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The flow generated by an active olfactory system of the red swamp crayfish

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Summary

Crayfish are nocturnal animals that mainly rely on their chemoreceptors to locate food. On a crayfish scale, chemical stimuli received from a distant source are dispersed by an ambient flow rather than molecular diffusion. When the flow is weak or absent, food searching can be facilitated by currents generated by the animal itself. Crayfish employ their anterior fan organs to produce a variety of flow patterns. Here we study the flow generated by *Procambarus clarkii* in response to odour stimulation. We found that while searching for food the crayfish generates one or two outward jets. These jets induce an inflow that draws odour to the crayfish's anterior chemoreceptors. We quantified velocity fields in the inflow region using Particle Image Velocimetry. The results show that the inflow velocity decreases proportionally to the inverse distance from the animal so that it takes about 100 s for an odour plume to reach the animal's chemoreceptors from a distance of 10 cm. We compare the inflow generated by live crayfish with that produced by a mechanical model. The model consists of two nozzles and an inlet and provides two jets and a sink so that the overall mass flux is zero. Use of the model enabled us to analyze the inflow at various jet parameters. We show that variation of directions and relative intensities of the jets allows the direction of odour attraction to be changed. These results provide a rationale for biomimetic robot design. We discuss sensitivity and efficiency of such a robot.

Key words: chemical sensing, crayfish, PIV, flow measurement, biomimetics.

Introduction

In an aquatic environment, vital information about the presence and location of food is provided by chemical stimuli. In contrast to visual and acoustic stimuli, chemicals are dispersed relatively slowly by molecular diffusion and the ambient flow. Molecular diffusion is relevant for orientation of microscopic organisms (Blackburn et al., 1998) but is inefficient at transporting olfactory information to animals over distances longer than a few millimetres (Dusenbery, 1992; Weissburg, 2000). Large aquatic animals such as crayfish rely on the information extracted from macroscopic odour plumes. These plumes form downstream of the odour source by advection and turbulent diffusion (Balkovsky and Shraiman, 2002).

Animals can orientate towards an odour source by following the mean direction of the flow carrying odour molecules (odour-gated rheotaxis) or by evaluating parameters of the turbulent odour plumes (Vickers, 2000; Weissburg, 2000). Lobsters, crabs and crayfish have been shown to navigate towards odour sources using a combination of these strategies (Atema, 1996; Moore and Grills, 1999; Weissburg and Zimmer-Faust, 1994; Grasso and Basil, 2002).

Animal orientation under still water conditions such as in ponds, lakes, caves, or during slack tide, has been less studied. In aquatic environments with little or no ambient water movement, the flow created by an animal itself could help in odour acquisition and orientation. Understanding the active olfactory mechanisms of crayfish inhabiting stagnant waters requires consideration of the flow patterns created by an animal and the transport of odour stimulus to the chemoreceptors. This knowledge can be applied to the design of a robot searching for chemical sources under stagnant water conditions.

Crustaceans are well known for their ability to create directed water currents by pumping and fanning appendages (Herberholz and Schmitz, 2001; Atema, 1985; Budd et al., 1979; Burrows and Willows, 1969; Brock, 1926). Different appendages can create distinct currents. For example, gill currents ventilate the gills, abdominal swimmeret currents aid in locomotion, and it has been suggested that currents created by the anterior fan organs can be used for odour acquisition and chemical signalling (Breithaupt, 2001).

The fan organs of a crayfish consist of the flagellae of the three bilateral maxillipeds. As shown in Fig. 1A, fan organs are located below the frontal sensory organs including the antennules, which constitute the major chemoreceptors in decapod crustaceans. The distal part of the multi-segmental flagella bears a dense, single-layered array of feathered hairs emerging on either side of the stem (Fig. 1B). During a power stroke the hairs are erect; during a recovery stroke the hairs are tilted and the stem is flexed in order to reduce the drag (Fig. 1C). The fan organs can be used for chemical communication by generating a forward directed jet (Breithaupt and Eger, 2002; Bergman et al., 2005), or for odour acquisition by drawing water towards the head region (Breithaupt and Ayers, 1998; Breithaupt, 2001). In decapod crustaceans, odour stimulation

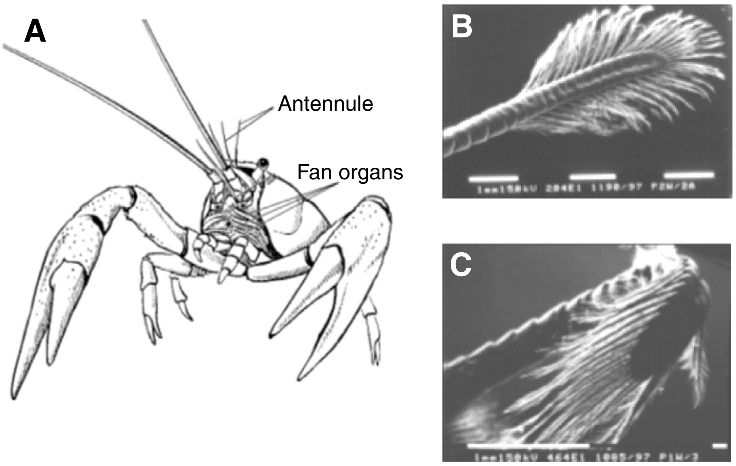

Fig. 1. (A) Location of fan organs and major chemoreceptors (antennules) of crayfish. The fan organs are multisegmental flagellae (exopodites) of the mouthparts (maxillipeds) and are feathered distally (B). (B,C) Scanning electron micrographs taken during the power stroke (B), showing the extended feathered hairs. During the recovery stroke (C) the feathered hairs are folded in. Scale bars, 1 mm. Reprinted from Breithaupt (Breithaupt, 2001) with permission of *The Biological Bulletin*.

