Emergence of Vortex Swarming in Daphnia

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Abstract

Swarming formation is a commonly observed group behavior in various biological systems. It is an example of emergent global pattern in a collection of individuals who follows simple-minded rules. In this paper we will discuss a special phenomenon of swarming, vortex swarming, that is observed in high-density population of *Daphnia*. Particular interest lays in the transition from a low-density, normal swarming state, in which rotation direction is equally probable among the Daphias, to the high-density, vortex swarming state, in which nearly all Daphnias rotate in one direction. We will examine the observations, mathematical models and simulations for both states, and discuss the possible parameters controlling the activation of vortex swarming formation.

I. INTRODUCTION

Swarm intelligence is ubiquitous in the biological world. It is the phenomenon of collective behavior emerged from each individual (agent) following a set of simple rules. The global pattern is often advantageous to the organisms, let it be maximizing food collection, avoiding predators, or aiding mating process and reproduction. There are strong motivations to understand swarm intelligence, and one of them is its applicability in designing high-performing artificial systems by constructing a collection of uncomplicated agents described by simple codes[1].

Swarming is an example of swarm intelligence. It is the occurrence of overall rotational motion in a group of agents. When all agents rotate in a single direction, vortex swarming is formed.

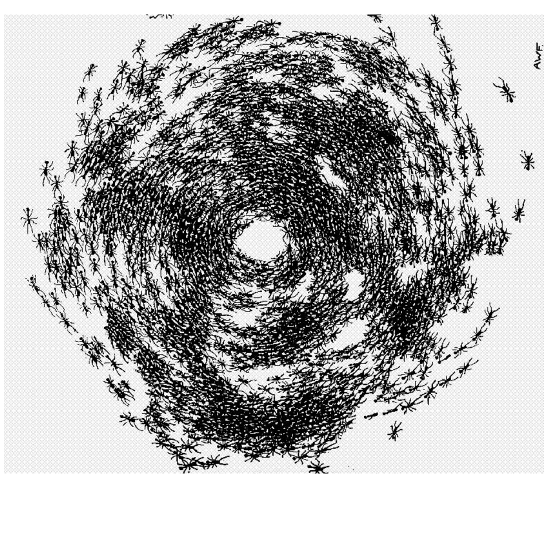

Fig. 1: A sketch of an army ants' swarming pattern from "Army Ants, a Study in Social Organization" by T. C Schneirla. Since the velocity vector of each ant is not specified, it is unclear if this depiction is a vortex swarming.

Daphnia is one of the many biological systems having been observed to practice swarming. It is more commonly known as "water flea", lives in clear water, and is often the prey of bigger organisms, for example paddlefishes, in the ecological system.

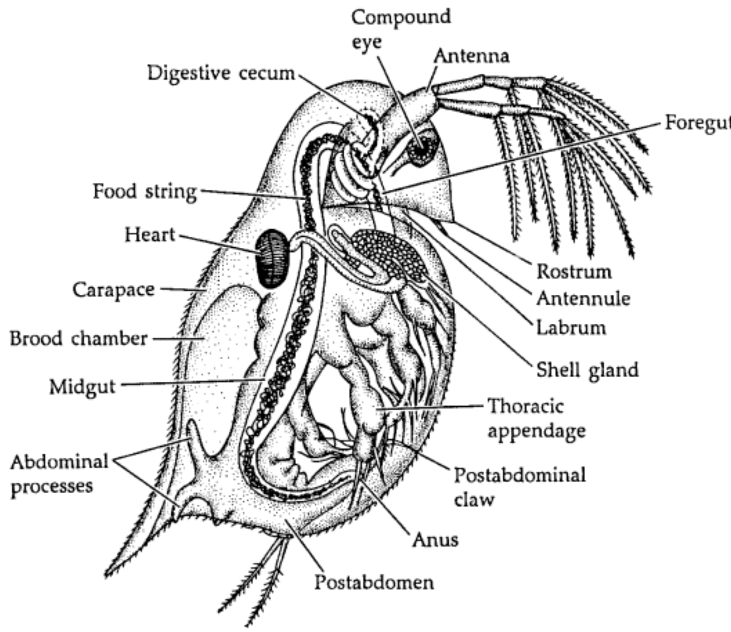

Fig. 2: LEFT[2] -- Typical body size of a daphnia is 1~3 mm. The average lifespan is about two weeks.
Fig. 3: RIGHT[3] -- Anatomic diagram of a daphnia. Daphnias have sensory eyes that detect light sources. They move in water by thrusting antenna in water.

