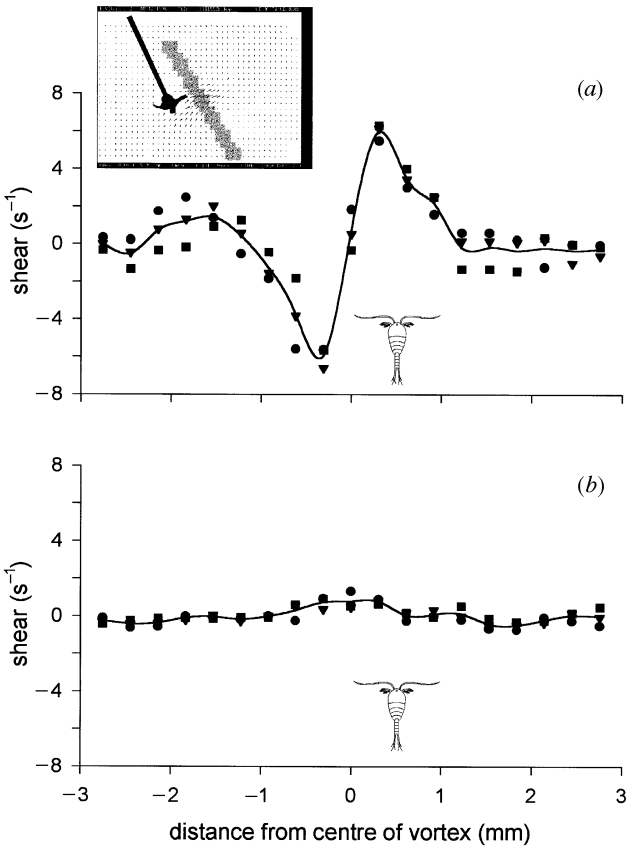

Figure 4. (*a*) Shear distribution at $t=0.08$ along the line across the centre of the vortex, perpendicular to the direction of the jet (see insert). Symbols indicate the value of the rate of shear in three cells across the line at each measuring point. The solid line shows a spline fit through the averages of each set of three points. Copepod is drawn to scale with the *x*-axis. (*b*) Shear distribution along the same line as in (*a*) behind the foraging copepod.

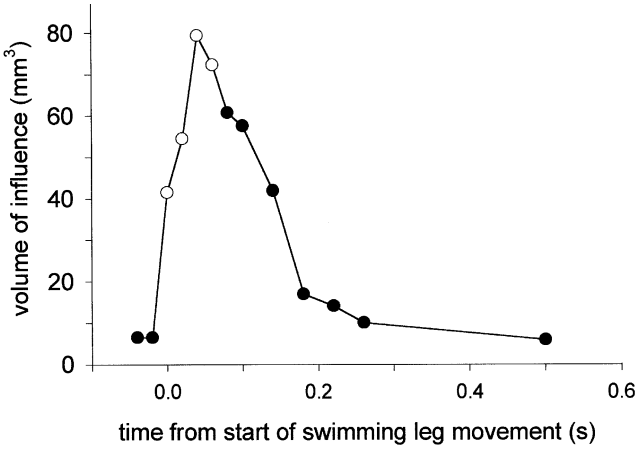

Figure 5. Development of the volume of the range ofinfluence after a hop. Open circles indicate those points in time where the swimming legs were moving.

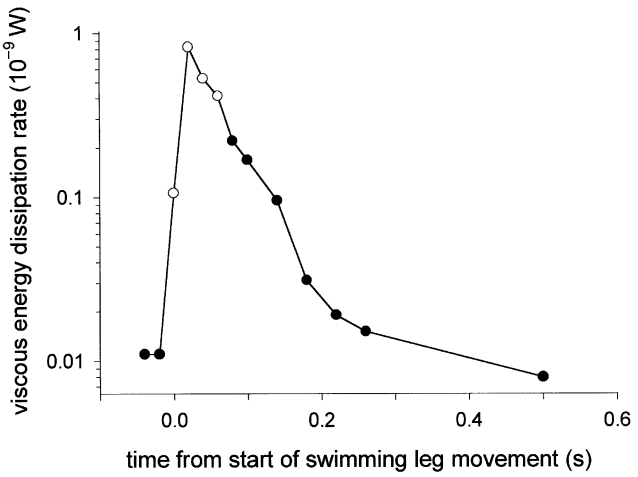

Figure 6. Rate of energy dissipation due to viscous friction after a hop. Open circles indicate those points in time where the swimming legs were moving.