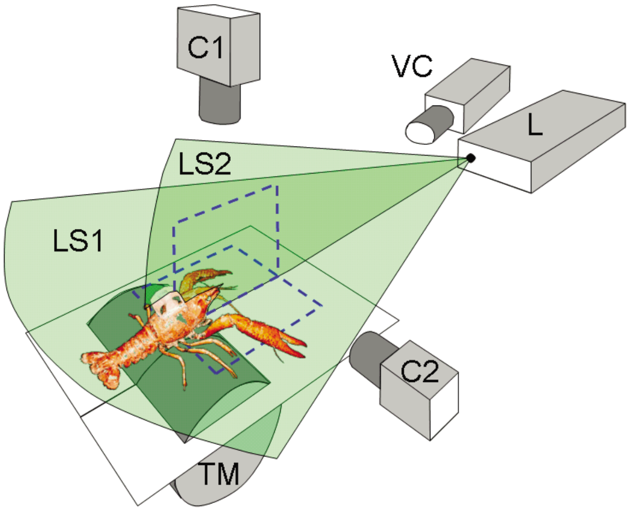

Fig. 2. Experimental setup. A crayfish is suspended above the treadmill (TM). A lasersheet is generated by a laser (L). A PIV camera is set to the position C1 (C2) and the lasersheet is aligned along the plane LS1 (LS2) to measure the two components of velocity field in horizontal (vertical) planes (blue broken boxes). A video camera (VC) is used to monitor the crayfish fanning activity.

generally initiates fanning activity (Atema, 1985; Brock, 1926). Crayfish (*Astacus leptodactylus*) were observed to increase the time spent fanning from about 50% to more than 90% of their time when encountering an odour plume (T.B., unpublished data). Inactivating the fan organs causes a dramatic decrease in their success in finding an odour source, indicating that fan organs are essential for chemo-orientation in still waters (T.B., unpublished data).

The red swamp crayfish *Procambarus clarkii* inhabits rice fields and other stagnant water bodies and therefore might utilize fanning as an active olfactory mechanism. The mechanism by which the fan-generated currents draw water towards the olfactory appendages is not understood. Here we investigate how the red swamp crayfish uses outward directed currents to generate an inflow that could serve for odour acquisition. We visualized the jets generated by a crayfish and used Particle Image Velocimetry (PIV) to quantify the flow velocity around the live animal.

In order to test a proposed mechanism for active odour acquisition we designed a mechanical model, an assembly of nozzles, simulating the flow pattern by producing the jets. The model enabled us to reproduce various velocity fields observed in crayfish. Behaviour of crustaceans has been used to develop algorithms for autonomous robots searching for chemical sources (Grasso, 2001; Ayers, 2004; Ishida et al., 2006; Martinez et al., 2006). Active generation of flow might help to locate chemical sources in a still environment. Our model can be used as a prototype design of robots orienting by chemical cues.

Materials and methods

Flow visualization and PIV measurements were conducted for five adult crayfish *Procambarus clarkii* (Girard 1852): one female and four males of 7–8 cm body length. A crayfish was suspended from a holder glued to its back (Fig. 2) in an aquarium 60 cm×60 cm×120 cm. A video camera (VC) was used to monitor activity of the animal fan organs, swimmerets and antennules. The crayfish was suspended above a double-wheeled, freely rotating treadmill (TM) with the walking legs of each side resting on a separate wheel. The treadmill was aimed to reduce agitation of the animal. It helped the crayfish to rest or to perform natural walking movements involved in olfactory search behaviour. To prevent animals from reacting to visual disturbances they were blindfolded by wrapping an opaque tape around the eyestalks and the rostrum. The animal's claws were removed by inducing autotomy since they interfere with flow measurements by shadowing the laser-sheet. Experiments with unrestrained crayfish showed that claws are kept motionless during odour acquisition so that their removal is not likely to affect the olfactory mechanism (T.B., unpublished data).

We visualized the jets created by crayfish by introducing water-based ink through a pipe of 0.6 mm i.d. in the proximity of the fan organs (Fig. 3). As will be discussed later, the flow around the crayfish consists of the outward jets produced by fan organs and the inflow carrying the odour towards the animal's chemoreceptors. To measure the velocity field in the inflow area we used a two-dimensional PIV system (Dantec Dynamics, Ltd, Copenhagen, Denmark) including a 125 mJ double pulse Nd YAG laser and a Hi-Sense 12-bit double-frame CCD camera (Dantec) with a resolution of 1280×1024 pixels. The FlowMap software (Dantec) was used to calculate the velocity field using the adaptive cross-correlation algorithm with two refinement steps and the use of deforming windows and high accuracy subpixel resolution. The interrogation area for the velocity calculation was set at 64×64 pixels, which is