Daphnia possesses several special characteristics that make it an interesting specie to study. Just like another popularly investigated organism, *Drosophila*, Daphnia also has short lifespan and quick reproduction rate. But unlike Drosophila, which has higher mutation rate that renders it ideal for genetic research, Daphnia is evolutionary completed. This means the specie has found the fittest phenotypes for its environment, and deviation/mutation is rare, so that the gene pool nearly does not fluctuate. Therefore researchers do not need to worry about the extra controlling parameter due to individual variations. Also, since Daphnia moves in water, its motion is slower than Drosophila and easier to observe and model. Below is a brief list of recent research interests on Daphnia.

1. **Sexual vs. Asexual Reproduction:** When a group of Daphnia is presented with an ideal environment, all its members would be female and they reproduce asexually. Therefore offspring are the identical genetic copies of their mothers, and reproduction cycle is very fast. But when the environment is less than ideal, half of its member shifts to male, and sexual reproduction dominates. Possession of both reproduction schemes makes Daphnia an ideal candidate for the study of the difference between sexual and asexual reproductions, and may help to understand why the former is more prominent among higher order organisms. Recently a study found the amino acid that triggers the transition between the two reproduction mechanisms in Daphnia[4,5].

2. **Optimal Foraging:** Daphnia acquires food by hopping in water. During each hop, water flows through Daphnia, which filters and intakes food. Given that Daphnia has attained its fittest evolutionary model, its hopping scheme would be the one that's most

optimal for its survival. In fact, studies have shown that Daphnia has a preferred hopping angle, which is the same angle that's most optimal for a simulated self-propelling Brownian-type hopping object to maximize food intake while minimizing energy usage[6]. Such study has useful applications in, for example, naval activities.

3. **Photoreceptor Mechanism:** It is believed that Daphnia is blind to infrared light, while being attracted to visible light[7]. This selection makes its photoreceptor in the compound eye interesting. Another study shows the effect on Daphnia's behavior due to urban light pollution[8]. It is yet to be understood exactly what is the molecular structure of Daphnia's photoreceptor, and what is the mechanism of its interaction with photons of different energy.

4. **Swarming and Vortex Swarming:** Daphnia is attracted to visible light, and when a light source is present, a single Daphnia would rotate around it (more precisely, hop in a random-walk fashion with average path forming a circle with the center being the light source). There is no preferred direction of rotation, in fact, a single Daphnia can change its rotational direction during an observation. When a group of Daphnia is present with a light source, each would proceed with the cycling motion, forming a low-density swarming pattern, with approximately half in clockwise rotation and the other counterclockwise. If the Daphnia concentration is high enough, the symmetry of equally-favoring-both-rotational-direction would break down, and the entire group would circle around the light source in a single direction, forming a vortex swarm. This phenomenon is of the interest of this paper.

II. Mathematical Model of Daphnia Motion[*]

Non-interacting Daphnia Model in an External Potential[**]

Each individual Daphnia is a self-propelled agent, and it is most often modeled as an active Brownian particle. An active Brownian particle can self-propel by intaking energy from its environment for conversion into kinetic energy. We will also incorporate fluctuations in particle motion by including a stochastic force term. With these considerations, the *i*-th particle would have position $\mathbf{r}_\mathbf{i}$ and velocity $\mathbf{v}_\mathbf{i}$ described by the following equations of motion:

$$\frac{d\vec{r}_i}{dt} = \vec{v}_i$$

$$\frac{d\vec{v}_i}{dt} = -\gamma({v_i}^2)\vec{v}_i - \vec{\nabla}U(\vec{r}_i) + \sqrt{2D}\vec{\xi}_i(t)$$

[*] This discussion originates from Reference 2, and mass of the particle is always set to unity.