4. DISCUSSION

(a) *Could hops increase encounter probability between potential mates?*

Our results indicate a 12-fold increase in the defined volume of influence of a foraging female. Assuming this can be translated into an increase in encounter radius of a similar order of magnitude, this equates to a very significant increase in encounter probability between males and females (Gerritsen & Strickler 1977). Gerritsen & Strickler (1977) assume the encounter volume to be spherical, with the organism positioned in the centre. The encounter probability is proportional to the square of the radius of this sphere. Following these calculations, the radius of the volume of influence around the hopping animal would be 2.3 times larger than that around the foraging copepod, and the encounter probability would be increased 5.24 times. However, the volume of influence is of course not spherical. During the hop it extends much further backwards in relation to the animal than forwards. A male will usually approach a female from behind (Katona 1973; Watras 1983; Doall *et al.*, this volume), and a fourfold increase in the range of influence in that direction would consequently result in a 16-fold increase in encounter probability.

According to Doall *et al.* (this volume), male *T. longicornis* tend to follow the swimming path of the female very accurately, seldom deviating by more than a couple of millimetres from the track. The antennules of the male span a distance of around 1 mm. A male encountering the wake of a hopping female, either head-on or at a tangent, will experience a variation in shear rate along the length of his antennules. This could provide information on the position of the female, but also on the orientation of the female respective to the male. As the aim of the male is to grasp the urosome of the female, this may be vital information.

Hydromechanical signals could also be picked up by organisms other than potential mates. Prey could use these signals as a signal to escape or hide, and unwanted attention from predators could be attracted. Therefore, such behaviour should be reduced in the absence of intended targets. The threshold value of a shear rate of $0.7\ s^{-1}$ for the defined volume of influence was, of course, an arbitrary one. Even if this threshold value were to be doubled or halved, it is clear from our results that males should be no more than a few millimetres away to be able to sense the velocity gradients.

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We have calculated a nearly 80-fold increase in viscous energy dissipation in the water. This is energy generated by the animal itself. The total energetic cost of this behaviour is of course higher, since muscle efficiency and mechanical efficiency will not be 100%. This indicates that this type of behaviour may be energetically very costly, an additional reason why hops should be performed only when there is a high probability of the signal being received.

It is difficult to assess how the volume of influence we defined relates to the actual encounter radius of the animal. We measured an increase in the volume of water where the shear rates exceeded a certain value. However, the encounter radius of the animal does not depend only on the signal in the water, but also on the sensitivity of the perceptive organs of the receiving male. The sensitivity of copepods to mechanical stimuli depends on the frequency of the signal (Lenz & Yen 1993; Yen *et al.* 1992; Hartline *et al.* 1996). Peak sensitivities occur particularly in the high-frequency range (around 1 kHz). Hartline *et al.* (1996) hypothesize that sudden, brief stimuli, such as the lunge of a predator, could cause high-frequency signals. The method of flow analysis we employed cannot resolve the frequency distribution of the hydrodynamical signals. If hops create stimuli of a higher frequency than the feeding current, it is possible that the sensitivity threshold for signals created by hops is lower than for disturbances created by the feeding current. In other words, the distance over which the signal can be perceived (encounter radius) could be increased more than is suggested by the increase in volume of influence alone. At the same time, high-frequency signals may attenuate at a different rate compared to lower frequency ones, which could also create discrepancies between encounter radius and volume of influence.

Maximum velocities reached during a hop range around 10–20 mm s^{-1} (L. A. van Duren, personal observation). This is in contrast to the high-velocity escape responses that *T. longicornis* is capable of, when they reach speeds of up to 80–100 mm s^{-1}, and show displacements of several centimetres. At the flow regime where copepods operate, a relatively small change in velocity has a large influence on the Reynolds number, i.e. on the ratio of inertial to viscous forces governing motion (Yen & Strickler 1996). Apparently, during a hop the copepod stops moving just as it has overcome the high drag forces due to viscosity. In terms of cost of swimming this does not appear to be very efficient. However, if the aim is to move a bulk of water to advertise your position, this is the only way to do it. If the animal were to continue to move its swimming legs it would rapidly move far away from the position of the signal, and as these signals appear to be very short-lived this could result in the male losing the trail altogether.

(b) *Alternative functions of hops*

Both male and female *T. longicornis* show hops in the complete absence of chemicals of the opposite sex. Females merely increased their hop frequency in response to the scent of males (Van Duren & Videler 1996). It is likely that this behaviour has more than one function. In view of the fact that hops are very suitable to shift a bulk of water away from a copepod, without displacing the animal over a great distance, these hops could well have a function in removing rejected algae or waste material. Due to the viscous flow regime that the copepods experience when feeding, waste products, unwanted particles and algae will accumulate in the water layer surrounding the animal. Shedding this surrounding layer of water is probably a necessary hygienic procedure, just like grooming the antennules. Strickler (1984) observed that grooming behaviour in *Eucalanus crassus* often coincided with a movement of the swimming legs, resulting in a hop.