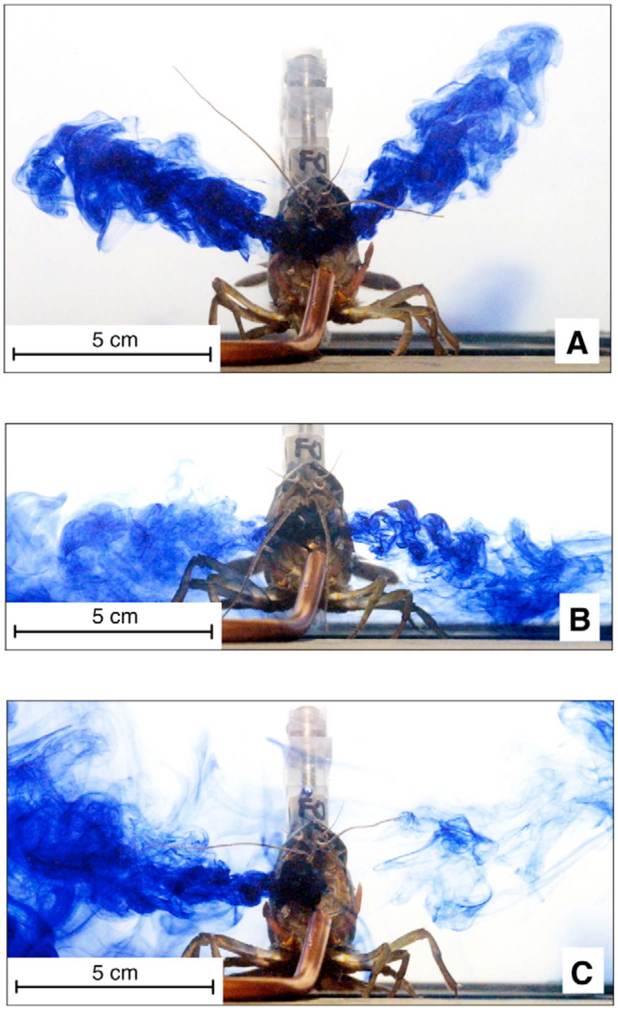

Fig. 3. Ink visualization of the jets generated by the crayfish fan organs. Bilateral jets directed at 25° and 40° upwards (A) and horizontally (B); unilateral jet directed horizontally (C). Water-based ink for a fountain pen was used. After the animal had been observed fanning for about 1 min, the ink was slowly released from a pipe of 0.6 mm i.d. placed in front of the animal fan organs. Caution was taken to prevent the ink from getting in contact with the animal's chemoreceptors. The photo in A was acquired 5 s, and in B and C, 30 s, after the beginning of the ink injection.

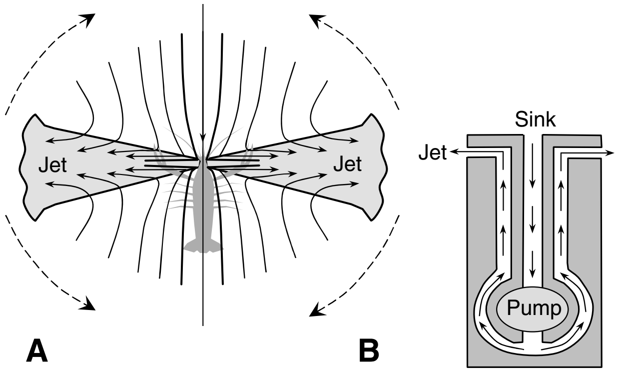

Fig. 4. The flow generated by crayfish fan organs consists of the jets and the inflow (A). The inflow converges towards the jets' origin and towards jets' axes. At a distance larger than the jets' length the flow is virtually unaffected by a crayfish fanning activity. The jets are generally out of horizontal plane, so the sketch shows a projection. To mimic the flow created by a crayfish, an assembly of an inlet and two outlet nozzles (B) was designed. The water was pumped through a closed loop providing fluid conservation, which is obviously the case for a crayfish.

6 mm×6 mm for measurements in horizontal plane and 3 mm×3 mm for measurements in vertical plane. The grid spacing was set at 75% of the interrogation area size. The calculated velocity field was refined by the range validation (all vectors exceeding 1 cm s^{-1} were omitted) and then by the moving average method over 3×3 grid points with the acceptance factor 0.05. A set of 30 sequential velocity fields was used to get an average flow field. Streamlines were calculated using MATLAB 7.0 software (The MathWorks Inc., Natick, MA, USA). Silvered hollow glass spheres of diameter 10 μm and density 1.03 g cm^{-3} were used as seeding particles. For PIV measurements of the horizontal velocity field the laser sheet and the camera were aligned at LS1 and C1 positions, as shown in Fig. 2. For measurements in the vertical plane they were set at positions LS2 and C2. Both the laser source and the camera were fixed on a frame attached to a vertical translational stage that allows measurement of the velocity field at various distances from the bottom. A time interval between the laser pulses was set at 50 ms to measure the low magnitude velocity in the inflow area. With this time interval the higher velocity within outward jets could not be resolved. Flow measurements within the jets were not attempted as the animal often changes the jet directions and these changes require re-alignment of the laser sheet and cameras.

After the crayfish was set to the measurement position, it was allowed to settle down for at least 30 min. When the animal was observed fanning with the swimmerets and walking legs inactive, the PIV was triggered to acquire data at a rate of 1 frame s^{-1}. Only the images acquired during the 30 s of each experimental run were taken for analysis. Following these 30 s the animal often ceased waving its fan organs reacting to the laser pulses. It is likely that the crayfish retinal or extra-retinal (Sandeman et al., 1990; Edwards, 1984) photoreceptors were stimulated by the light scattered by the animal's translucent body.

