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Phil. Trans. R. Soc. Lond. B 1998 **353**, 671-680
doi: 10.1098/rstb.1998.0233

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Observing free-swimming copepods mating

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Planktonic copepods are small transparent animals swimming in water. To observe how a male finds its mate, special optical systems had to be designed. The animals are treated as phase objects and matched spatial filters allow three-dimensional recordings of the swimming behaviour in a 1-litre vessel. Application of the techniques described shows how a male cyclopoid copepod swims for 20 s in synchronicity with the female before mating. Results stemming from observations with this optical system are published in this volume.

Keywords: cyclopoid copepods; mating; phase objects; spatial filtering

1. INTRODUCTION

Hensen (1887) coined the term 'plankton' on the suggestion of his colleague, Förster, for what was then known as 'Auftrieb', the material fished from the seas by fine-meshed nets. He defined 'plankton' as 'Alles was im Wasser treibt, einerlei ob hoch oder tief, ob todt oder lebendig' (Hensen 1887, p. 1). He then went on to discriminate between mero- ('periodischen') and holo- ('perenir-enden') plankton, but he made it clear that the essential criterion is that 'die Thiere willenlos mit dem Wasser treiben'. He emphasized that the copepods 'ogleich lebhaft schwimmend, werden doch willenlos mit dem Wasser fortgerissen'. Zooplankton has been marked since then as the marine or aquatic community of ever-drifting small animals, totally subject to the physical forces moving the surrounding waters; in short, it is perceived as living a 'life at random'.

The above definition of the term 'plankton' may have been too encompassing for most investigators. Hutchinson (1967) summarizes the many distinctions given to plankton of different size and composition, however, the notion of randomness remained and has become one of the paradigms of marine and aquatic biology. As paradigms tend to guide the approaches to research (Kuhn 1970), the tendency has been to minimize planktonic animals to points in space or to milligrams of material per square metre of surface area, integrated over entire water columns. For example, studies in the predator-prey relationships of zooplankton have involved modelling the encounter rates between different kinds of moving 'dots' in a three-dimensional space (Gerritsen & Strickler 1977). This applied mathematical approach focused on the underlying principles of search and encounters under different regimes (e.g. Koopman 1956; Kohlas 1967). Gerritsen & Strickler (1977) assumed that their animals are randomly distributed in space and move in random directions independent of each other and of any environmental parameters (figure 1a). They also assumed that the encounter volume is a sphere and defined an encounter as when a prey swims into the encounter volume of a predator. Giguère *et al.* (1982) adapted the equations to

include elongated predatory animals with cylindrical encounter volumes.

This mathematical approach, extending the paradigm to the fullest, met with considerable success. Rothschild & Osborn (1988) modified the equations to include small-scale turbulence, again a random factor, to show that turbulence can enhance encounter rates between the 'dots'. Current attitudes on the relationships between turbulence and plankton (Marrasé *et al.* 1997) indicate that the paradigm is still determining research agendas.

There is, however, one problem with this paradigm: mating. If the animals, males and females of different species, were randomly distributed and swimming (slowly when compared with the forces of nature) in random directions, there may be too few encounters between mates to ensure a next generation. The problem is primarily one of human perception. Assuming that each litre of water within the upper 200 m of the water column of all surface waters contains on average two copepods, the estimate of one hundred billion trillion copepods alive today would seem enough to provide successful mating encounters. However, the average distance between potential mates may be too great, metres to tens of metres, for these millimetre-scale animals, swimming in random directions at millimetres per second, to encounter each other within the temporal window of sexual receptivity.

Katona (1973) provided evidence that copepods may use pheromones to enlarge their encounter radius (figure 1b). This may work but it may be energetically very costly for animals as tiny as copepods to create a sufficiently large 'active space' (Bossert & Wilson 1963). Two behavioural patterns could increase the numbers of animals per volume and, therefore, decrease the distances between them. First, the pattern of 'diel vertical migration' brings the animals into the upper layers of the water column at night. In the late afternoon they would begin to show a bias according to changes in the ambient light regime (e.g. Strickler 1970). They would swim less in the direction of gravity under decreasing light conditions than when the light intensity is constant (figure 1c). For most of their lives gravity is the only environmental cue for orientation in these animals and, since most are negatively buoyant,