[**] Detailed discussion on active Brownian particle theory and its adaptation in Daphnia motion can be found in Reference 9~11.

The first deceleration term, $\gamma(v_i^2)$, comes from the non-linear friction controlled by the difference of the intrinsic friction between the particle and the environment, γ_0, and the energy depot that the particle holds, $e_i(t)$:

$$\gamma(v_i^{\,2}) = \gamma_0 - d_2 e_i(t)$$

where d_2 is a constant parameter that describes the conversion rate of internal energy to external kinetic energy.

We can further express energy depot as a function of other parameters: flux of energy into the particle's internal depot (q_0), and loss of internal energy due to metabolism and various dissipations (c). Knowing that energy depot $e_i(t)$ should be proportional to incoming flux of energy and inversely proportional to rate of energy loss (internal energy loss, ie. metabolism, plus external energy loss, ie. particle motion) gives the following equation for $\gamma(v_i^2)$:

$$\gamma(v_i^{\,2}) = \gamma_0 - d_2 \frac{q_0}{c + d_2 v_i^{\,2}}$$

The external potential $U(\boldsymbol{r}_i)$ in the second term is created by light source in our case. We will assume that it follows a simple quadratic rule so that the force is attractive with strength a and linear in $\boldsymbol{r}$:

$$U(\vec{r}) = \frac{a}{2}\vec{r}^{\,2}$$
$$\vec{F} = -\vec{\nabla} U(\vec{r}) = -a\vec{r}$$

And the last term, $\xi(t)$, is the stochastic force with strength D. We will discuss the result of simulation using these equations of motion in the next section.

Interacting Daphnia Model in an External Potential (Avoidance Model)

The previous model treats all Daphnias as uncoupled individuals, but we are interested in describing the vortex swarming pattern, which is most likely triggered by particle interaction, since it is only observed in high-density population. To device equation of motions incorporating the correct interaction, we need to understand the cause of vortex swarming. Several possible agent-agent interactions have been proposed and simulated: individual's velocity coupling with local average velocity, individual's orientation coupling with local average orientation, individual's position coupling with local center of mass position, individual's angular momentum coupling with local average angular momentum, and finally hydrodynamic interaction between agents[2]. Although all of the above result in simulations that successfully depict swarm structure and even single-direction vortex swarming, they have low biological relevance because they are unlikely practiced by Daphnia.

We will therefore only discuss the avoidance model, which assumes that each Daphnia's aversion of colliding with other Daphnia is the cause of vortex swarming in high-density population. Later we will look at simulation results of this model, as well as observation of actual avoidance mechanism in Daphnia system.

There are two ways to include avoidance into our model. First, we can simply start with our previous uncoupled equation of motions, and add an extra term to describe avoidance as an agent-agent repulsive force. The strength of this force term is biologically related to the sensitivity and range of Daphnia's sensory system. The second method is more complicated mathematically. It is an adaptation from the pedestrian movement model[2], which in the end also gives us an additional repulsive force term that we insert into the previous uncoupled formula. Both of these modifications result in satisfactory vortex swarm simulation, so we will only discuss the mathematically succinct first method.

We will start with assuming the repulsive avoidance "force" between two agents *i* and *j* depends on the inverse of their distance to the power *m*:

$$\vec{f}_{ij} = \frac{g}{(r_{ij}^{\varepsilon})^m}\vec{r}_{ij}$$

where g is the force strength, $\boldsymbol{r}_{ij}$ is the displacement vector, and r_{ij} would have been the displacement magnitude, but instead we are using the offset r_{ij}^{ε} to avoid singularity for close separation:

$$r_{ij}^{\varepsilon} = \sqrt{\varepsilon + \vec{r}_{ij} \cdot \vec{r}_{ij}}$$

This avoidance force is not yet biologically correct. Daphnia only senses others in front of it, those behind them would not alter its course. Therefore we correct the model with a prefactor w_{ij}^{ε} that filters unwanted effect from particles out of the visual range:

$$w_{ij}^{\varepsilon} = v_{rel} \cdot \hat{r}_{ij}^{\varepsilon} \quad \text{if} \quad v_{rel} \cdot \hat{r}_{ij}^{\varepsilon} \geq \eta$$
$$\text{else} \quad w_{ij}^{\varepsilon} = \eta$$

where η accounts for agent's angle of perception ($\eta = 0$ means a visual angle of 180°, and $\eta > 0$ means a smaller visual angle).