To simulate the flow generating mechanism involved in chemoreception of the crayfish we designed a mechanical model, a closed loop pump–nozzle assembly with one inlet and two outlets, as sketched in Fig. 4B. The assembly mimics the far field flow, initiated by the jets that are generated by the fan organs, preserving the amount of water involved in the motion. Fluid mass conservation is achieved by feeding the outlet nozzles with the fluid pumped from the sink *via* a closed loop. As in live crayfish, an inflow replaces the fluid drawn in by the sink and subsequently ejected as jets, and the fluid entrained by the jets. The nozzle assembly allows generating horizontal sideward jets, jets directed 45° backwards and jets directed 45° upwards, and was built to match the size scale of a crayfish. Velocity of the flow induced by the model was measured using the same PIV arrangements as for the crayfish and the flow rate through the nozzles was adjusted to make the magnitude of the inflow velocity close to that observed in experiments with live animals.

Results

We observed a crayfish producing one or two jets by waving the fan organs of one or both sides (Fig. 3). The jets' direction varied from 90° to the animal plane of symmetry to 45° upwards and 45° backwards. Jets extending over a length of more than 10 cm were observed. Fanning was generally accompanied by flicking of the lateral antennules, a behaviour that enhances olfaction in decapod crustaceans (Koehl et al., 2001; Koehl, 2006). Flicking occurred at multiple heights as the antennules were slowly swept downwards. Flicking and downward sweeping occurred only rarely when the animals were not fanning, indicating the close link between fanning and olfactory sampling. The animals occasionally walked on the treadmill while waving the fan organs, but most of the time their walking legs were steady.

The outward jets induce an inflow converging towards the fan organs and the jets themselves. A typical flow field measured by PIV in the vertical plane is shown in Fig. 5. Note that the antennules are lowered in front of the fan organs, thereby exposing olfactory receptors to the incoming flow. The streamlines in Fig. 5 are more or less horizontal at the level of fan organs, which suggests that one can study the horizontal inflow structure by measuring the velocity field at this height. Examples of the flow field measured in the horizontal plane are shown in Fig. 6. Since the instantaneous velocity field (Fig. 6A) appears too irregular, we use the averages over the 30 sequential images. Visual observation shows that the crayfish changes its fanning behaviour over a timescale of minutes, so we used the 30 s average to illustrate the actual range of the odour attraction. The streamlines leading to the animal chemoreceptors illustrate that the sector of odour attraction may vary. The jets were out of the plane of measurement in most of the experiments with live animals, which may create an illusion of breaking the conservation of fluid mass.

To understand how the configuration of jets affects the inflow, we measured the velocity field around the assembly with nozzles directed horizontally, 45° upwards, 45° backwards, and with one nozzle blocked. The corresponding four samples of the model-generated flow field are shown in Fig. 7. The inflow patterns resemble those generated by the animal (Fig. 6), illustrating how the flow outside the jets converges towards the jets' origin (nozzle assembly), and towards the jets' axis.

Since odour tracking is a time-dependent process, we investigated how long it takes for the inflow pattern to adjust to a changed configuration of the jets. Experiments with the flow-through nozzles switched on from rest showed that the steady flow field is stable within several seconds after starting the pump.

To assess the range of odour acquisition, the flow velocity as a function of distance from the fan organs/sink along the streamlines (broken lines in Fig. 6A–D and Fig. 7A–D) is plotted for the live animal in Fig. 8A–D and the mechanical model in Fig. 9A–D. The slopes of the plots show that the flow velocity is somewhat inversely proportional to the distance from the fan organs, i.e.:

$$V \approx V_0 \frac{s_0}{s}, \qquad (1)$$

where V_0 is the fluid velocity at a distance s_0 from the fan organs. The time required for the odour patch located at a distance L from the fan organs to reach the crayfish antennules can be estimated by integrating the inverse velocity by the distance:

$$T \approx \int_0^L \frac{1}{V}\,\mathrm{d}s \approx \int_0^L V_0 \frac{s}{s_0}\,\mathrm{d}s = \frac{L^2}{2V_0 s_0}. \qquad (2)$$

Assuming velocity $V \approx 5$ mm s^{-1} at $s_0 \approx 10$ mm (as in Fig. 8B), we can infer that an odour patch located 100 mm away from the crayfish fan organs would reach the chemoreceptors in approximately 100 s. This time interval increases quadratically with L, rising to approximately 4 min for a distance of 150 mm. For comparison, solution of the diffusion equation for the point source [(for example, see Batchelor, 2000), p.187] shows that the characteristic time of molecular diffusion at a distance of 100 mm is measured in days.