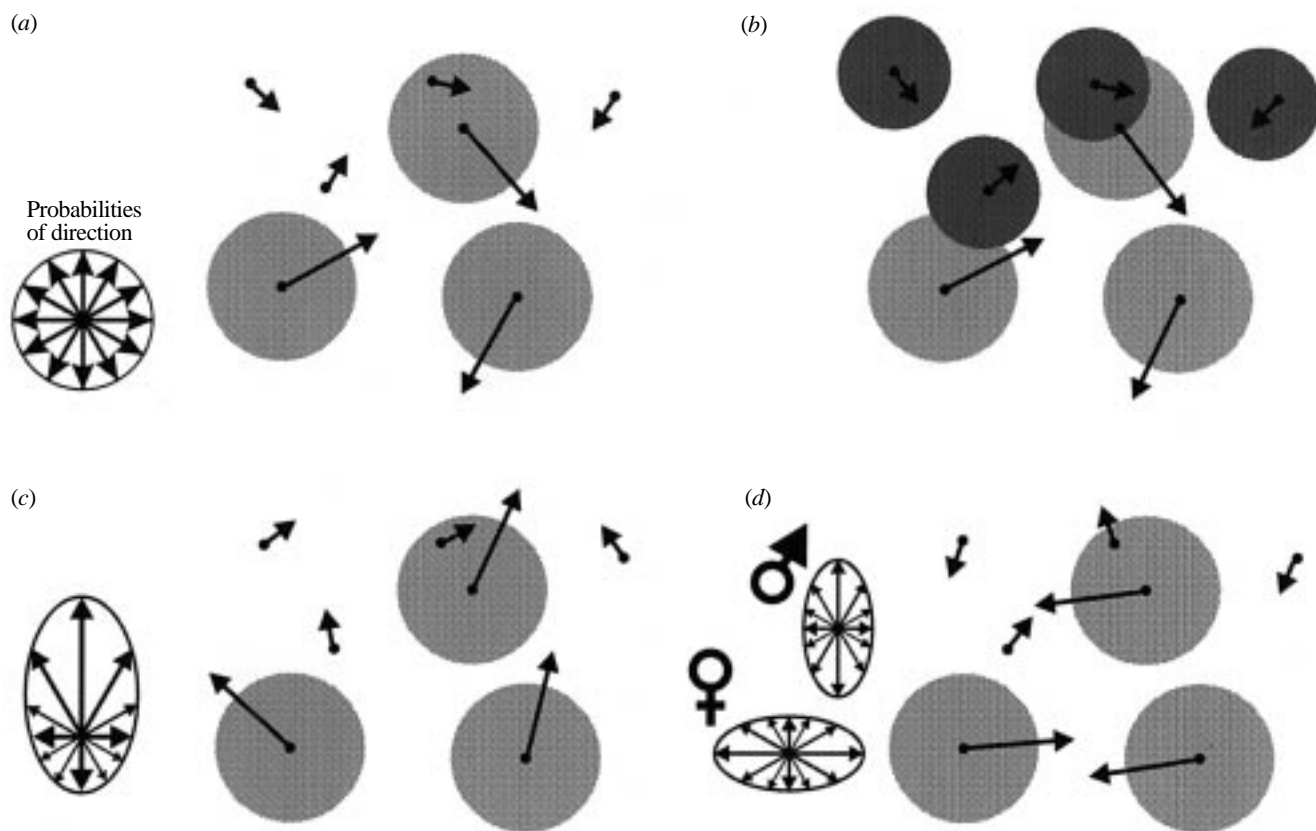


Figure 1. The assumptions governing models of encounter rates (males represented by long arrows, higher velocity, and with encounter sphere; females with shorter arrow): (a) swimming in random directions; (b) swimming in random directions but females producing active space with pheromones; (c) swimming directions biased by vertical migration; (d) males swimming preferentially in the vertical plane, females in the horizontal plane.

they can perceive 'down' (Strickler & Bal 1973). Second, Gerritsen (1980) showed that encounter rates would increase if one sex swims mostly in the horizontal plane and the other mostly in the vertical plane (figure 1*d*). Yen (1988; see also Brewer, this volume) observed that zooplankters behaved in exactly this way. Hence, the concept of a 'life at random' may not be an adequate description of the planktonic realm.

The central question is: how do zooplankters of the same species and opposite sex encounter? Once mates encounter each other there may be elaborate courtship behaviours before mating takes place. Jurine (1820) described the mating process in a variety of zooplanktonic crustaceans in remarkable detail (figure 2) based on observations of live animals. Blades & Youngbluth (1979) observed how the fifth legs of some calanoid copepods and their complex spermatophores function as a 'lock and key' mechanism and act as mechanical isolation mechanisms (Mayr 1970). These observations, as well as Katona's (1973), were made by adding males and females to a small volume of water contained in a laboratory vessel. In nature, however, mates have to encounter each other first.

Strickler (1970) observed continuously 50–80 cyclopoids in a 5-l vessel for more than 2 h using infrared illumination. The animals avoided each other, some followed others for a short distance and some seemed to stake out a small 'territory', carefully termed the 'lingering space'. With the development of a modified Schlieren technique (Strickler 1977), the swimming tracks of moving zooplankters could be recorded (figure 3) and inferences drawn

about recognition of each other's 'territory' and potential mates (Kerfoot *et al.* 1980). After such observations Yen & Strickler (1996) proposed that 'footprints', species-specific mechanical disturbances possibly in conjunction with chemicals, may provide copepods with significant information, dispelling the notion of a life at random.

To test whether additional cues and behaviours are involved in encounters between the sexes of copepods new techniques had to be designed. In this paper, the design and development phase of these techniques is described and discussed, highlighting the feedback loops in which results have led to further redesigns and improvements. The results of targeted research into mating encounters between copepods are discussed in other contributions to this volume (Doall *et al.*; Weissburg *et al.*; Yen *et al.*).

2. METHODS

(a) *Optical signal processing*

In Strickler & Hwang (1998) the difficulties in observing planktonic life in the oceans and in the laboratory were outlined. The majority of marine and aquatic life forms are small and transparent. It is necessary to observe animals in the 100 μm to 5 mm size range, as well as their food, algal cells of 5 μm to 1 mm. In addition, the animals require adequate space so that their behaviour is not influenced by 'wall effects' (Zaret 1980). These three constraints (transparency, small size, large volume) have been overcome by treating the animals and the algae as phase objects and applying an optical system that