(c) *The combination of chemical and mechanical signals in mate seeking*

It is now widely recognized that searching for food in copepods is a process where mechanoreception and chemoreception work in conjunction (Poulet & Gill 1988). The same probably holds for mate seeking and it is likely that there will be significant differences between species. The results of Doall *et al.* (this volume) indicate that males of *T. longicornis* are able to sense trails of female conspecifics up to 10 s after the female has travelled through a particular volume of water. The males accurately followed trails of females over a length of 6.5 mm. Neither the mechanical effects of the feeding current nor the mechanical effects of a hop of this species would be traceable over this time or over this distance. For *T. longicornis*, chemical signals are therefore likely to be the primary mechanism for long-range mate location. The experiments by Doall *et al.* (this volume) showed that males often lost a female trail at places where the female had jumped, implying that for long-range tracking hops may even be counterproductive.

Van Duren & Videler (1996) did not observe a specific behavioural reaction in the swimming behaviour of the males to water conditioned with female scent that was completely mixed in. This is not surprising, as no trails or gradients in pheromones were present for the males to track. The only reaction that males showed to this 'unstructured' scent was a marked decrease in inclination to escape. This in itself is probably an important reaction, since copepods normally react to any mechanical disturbance with an escape response (Strickler 1975).

Mechanical signals, such as hops, could serve as a strong but short-lived directional cue for the close-range location. Katona (1973) found that in *Eurytemora affinis* and *Eurytemora herdmanni* vibrations or water currents did not play an important role in mate seeking. However, he observed that in *Pseudodiaptomus coronatus* mechanical signals probably played an additional role in mating. Contrary to the first two species, male *P. coronatus* did not mate with immobile freshly killed females, but they did mate with moving ones.

Alternatively, hops could serve as an indication of the reproductive state of a female. The responses of males to chemical cues do not appear to be very specific. Males apparently follow and even attempt to mate with other males (Doall *et al.*, this volume), as well as with copepods from related species (Katona 1973). If signals such as these hops were only given by females willing to mate, futile mating attempts could possibly be avoided. Such a mechanism was also suggested by Watras (1983). He found that males of four species of *Diaptomus* mated significantly

more often with gravid females than with non gravid females. He suggested that discrimination between these females could occur either on the basis of pheromones or on the basis of behavioural changes in the females.

Female *T. longicornis* perform hops in the absence of physical presence of males. Escape responses from females upon physical encounter with males are reported for both cladocerans and copepods (Brewer, this volume; Tsuda & Miller, this volume; Watras 1983). The function of such escape responses prior to mating is still unclear.

(d) *Methods*

The PIV method is a particularly useful tool to investigate short-lived flow phenomena, such as the signals created by hops. All the other flow analysis methods based on particle movement that have been applied to investigate flow around copepods have involved integrating results over a relatively long duration, from 30 s up to several minutes (Yen *et al.* 1991; Fields & Yen 1993; Bundy & Paffenhöfer 1996; Tiselius & Jonsson 1990). For steady flow phenomena, such as the feeding currents of certain species of copepods, this may not cause too many problems. Short-lived signals, and certainly the attenuation of such signals, however, could not be investigated with these methods.

Although tethering of copepods does not significantly affect the types of behaviour they display (Hwang *et al.* 1993), it may have had some influence on the morphology of the flow field and in particular on the volume of influence that we calculated (Bundy & Paffenhöfer 1996). Instead of moving its body through water, the animal is moving water past its body. Tethering is known to increase the volume of water displaced by the animal (Bundy & Paffenhöfer 1996; Emlet 1990). Hops, however, characteristically do not result in a large displacement of the copepod (a couple of millimetres, as opposed to, for example, several centimetres during an escape response) and the effect of tethering is unlikely to be large enough to affect the main conclusions of these experiments.

We have only PIV data on the one hop analysed in this paper. Therefore, we have no information on how variable these flow phenomena are between individuals or even between different hops of one individual. Similar research on other species could provide answers on species specificity of such signals.

This research shows that hops certainly have the potential to increase encounter probability between male and female copepods. The question as to whether they actually are used as such has not been fully answered yet. If they are, their precise function within the complex of mate-seeking behaviour remains to be investigated. Understanding perception and communication between copepods certainly requires very detailed knowledge of the combination and interaction between chemical and mechanical signals.

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