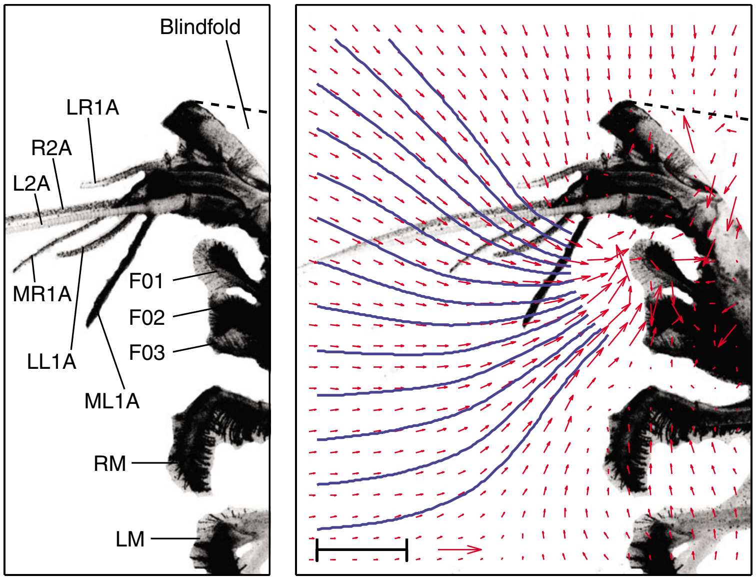

Fig. 5. Right, the flow field measured at the crayfish plane of symmetry (vertical laser sheet LS2 in Fig. 2) averaged over 30 instantaneous measurements (30 s). The fluid converges towards the fan organs in the plane of measurements and escapes in the form of jets in a perpendicular direction (not shown). Reference segment at the bottom, 2 cm; reference vector, 1 cm s^{-1}. The negative image of the crayfish cut from a PIV image is shown for reference. The broken line indicates the contour of the blindfold which is shaded from the laser sheet and thus is not visible in the image. The animal's appendages are denoted on the left; LR1A, lateral right antennule; R2A, right second antenna; L2A, left second antenna; MR1A, medial right antennule; LL1A, lateral left antennule; ML1A, medial left antennule; FO1, FO2, FO3, extended exopodite of fan organs 1 to 3; RM, LM, endopodite of right and left third maxilliped. Note that lateral antennules LR1A and LL1A are lowered in front of the fan organs, exposing chemoreceptors to the inflow.

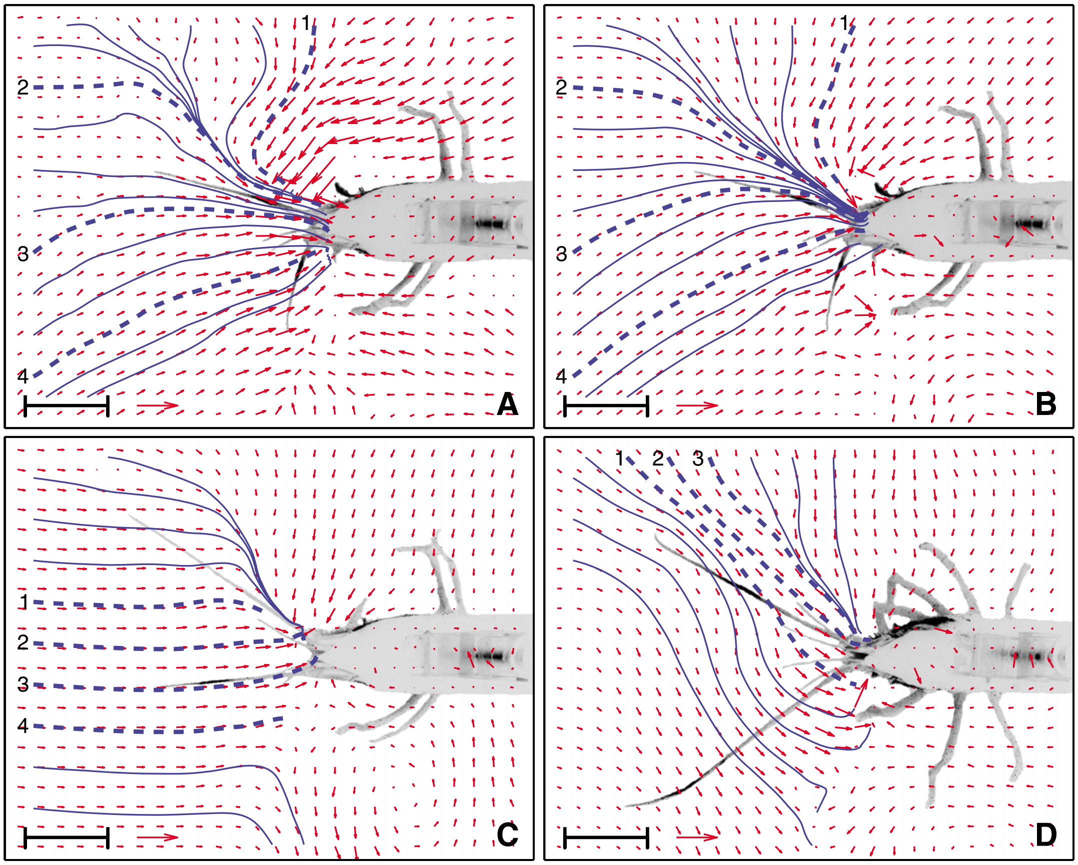

Fig. 6. Examples of the velocity field generated by a crayfish measured in a horizontal plane LS1 (Fig. 2). (A) The instantaneous velocity field (B–D) averages over 30 instantaneous measurements taken at 1 s time intervals. Velocity field A is one of those used to obtain the field C. Fields A–C were recorded from a female animal; the field D was recorded from a male. The fluid converged towards the animal head region, escaping within the jets located outside the plane of measurement. Negative images of the animal cut from a PIV image are shown for a reference. Reference segments at the bottom left, 2 cm; reference vector, 1 cm s^{-1}. The jets created by the animal are outside the plane of measurement and thus are not observed in the vector field. Profiles of the horizontal fluid velocity along the enumerated streamlines (broken lines) are correspondingly plotted in Fig. 8A–D.

Discussion

We have described a mechanism that crayfish may utilize to assess odour stimuli in a stagnant water environment. Using the anterior fan organs, a crayfish creates jets (Fig. 3) so that the flow induced by these jets (Figs 5 and 6) draws water samples from a distance to the animal's chemoreceptors. A schematic of the flow around the crayfish is sketched in Fig. 4A. To detect odour stimuli in the stagnant environment effectively, the animal induces a flow causing a large volume of surrounding fluid to converge into the relatively small space accessible by its chemoreceptors.