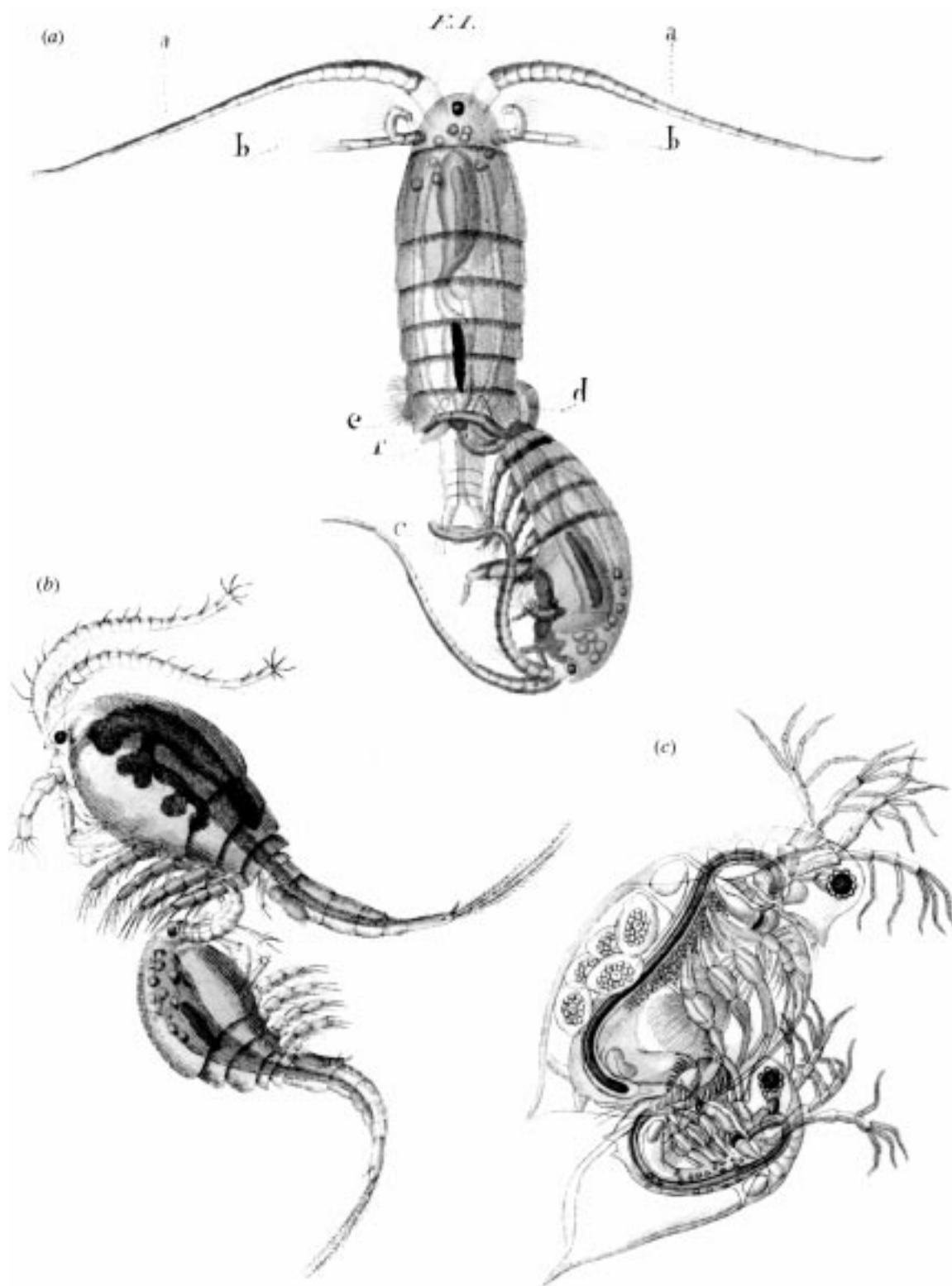


Figure 2. Early illustrations of mating behaviour in various freshwater zooplankton: (a) *Diaptomus*, (b) *Cyclops* and (c) *Daphnia pulex*. All from Jurine (1820).

functions as an optical signal processor (VanderLugt 1992) using matched spatial filters. It is derived from the classical Schlieren system (Toepler 1866) and has, instead of a slit as the first spatial filter and a knife-edge as the matching one, a point source (pinhole) as the first and a stop as the matching one (figure 4).

The light source is either a helium-neon laser (632 nm wavelength) or a near-infrared laser diode (890 nm wavelength) with energies of less than a milliwatt. The collimated laser beam of about 3 mm diameter is focused by a 10× microscope objective into the pinhole of the spatial filter. The concentric waves passing the filter are

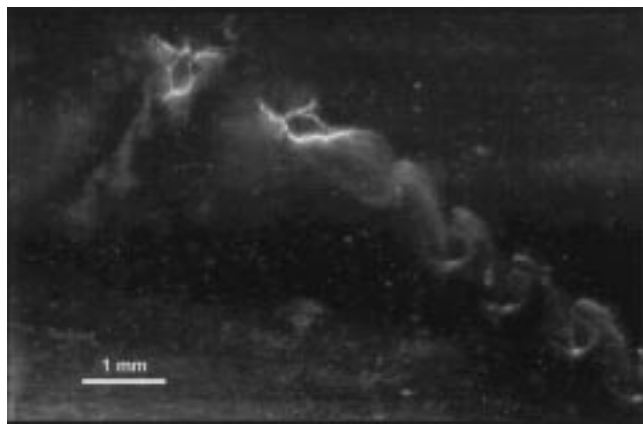


Figure 3. One field from a video of swimming zooplankters in a Schlieren optical system. *Cyclops scutifer* (right) shows a typical hop and sink pattern with distinct hydrodynamic disturbances. *Daphnia pulex* (left) disturbs the water much less. These footprints are visualized using a small density gradient in the medium.

collimated by a spherical mirror (Newport Corp., $F/9$) producing a collimated light beam of 150 mm diameter. As the aspect ratio of TV frames is 3:4 and the system is designed to observe moving animals without losing them in the largest volume with greatest depth (z -axis), a vessel 90 mm wide and 120 mm high is used. This vessel is located within an outer vessel. The water surrounding the inner vessel serves as a water jacket and is kept at a constant temperature appropriate for the experimental organism. The outer vessel serves also as an optical element that eliminates additional diffraction due to the unequal passage of light through and around the observation arena.

As an objective another spherical mirror of 150 mm diameter is used in combination with a high-quality photographic lens as the eyepiece (Carl Zeiss Hasselblad). Exchanging the eyepiece lens (80 mm, 150 mm or 250 mm) defines the observation arena: the full vessel with the 80 mm lens, smaller volumes at higher focal lengths. This is achieved without changing the optical path or the distances between the elements. The use of large-format camera lenses allows the TV camera to be dynamically repositioned to follow a swimming animal. The TV camera is mounted on its side to permit recording over the full frame even though this has the disadvantage that the animals appear to sink to the side of the monitor instead of downwards.

The focal plane of the objective is also the plane of the 2D Fourier transform of the collimated light beam and all other incoming optical information (Strickler & Hwang 1998). The parallel light (DC signal) is focused at the origin of the transform and removed by a binary filter, a black dot on the optical axis. When the observational vessel is filled with filtered water additional binary filters are used to eliminate any impurities in the optical system. A video camera (Sony, Model XC-77 with IR filter removed) is used which is sensitive in the near-infrared range and allows recording at ambient visual light intensities similar to or lower than natural levels. The use of digital imaging equipment (Amiga 4000 PC with V-Lab video board) provides a temporal resolution of 17 ms between observations (60 fields s^{-1} or $60 \text{ JPEG files s}^{-1}$). This resolution is only just sufficient because most planktonic animals can accelerate to speeds many times their body lengths (e.g. Strickler 1977). In addition, the use of a matched filter optical path records the position of particles smaller than the geometric resolution would allow because the light dispersed by the particle is registered.