Inserting the prefacor and summing over all other particles to get total avoidance "force" for agent *i,* we get:

$$\vec{F}_i = \sum_{i \neq j} \vec{f}_{ij} = \sum_{i \neq j} w_{ij}^{\varepsilon} \cdot \frac{g}{(r_{ij}^{\varepsilon})^m}\vec{r}_{ij}$$

Finally our overall equation of motions would be the uncoupled version plus this avoidance force:

$$\frac{d\vec{r}_i}{dt} = \vec{v}_i$$

$$\frac{d\vec{v}_i}{dt} = -\gamma(v_i^{\ 2})\vec{v}_i - a\vec{r}_i + \sqrt{2D}\vec{\xi}_i(t) + \sum_{i \neq j} w_{ij}^{\ \varepsilon} \cdot \frac{g}{(r_{ij}^{\ \varepsilon})^m} \vec{r}_{ij}$$

III. Simulation Results*

Simulation of Non-interacting Daphnia Model in an External Potential

Computer simulations were preformed using the active Brownian particle models derived in previous section. We start with the simulation of the non-interacting and uncoupled version with the following equation of motion for each agent *i*:

$$\frac{d\vec{r}_i}{dt} = \vec{v}_i$$

$$\frac{d\vec{v}_i}{dt} = -\gamma(v_i^{\ 2})\vec{v}_i - \vec{\nabla}U(\vec{r}_i) + \sqrt{2D}\vec{\xi}_i(t)$$

Single-agent simulation shows the correct circulatory path around the source of potential field (Fig. 4). In an N-agent simulation, in which each agent obeys the above equation of motions, swarm formation occurs as all agents exhibit the same rotational motion, but the directions of rotation do not unify at high density, and no vortex swarm emerges (Fig. 5).

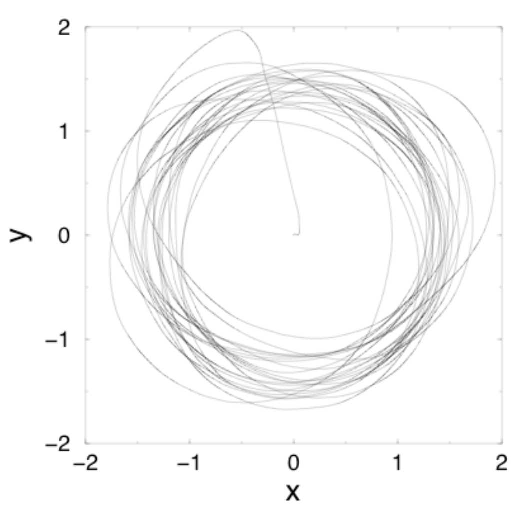

Fig. 4: Simulation result of the trajectory of a single agent obeying the active Brownian particle model with external potential field. Simulation duration is t = 200, and parameters are: $\gamma = 5.0$, $d_2 = 1.0$, $q_0 = 10.0$, $c = 1.0$, $D = 0.05$, and $a = 0.5$, with trivial initial condition.

* Simulation results are proposed by Reference 2.