The most important fact revealed by the PIV measurements is a surprisingly slow decay of the inflow velocity with the distance from fan organs, as plotted in Fig. 8. The slow decay is explained by a fluid entrainment by jets. Indeed, if the entrainment were insignificant and the inflow were formed only by a point sink at the location of fan organs (the origin of jets), one would expect the inflow to be spherically symmetric [(see Batchelor, 2000), p. 89]. In that case the flow velocity would decrease as the inverse square of the distance from the fan organs, and the travel time *T* for the odour patch to reach the crayfish chemoreceptors (Eqn 2) would be proportional to the third power of the distance *L* to the odour source. This would increase the travel time to 10 min for the distance of 100 mm and to 40 min for the distance of 150 mm, indicating efficiency of the jet-based odour acquisition mechanism used by crayfish.

Fluid entrainment by a single jet has been described theoretically (Schneider, 1981). Schneider showed that a turbulent jet acts as a line sink with respect to the surrounding fluid. This leads to the axial rather than spherical symmetry of the flow field, hence to a slower decay of velocity with distance. The velocity decay is now proportional to the inverse distance from the jet axis (a line) instead of the inverse squared distance from the sink (a point). The secondary flow induced by a turbulent jet and decay of the jet itself were described analytically (Kotsovinos and Angelidis, 1991). However, the results of this paper cannot be extended to a case of two jets because the Navier–Stokes equations governing fluid motion are not linear. Moreover, the relatively weak jets created by a crayfish cannot be considered as fully developed turbulent jets, and the presence of a rigid boundary, the bottom of the tank, affects the flow.

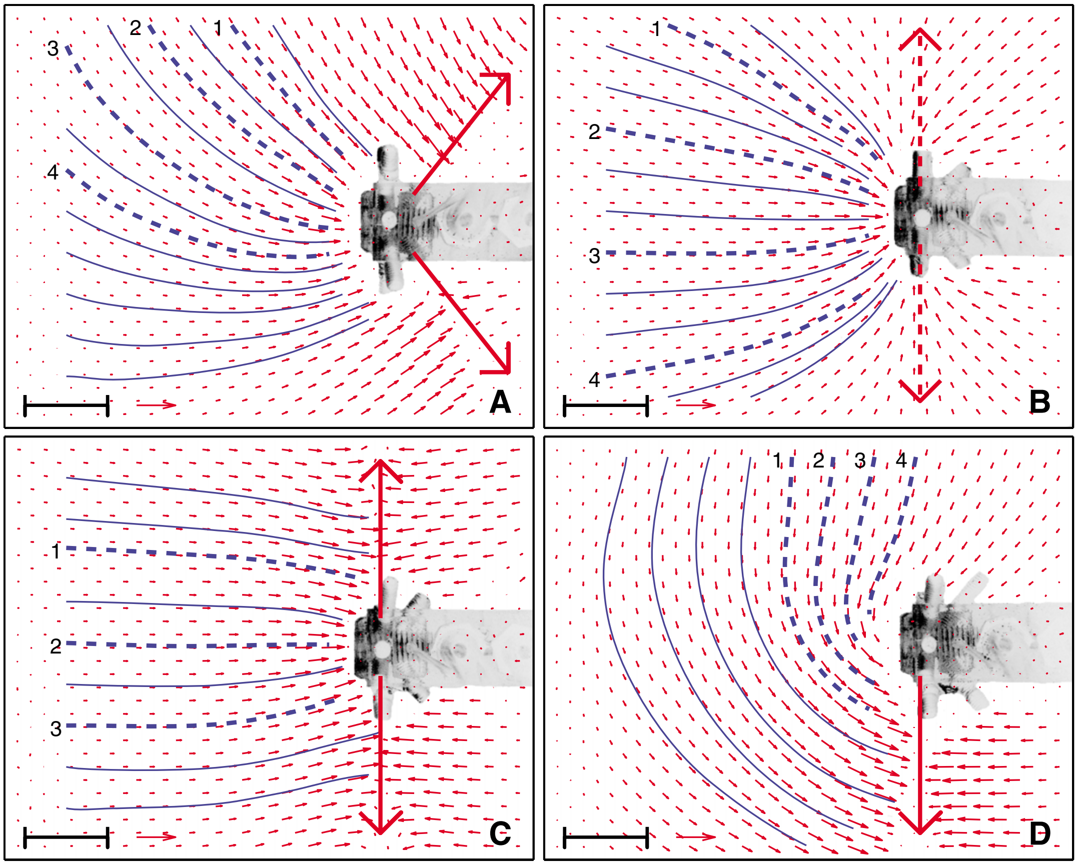

Fig. 7. Velocity field generated by the mechanical model (Fig. 4B) measured in a horizontal plane LS1 (Fig. 2). Negative images of the device cut from a PIV image are shown for a reference. The positions of the jets produced by a model are indicated by bold red arrows. Two jets directed to the sides (C), 45° backwards (A), 45° upwards, off the plane of measurement (B), a single jet directed to the left (D). Reference segment at the bottom left, 2 cm; reference vector, 1 cm s^{-1}. Short arrows at jet locations and over the model correspond to the 'noise' of image processing software and are not indicating any real values of fluid velocity. Profiles of the horizontal fluid velocity along the enumerated streamlines (broken lines) are correspondingly plotted in Fig. 9A–D.

The above argument suggests employment of direct numerical simulation to model the flow induced by the jets. However, simulation of a system of jets is a problem on its own, so in the present study we do not investigate the inflow structure any further. We merely observe that the range of odour acquisition, i.e. the range in which the inflow rate decreases slowly with the distance, is defined by the jet length (Fig. 4A), and that the jet length may exceed 10 cm as the jet visualization has shown.