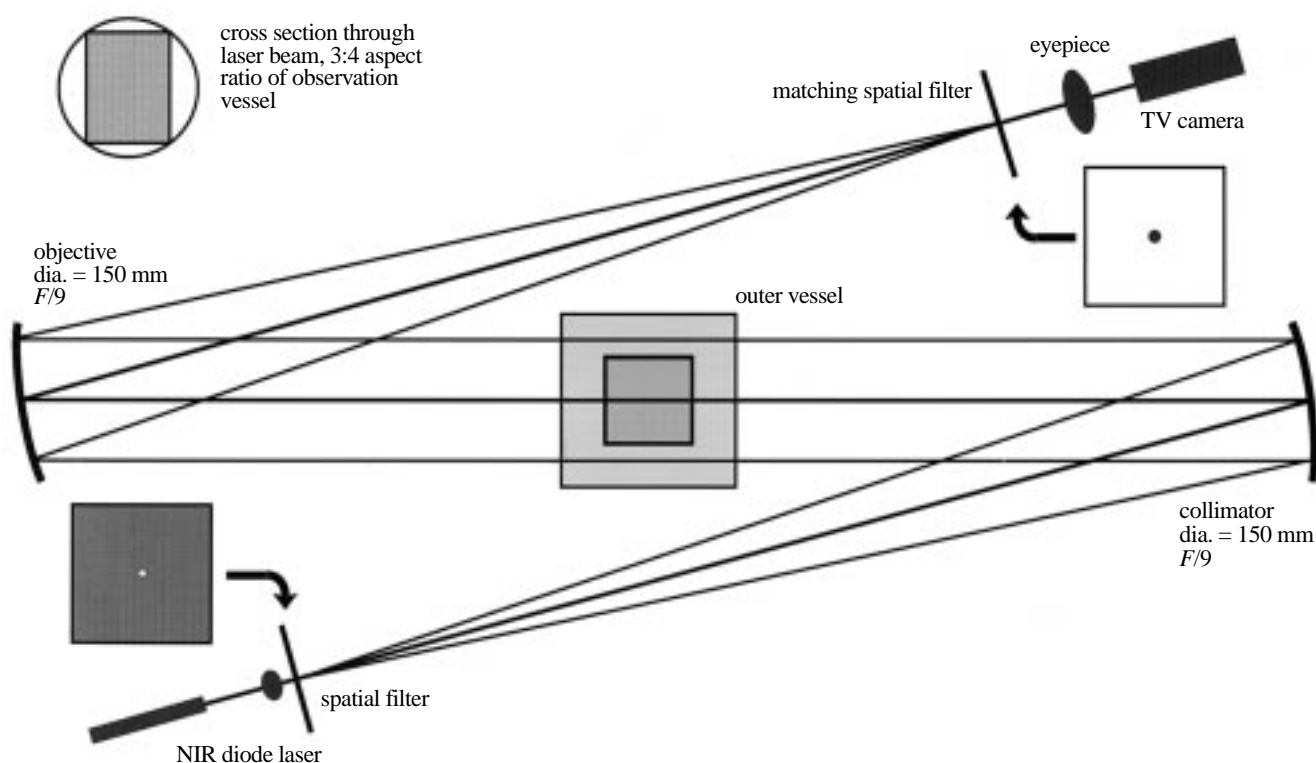


Figure 4. Optical system with matched spatial filters used to visualize phase objects swimming in the inner water vessel.

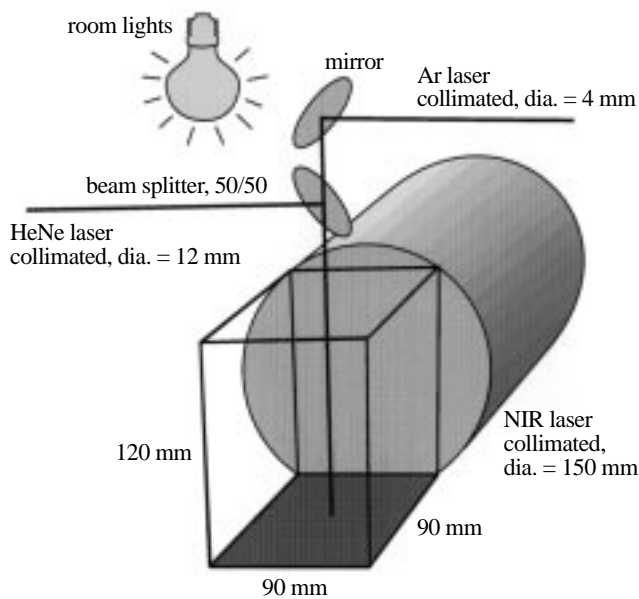


Figure 5. Use of the strange attractor to concentrate the swimming animals in the centre of the vessel.

(b) Laser beam as a strange attractor

Mandelbrot (1982) introduced fractal geometry to biologists and with it the concept of a strange attractor. In practice this means a physical or chemical property which attracts free-swimming animals causing them to swarm within a subset of the space within the vessel. Most crustacean zooplankters are attracted to a vertical laser beam of blue or red colour, but they are not attracted to a horizontal beam. The motions of the animals in a vessel of about 1-l volume were recorded using a near-infrared laser for observation (figure 5). A 10 mW argon laser beam was projected, via a mirror, through a beam splitter into the vertical symmetry axis of the vessel. The beam splitter allowed the addition of a concentric red helium-neon laser beam of the same power. Trial experiments had shown that the blue laser beam is sufficient to act as a strange attractor, whereas the red beam alone is barely perceived as an attractor. No beam does not concentrate the animals within the inner volume of the vessel.

(c) Observing in three dimensions

The strange attractor provides a method for keeping the animals away from the vessel walls. The problem now is to observe them in three dimensions and to obtain $x/y/z$ data over time for each animal within the vessel. Stereo vision is based on perceiving a scene with two vision receptors some distance apart. The two pictures then are compared and the third dimension, the axis perpendicular to the base line between the two receptors, is estimated. However, the smaller the distance between the receptors in relation to the distance to the scene (angle α in figure 6a) and the larger the single pixels, the larger is the error estimating the distance to the scene (Δy in figure 6a). This error is smallest when the angle α is 90° .

Stereo reception necessitates the use of two receptors. The use of two TV cameras and two videotape recorders allows the comparison of two fields taken perpendicularly, x and z values from one field and the corresponding y and z values from the other. However, the two recording

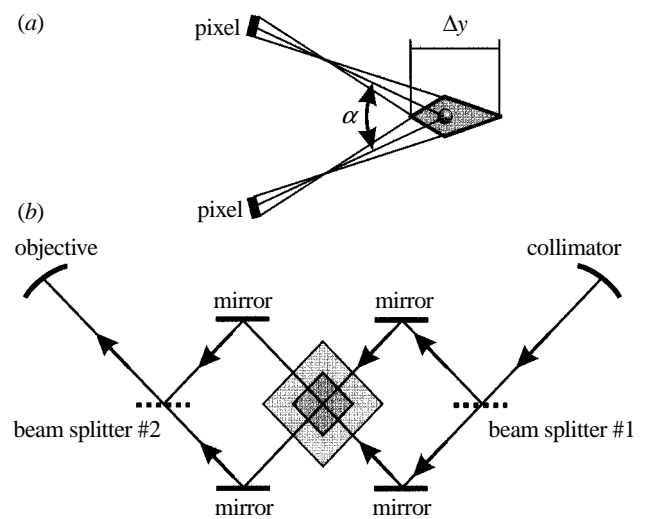


Figure 6. Schematic of the three-dimensional observation system demonstrating (a) why an angle of 90° allows the smallest error in estimation of coordinates, and (b) the optical pathway allowing observation of both front and side views with a single camera.

system must be synchronized. The two systems can be synchronized electronically (Strickler 1985; Crenshaw 1991). However, the design of the optical system used here allows an optical synchronization that necessitates only one recording system (figure 6b).