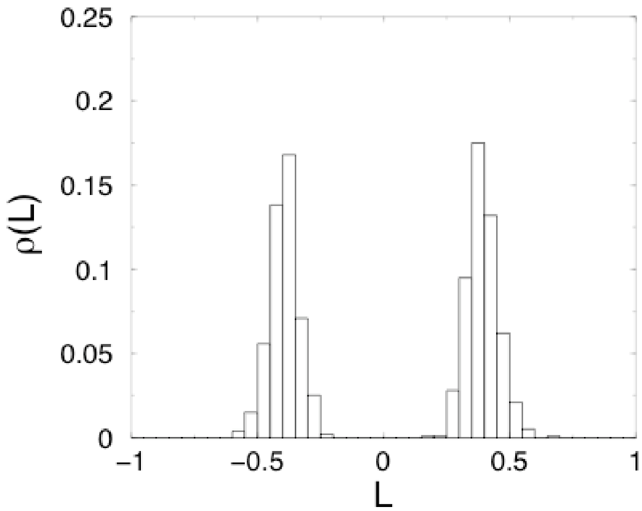

Fig. 5: Angular momentum distribution for an N-agent simulation. The signs of L indicate the two rotational directions. Here we can see that both directions are approximately equally favored, meaning no formation of vortex swarming arises from the non-interacting model.

Simulation of Interacting Daphnia Model in an External Potential (Avoidance Model)

The modified active Brownian particle model that includes the agent-agent avoidance interaction demonstrates the vortex swarming pattern expected for high-density Daphnia system (Fig. 6).

$$\frac{d\vec{r}_i}{dt} = \vec{v}_i$$

$$\frac{d\vec{v}_i}{dt} = -\gamma(v_i^{\,2})\vec{v}_i - a\vec{r}_i + \sqrt{2D}\vec{\xi}_i(t) + \sum_{i \neq j} w_{ij}^{\ \varepsilon} \cdot \frac{g}{(r_{ij}^{\ \varepsilon})^m}\vec{r}_{ij}$$

Therefore we now have a model that correctly exhibits vortex swarm. Next we will review the observations of the Daphnia system, and especially investigate if we can identify any avoidance mechanism in their motions.

IV. Observation of Daphnia Motion

A Daphnia experiment typically has the following setup (Fig. 7). A vessel with transparent bottom that holds the animals is placed in a dark room, and an inferred light source, to which Daphnia is believed to be blind, illuminates a horizontal layer of the vessel. A mirror is placed below the vessel and captures the reflected two-dimensional image of the illuminated layer, which is recorded by a camera in night mode. The image is simultaneously recorded and analyzed by a computer. We can insert visible light source into the vessel to create the attractive potential.