To produce continuous jets as visualized in Fig. 3, a row of the three exopodites is located on each side waving with the phase shifts of 120° (Breithaupt and Ayers, 1998). In contrast, the fanning appendages aimed to produce thrust, the swimmerets, are arranged to generate a less regular excurrent, which induces suction at the locus of the appendages and much weaker suction along the extended line such as the jet axis. Extreme examples of the thrust-producing excurrent with the minor fluid entrainment are the vortex street produced by a fish (Sfakiotakis et al., 1999) or a trail of vortex rings produced by a jellyfish (Dabiri et al., 2005). The latter is commonly observed in the form of smoke rings and described in, for example, Batchelor (Batchelor, 2000), p. 22.

To locate a source of an odour, crayfish need to sense the direction to the source. In a riverine environment the source is somewhere upstream. In still water an animal can navigate by comparing the local intensity of the odour at different locations through the plume (Atema, 1996). However, the animal movement may stir up the water and destroy the pattern of odour patches formed by the source. Walking through the open environment would also increase predation risks and may be energetically expensive. The crayfish may overcome these difficulties in scanning the environment by varying the jet pattern, thereby drawing odour molecules from different directions to its chemoreceptors (Figs 6, 7). The original pattern of odour patches is changed by the inflow in such a way that the strongest chemical signal, i.e. the odour patch washed off from a chunk of food, approaches the animal from the direction of the food locus. This mechanism of odour acquisition may significantly reduce predation risks compared to odour tracking by walking where the crayfish acts as a moving visual target. The hydrodynamic disturbance created by jets is only detectable from a short distance (a jet length) and is therefore less conspicuous than a walking crayfish. When the bottom of a pond or a lake is covered by

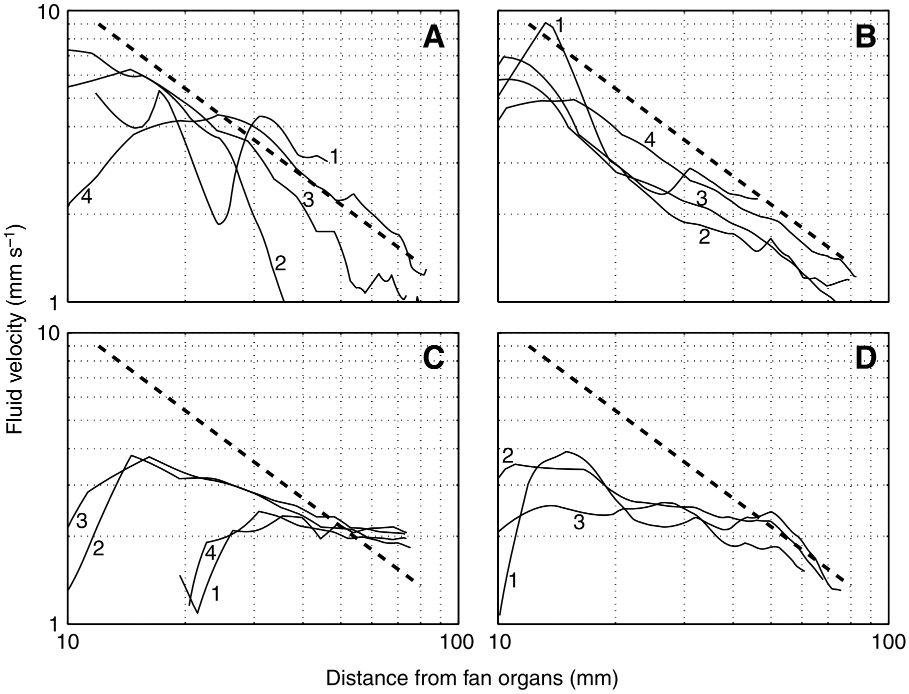

Fig. 8. Absolute value of fluid velocity plotted *vs* distance from the crayfish fan organs along the corresponding enumerated streamlines in Fig. 6A–D. Broken lines correspond to the velocity inversely proportional to the distance, as in Eqn 1.

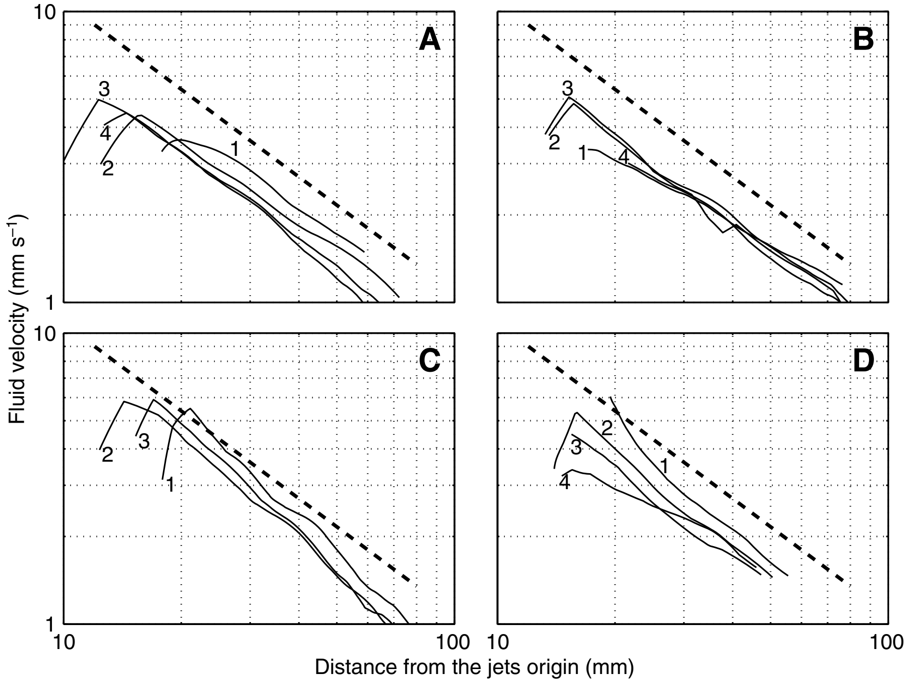

Fig. 9. Absolute value of fluid velocity *vs* distance from the jets origin along the enumerated streamlines corresponding to those in Fig. 7A–D. Broken lines correspond to the velocity inversely proportional to the distance, as in Eqn 1.