The collimated beam is split into two beams of equal strength (beam splitter 1 in figure 6b). Two mirrors direct these beams through the observation vessel at an angle of 90° . Two additional mirrors redirect the beams on to a second beam splitter, which combines the two beams into one. The use of matching spatial filters can filter out all the undesired information from each beam. The two beams are set up so that in any one frame the x/z is one line lower in the z -axis than the superimposed y/z picture. In this way the x , y , z coordinates of every animal can quickly be read without having to establish which image corresponds to which view.

The optical arrangement shown schematically in figure 6b is shown in figure 7. The system is set up on an optical table (Newport Corp.) which is isolated from vibrations and totally covered so that the blue laser beam in the observation vessel is the only visible source of light. The expanding beam from the first spatial filter is folded to save space, as is the beam between objective and eyepiece. For adjusting all mirrors and the large water vessel, a helium-neon laser was used and then replaced by the near-infrared laser for experimentation.

(d) Live material for testing

For the observation of mating in cyclopoid copepods, live material of both sexes of *Cyclops scutifer* was caught from Lake Meach (Province de Quebec, Canada) in Spring 1978. Approximately 80 *C. scutifer* and 150 *Bosmina coregoni* were placed in the 5-l vessel, fully exposed to daylight. The light source for the optical path (figure 4) was a xenon high-pressure burner (Carl Zeiss) and 16 mm black and white cine film (Kodak Plus-X Reversal) at 25 frames s^{-1} was used for recording with a Bolex-EL camera. For testing the effectiveness of the optical

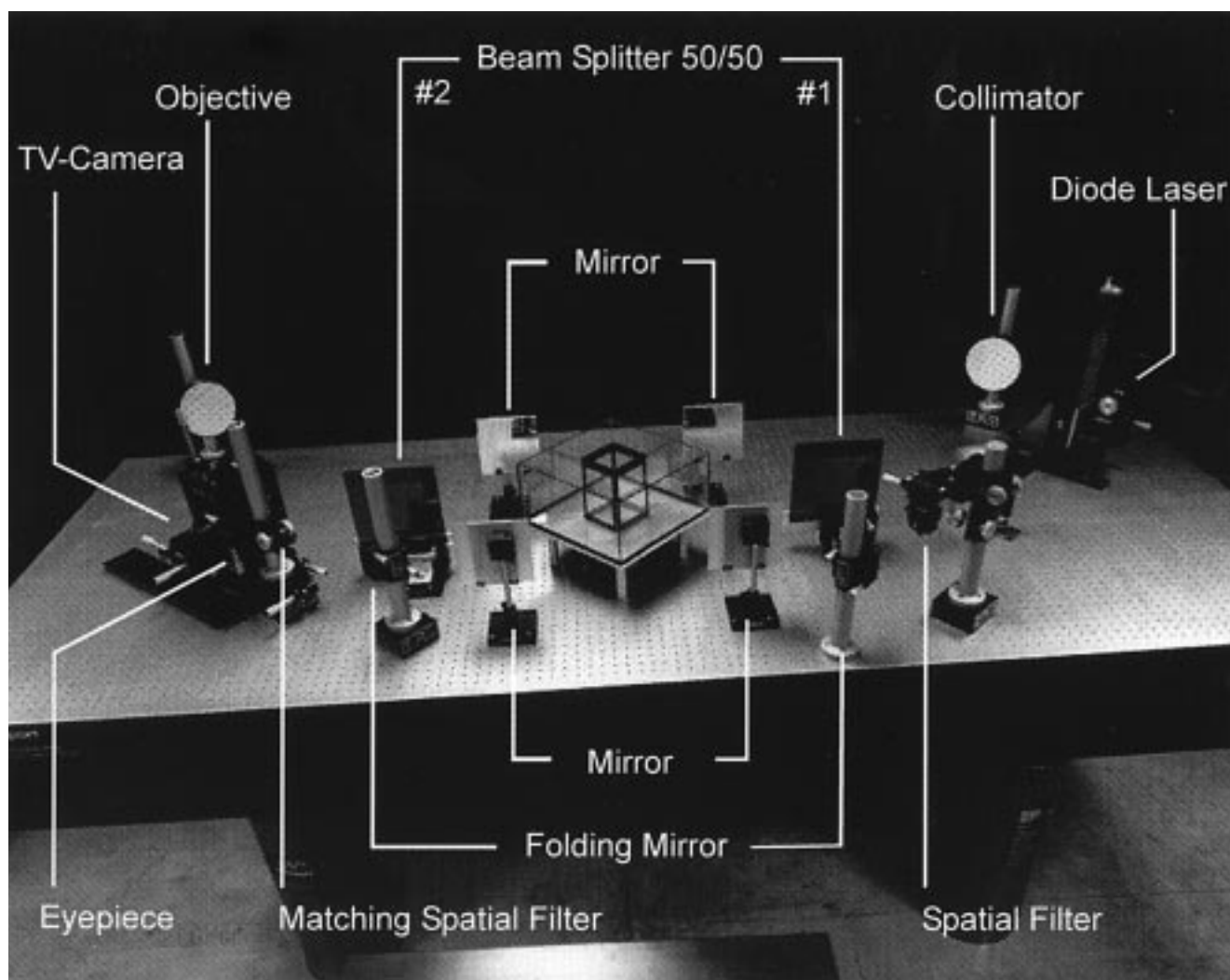


Figure 7. Optical table (3 m × 1.2 m) with the optical, three-dimensional observation system used to study swimming behavior of zooplankters (table and all components, Newport Corp.)

designs, laboratory cultures of *Daphnia pulex*, *Cyclops scutifer* and *Chydorus sphaericus* were used.