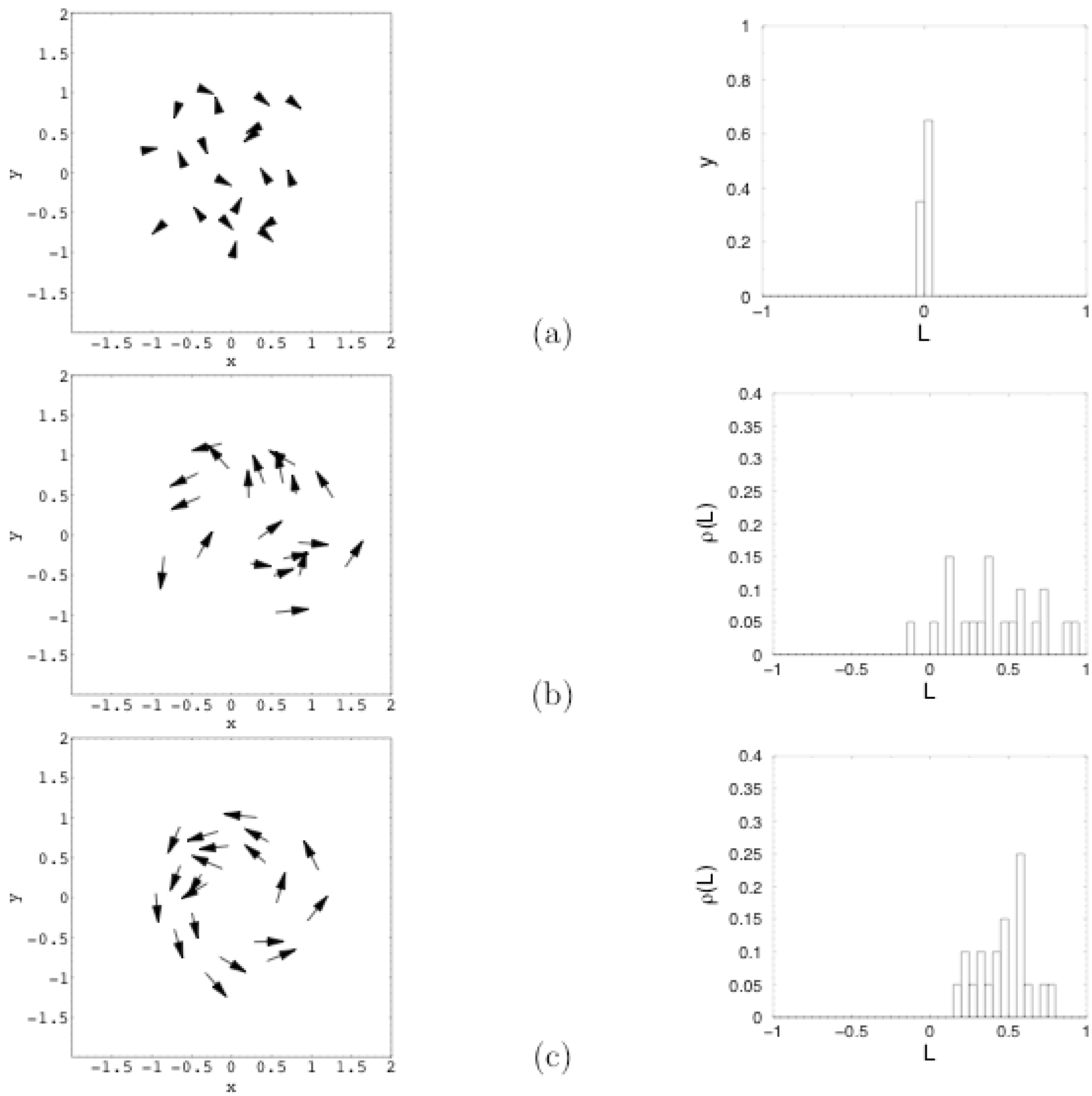

Fig. 6: Computer simulation of the active Brownian particle model enhanced with agent-agent avoidance interaction. On the right are snapshots of spatial distribution with velocity vectors at different time, and on the right are the angular momentum distributions at the corresponding time: (a) t = 0, (b) t = 8, and (c) t = 55. We can clearly see the vortex swarm pattern in (c).

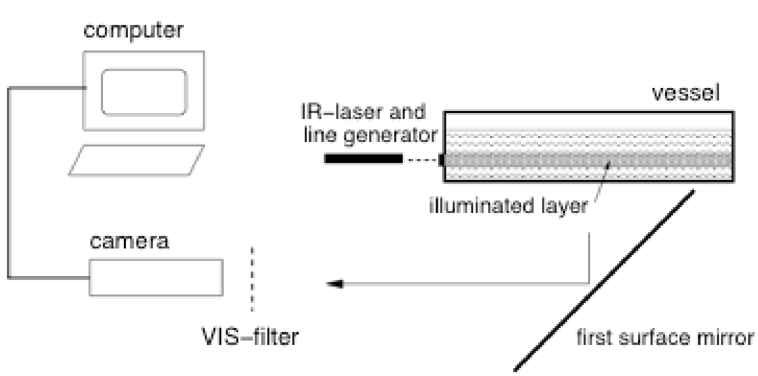

Fig. 7: A schematic diagram of Daphnia experiment setup.

Observation of Swarm and Vortex Swarm

As discussed previously, Daphnia shows a swarming pattern when a visible light source is placed in the vessel. If we increase the density in the vessel, then a vortex swarming would be seen (Fig. 8). The recorded movie of this experiment is accessible at http://summa.physik.hu-berlin.de/~frank/web-mos.html.