plants, scanning the environment with the help of jets also becomes energetically profitable, since the macrophyte stalks are less of an obstacle to the flow than they are to a walking crayfish.

To show that production of the jets is energetically affordable, we make an estimate based on parameters measured by Breithaupt (Breithaupt, 2001). Consider six appendages of the area A=10 mm^2, each waving with frequency f=6 Hz, amplitude a=5 mm, and velocity amplitude $u=2\pi fa\approx 20$ cm s^{-1}. Water density ρ=1000 kg m^{-3} and its kinematic viscosity ν=0.01 cm^2 s^{-1}. The Reynolds number of the flow around an appendage can be estimated as:

$$Re = \frac{u\times a}{\nu} = \frac{20\times 0.5}{0.01} \approx 1000\,, \qquad (3)$$

so that we can assume that the forces to be overcome by an appendage are defined by dynamic terms. Taking the drag coefficient to be 1 [(Prandtl and Tietjens, 1934) p.100], we have:

$$F_{\mathrm{drag}} \approx \tfrac{1}{2}\rho u^2 \times A = \tfrac{1}{2}1000\times 0.2^2\times 10^{-5} = 2\times 10^{-4}\ \mathrm{N}\,. \quad (4)$$

To calculate the force due to the acceleration of the fanning appendage (F_{acc}) we estimate its added mass as the mass of fluid of the volume equal to the cube of its span, i.e. as $A^{2/3}$:

$$F_{\mathrm{acc}} \approx \rho\times A^{3/2}\times 2\pi fu = 1000\times 10^{-15/2}\times 2\pi\times 6\times 0.2 \approx 2\times 10^{-4}\ \mathrm{N}\,. \quad (5)$$

We neglect the force associated with acceleration of an appendage itself because the mass of the appendage is significantly less than the mass of the fluid it accelerates by a stroke. Assuming that the fans are active for, at most, 50% of the time (being a very conservative estimate based on observations of *P. clarkii* activity in holding tanks; T.B., unpublished observations) we can calculate the energy required to wave the six appendages for 12 h a day for 1 week as:

$$E \approx (F_{\mathrm{drag}}\times a + F_{\mathrm{acc}}\times a/2)\times 6\times 7\times 12\times 3600\times 6 \approx 10\ \mathrm{J} \approx 3\ \mathrm{cal}\,. \quad (6)$$

Allowing for the variability of the appendage area, the beat frequency, and the efficiency of the muscles driving the fan organs (10%), the estimated energy can be up to 100 cal. This is 10 times less than the total energy of approximately 1 kcal gained by feeding, which corresponds to one shrimp fed to an animal every week. The fact that the energy expenses of fanning are not negligible may explain why the crayfish does not produce stronger jets to extend the range of odour acquisition.

Observations of an unrestrained crayfish show that it may use the fan organs both when walking and when hiding in a shelter. It suggests that the animal creates the inflow both to assist active search for food and to detect the food appearance in the vicinity of the shelter. To describe the exact way in which the crayfish utilizes the inflow it generates with the fan organs and to find if it uses the swimmerets to alter the flow, behavioural experiments are required involving the unrestrained animals in a large tank.

Experiments with the model (Fig. 7) suggested that the mechanism of odour attraction employed by the crayfish could well be adopted to design devices for finding chemical sources in stagnant fluids. Instead of scanning a region of interest with a probe, fluid from the region can be attracted distantly and driven through a significantly smaller sampling volume. Nozzle assemblies generating one or several jets should be more efficient in drawing distant odour patches to sensors than devices creating a point sink flow. Unlike the live animals, a man-made mechanic assembly has fewer restrictions on the parameters affecting performance of the system. By optimizing nozzle profiles the jets can be made more regular and by increasing the pump power jets can be made considerably longer than those generated by a crayfish. The intensity, the number, and the alignment of jets could be altered to obtain a desirable pattern of the inflow. Placing sensors at different locations around the nozzles would enable determination of the direction to the chemical source. Measurements of the time lag between switching the jets on and arrival of an odour plume would add data about the distance to the source.

With the inflow induced by excurrent jets, the range of odour acquisition and the directional sensitivity of the robot are defined by the length of jets rather than by physical size of the device. This would allow design of a relatively small probe with ability to access the obstructed area of interest. In some cases, induction of the inflow by jets would eliminate necessity of direct access to the area enabling, for example, chemical sensing through the mesh. Probes consisting of a sink, nozzles, and chemical sensors can be employed to search for leaks from oil or gas pipelines, to search chemical sources at the ocean bed, or for non-invasive flow monitoring. The idea is not restricted to the aquatic environment and can be used, for example, for the monitoring of plantations where access to the area of interest is restricted by stalks. A probe producing the inflow can be swept between the plant patches to measure the pesticide content or to sample the pollen.

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