3. RESULTS

(a) *Mating in Cyclops scutifer*

Analysis of the 30 s before a mating event shows no contacts for the first 10 s and no perception of each other by either sex (figure 8). After 10 s the male appears to perceive the female, matching his swimming pattern to hers jump for jump. Cyclopoid copepods show the typical hop and sink swimming pattern with about one jump s^{-1} and each jump covers a distance of 1–2 mm (figure 3). For the next 20 s the male followed the female remaining at a distance of about 2–3 mm from the female, about two jumps behind (figure 9). The synchronization in swimming motions is best seen in figure 10, where the speeds of both sexes are plotted. For a period of 20 s (A to B in figure 10) it shows remarkable synchronization, maybe with an undetectable time lag between male and female. After 20 s of following the female the male executed one larger jump bringing himself into contact with the female (B in figures 9 and 10). The male grasped the female and transferred the paired spermatophores on to the genital

double-somite and after less than 3 s they separated (C in figures 9 and 10).

(b) *Swarming around a strange attractor*

The effectiveness of the vertical laser was demonstrated using hundreds of *Chydorus sphaericus*. The videotape was started while the room lights were on (figure 11a) and all animals were concentrated on the bottom of the vessel, mostly in the left corner. Two seconds after the room lights were turned off, with the light regime consisting of only the strange attractor, the animals swam up off the bottom, into the middle of the vessel (B to C), to be concentrated within the laser beams (D to F). For animals of only 0.3 mm in size this swimming performance is quite remarkable. Some swam 300 body lengths in 20 s. However, repeated experimentation showed that the response ceases after about 10 repeats of light and dark alternations, probably through habituation.

(c) *Three-dimensional observations*

One field with *Daphnia pulex* swimming around the strange attractor is shown in figure 12. The matching filter is set up to highlight the positions of the animals, and not the details of the animals or the algae (see

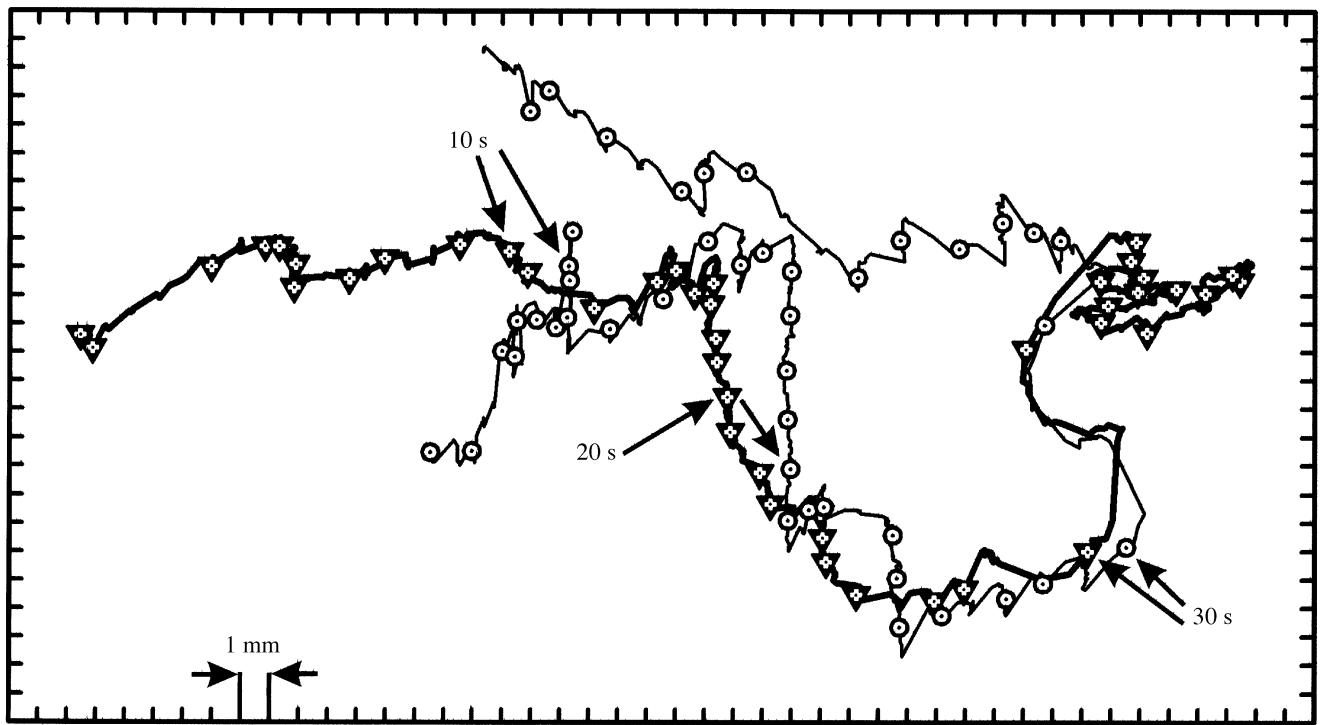


Figure 8. Observation of mating in *Cyclops scutifer*. The male (inverted triangles) swims at random until encountering a female (circles) after 10 s. The male follows the female for the next 20 s, at 30 s they mate. The interval between markers is 1 s.

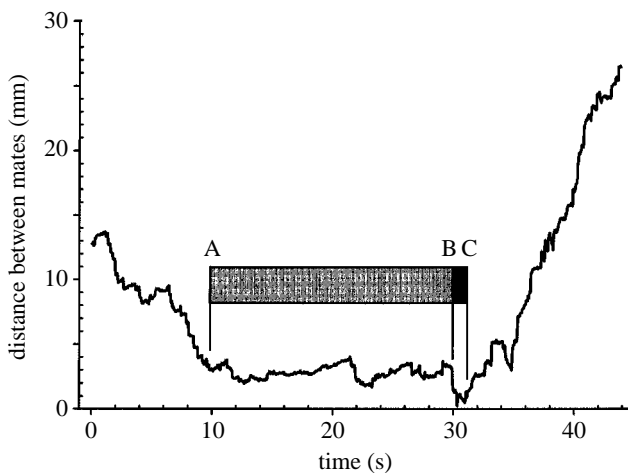


Figure 9. Distance between male and the female during the observed mating. Between A and B the male maintains a more or less constant distance from the female. Mating takes place during the phase from B to C.

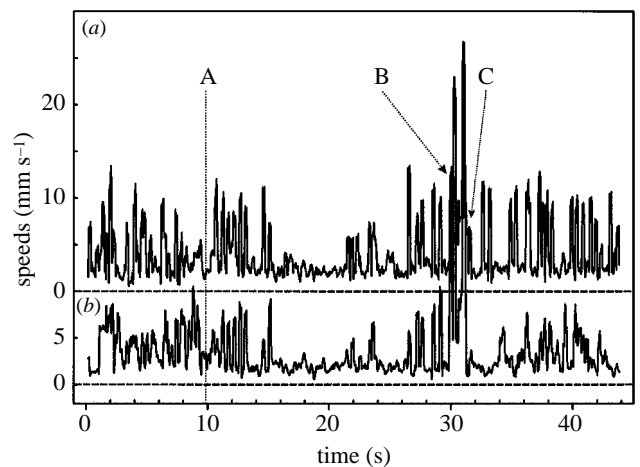


Figure 10. Swimming speeds of (a) female and (b) male during the observed mating. Note the synchronized swimming during the phase from A to B and the high speeds during mating (B to C).

Strickler & Hwang (1998), for details on spatial filtering). The one line difference between the x/z and y/z images allows rapid identification of the coordinates. The resultant video is analysed in sections of about 30 s subdivided into about 1800 pictures, as in figure 12. One picture can be viewed at a time and by clicking with the mouse on the positions of the animals, the coordinates of these positions can be stored in a spreadsheet and the next picture (even or uneven field of a video frame) is automatically exposed. Alternatively the picture can be transferred to a series of JPEG files which can then be analysed using graphics programs such as Photoshop (Adobe).

The data on the spreadsheet are in the form of time with as many $x/y/z$ coordinate triplets as there are animals. Analysis programs, for example SigmaPlot (SPSS), are used for processing the coordinates. Figure 13 is a rendering of one data set at one point in time (same as figure 12). The program also allows rotation of the volume in order to see, for example, down the blue laser beam, or the viewpoint in three dimensions can be attached to one animal so that all other animals, their positions and swimming directions are viewed dynamically from the moving standpoint of the one individual. Using this system it is possible to examine the mating behaviour of zooplankters

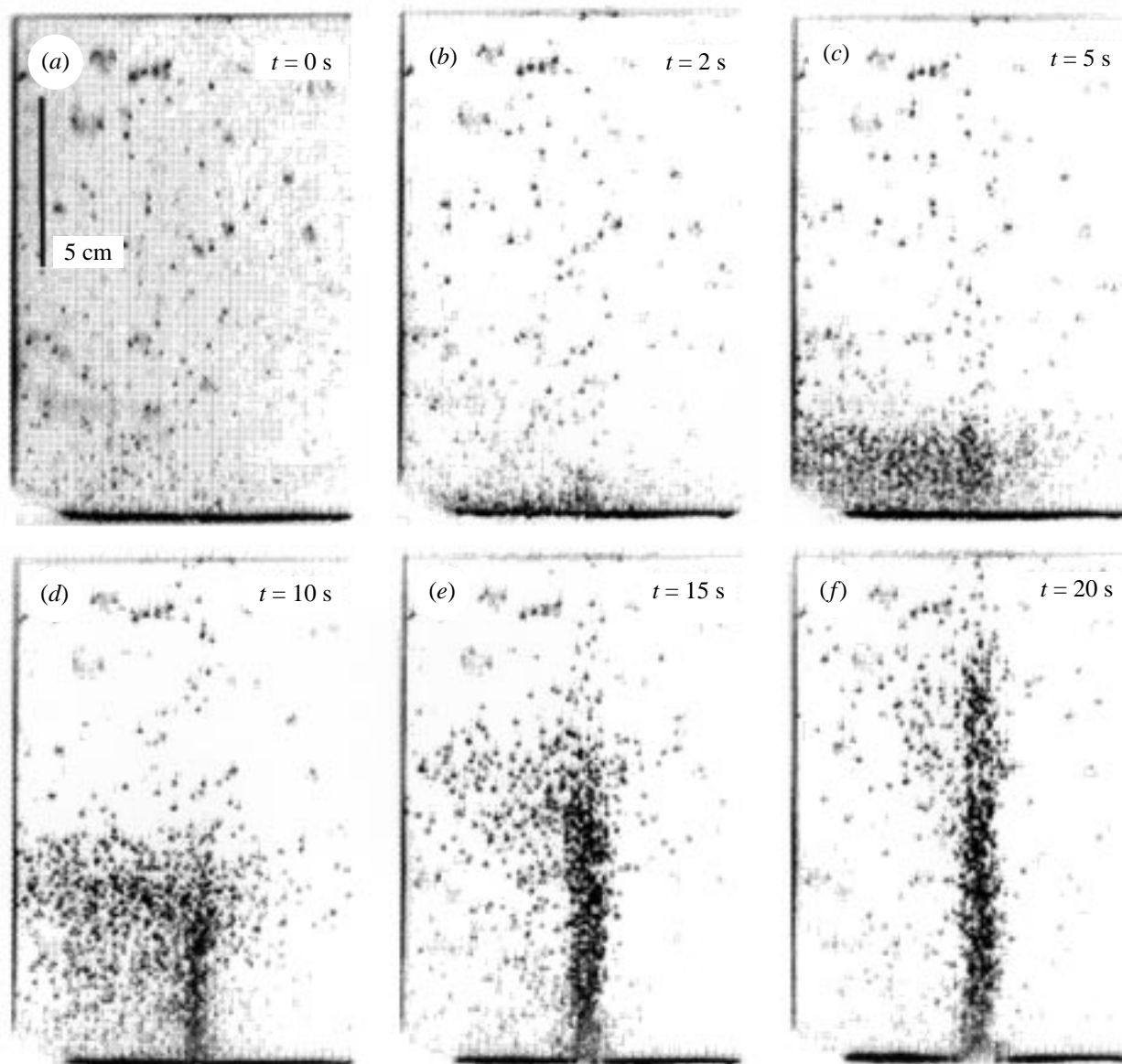


Figure 11. Six fields from a video of swimming *Chydorus sphaericus*. (a–c) When illuminated by ambient room lights the animals are located on the bottom of the vessel. (d–f) When the lights are turned off they leave the bottom and swim towards the strange attractor.

at the appropriate spatial and temporal scales (Doall *et al.*; Weissburg *et al.*; Yen *et al.*, this volume).

4. DISCUSSION

(a) *Mating in Cyclops scutifer*

The ‘jumping in synchronization’ of *Cyclops scutifer* closely resembles the ‘tandem running’ of ants (Wilson 1959; see Hölldobler & Wilson 1990). In ants it helps to recruit a nestmate, and the follower stays in antennal contact with the leader. In planktonic copepods the two individuals do not have to stay in direct contact because viscosity connects them over a distance of 2–3 mm anyway. During this phase the male may be confirming that the female is conspecific and ready to mate, as females of other species differ in frequency of jumping and in jump length (J. R. Strickler, unpublished observations). Pairs of mixed species composition, therefore, will not remain in synchronization during this 20-s long

phase of the mating behaviour. The simultaneous execution of jumps may also provide information to the female, for example, that the animal following is not a predator. However, during a jump the antennules are used for locomotion and may not perceive any information (Strickler 1977). Hence, the female may not perceive that a male is following and may execute an escape reaction only when grasped by the male (B in figures 9 and 10). This may also explain why mating is executed in such a short time and why the animals display high speeds between B and C in figure 10.

(b) *Observing in three dimensions*

The cine film used in observing *Cyclops scutifer* mating (figures 8, 9 and 10) is of limited use because the spatial relationship between the two animals in all three dimensions cannot be determined. The mating event took place in a space 45 mm wide and 25 mm high and happens to be in perfect focus throughout. For animals swimming faster

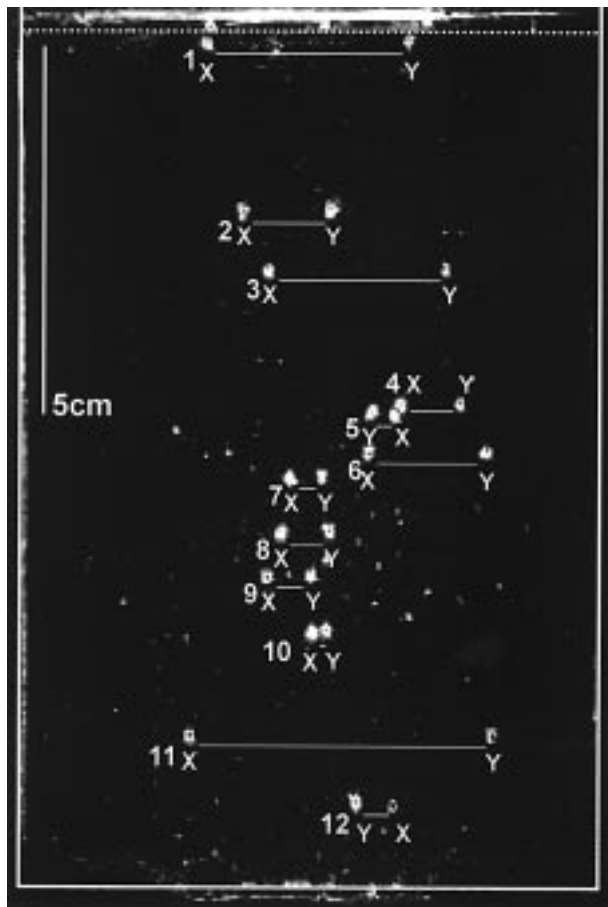


Figure 12. One field from a video of swimming *Daphnia pulex*. The optical system allows front and side view information in the same field and read-out of all three coordinates (x , y and z).

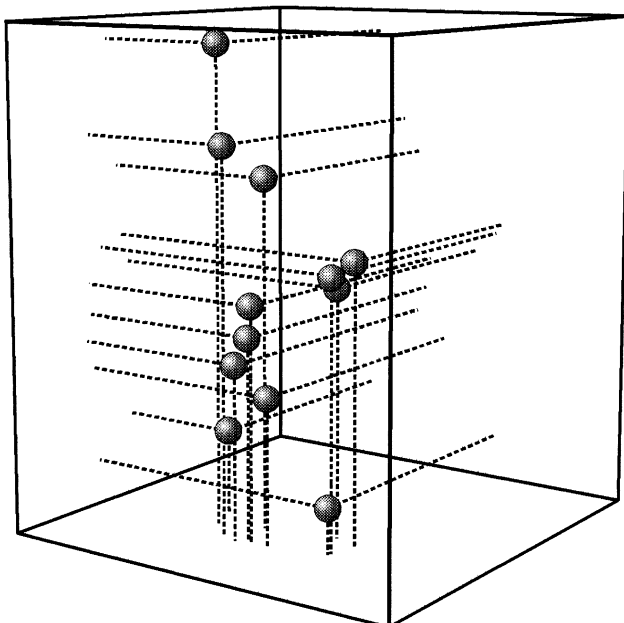


Figure 13. Three-dimensional representation of the spatial information derived from the field of figure 12. The vessel is 90 (width) \times 90 (length) \times 120 mm (height).

than *Cyclops scutifer* this space may be larger, but it is likely that any mating between planktonic copepods will be on a temporal scale of between 10 and 100 s. Additionally, this preliminary cine study demonstrated that there is informa-

tion flow between the partners, at least unidirectionally from female to male. To observe mating in free-swimming planktonic copepods it is necessary to maintain them near the centre of the observation vessel by stimulating them to the centre before reaching the walls of the vessel. Therefore the animals will be swimming for more than 100 s within the vessel and along convoluted paths without being disturbed by an encounter with the walls. In addition, the density of animals in a 1-l vessel must be kept low enough to prevent a too high frequency of encounters or they may react constantly with escape jumps.

Read-outs of the full length time series of the coordinates of each animal are necessary. As will be shown in the contributions of Doall *et al.*, Weissburg *et al.* and Yen *et al.* (this volume) local information may still be around changing the swimming pattern of an animal tenths of seconds after another one passed a location. Without precise three-dimensional time series it would be very hard to infer and estimate parameters involved in the full mating behaviour of crustacean plankton.

(c) *The paradigm of plankton*

Plankton, the ever-drifting community of small animals and algae, may not have a 'life at random'. For them, at their scales, water may not be so turbulent because their lives happen to be close to or below the scales of Kolmogorov (Granata & Dickey 1991). Whether the information put into the surrounding water by a swimming animal (the footprints in Yen & Strickler (1996) or the chemicals in Yen *et al.*, this volume) stays as laid down or is stretched out due to strain and vorticity, it is still there in such a way that animals using this information can follow the information and catch up with its source. Further research, especially into the mating biology of zooplankton, should clarify the point that a paradigm shift may be in order.

Support from grants (National Science Foundation USA OCE-9402910 and OCE-9409073) are acknowledged. Ms Eleanor Hing Fay digitized the data for figures 8, 9 and 10 and Professor Yen sent her students with male and female copepods to Strickler's laboratory creating the challenge to design the optical three-dimensional system.

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