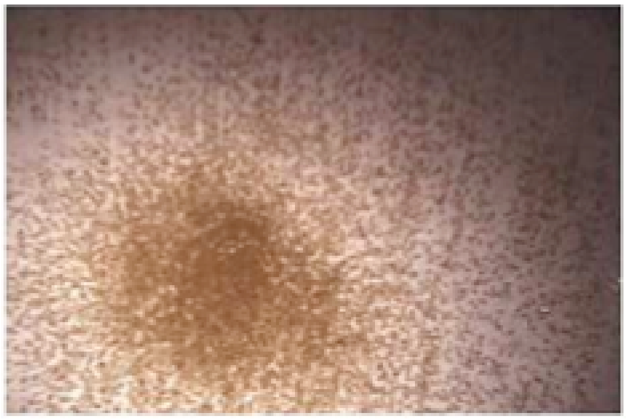

Fig. 8: A snapshot of vortex swarm during a high-density population experiment.

Observation of Avoidance Mechanism

We are also interested in observing avoidance mechanism so that our model would be biologically relevant. To do so we place very few Daphnia in the vessel without visible light source, and let them move freely in water. Their paths were recorded and examined, and avoidance maneuver was indeed observed (Fig. 9).

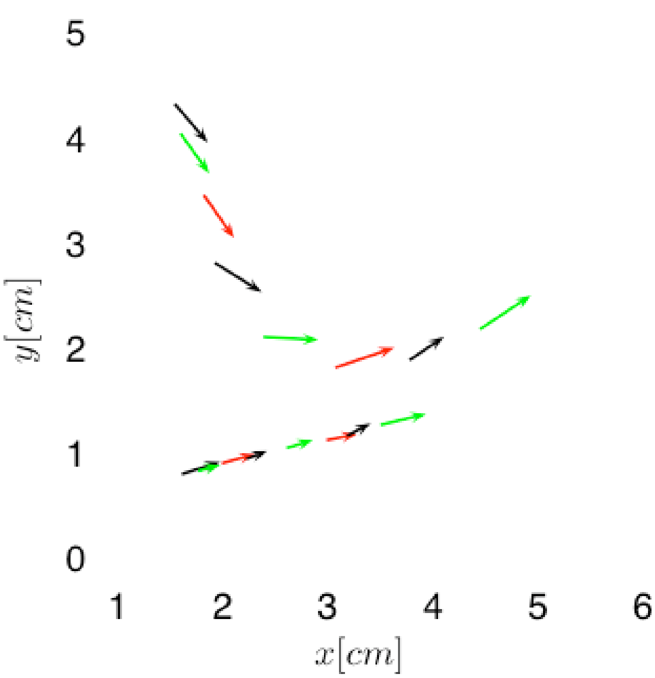

Fig. 9: The trajectories of two Daphnia in experimental vessel that demonstrate avoidance mechanism. The different color of the arrows corresponds to different time step (every 0.2 second).

V. Conclusion and Discussion

Daphnia is attracted to visible light, and when such a source is present, each individual would rotate around it. If population concentration is low, then the two rotational directions would be equally probable; but if the population concentration exceeds a critical value, then the swarming becomes a vortex swarm, such that rotational direction becomes single-valued for all agents.

This vortex swarming is studied by constructing a model that assumes each Daphnia behaves like an active Brownian particle that follows avoidance mechanism. Such model produces simulations that retain the vortex swarming feature as seen in the actual Daphnia experiment. Moreover, the practice of avoidance mechanism can also be identified in Daphnia motion in experiment.

So far the studies on Daphnia vortex swarming focus on the two individual states separately: the low-density swarming state and the high-density vortex swarming state. We still need an investigation at the transition between the two, and this transition is not depicted in the current models. As we can see in Fig. 6, our model exhibits vortex swarm even with very few agents present. An ideal model should allow us to vary parameters and observe the phase transition.

This also brings us to the discussion of relevant parameters. So far we know the vortex swarming transition is controlled by the population concentration parameter, but it is likely that there are other parameters in control: velocity of agents, mass of agents, and size of agents, which our current model does not fully accommodate. Eventually we would want a generalized model for any multi-agent system with a vortex swarming phase that's activated by different parameters. Such model would aid our understanding in swarm-to-vortex-swarm phase transition, and perhaps we can relate such phase transition in biological system with those more qualitatively analyzed in physical systems.

Acknowledgement

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References

1. Bonabeau, E., Dorigo, M., Theraulaz, G. "Swarm Intelligence: From Natural to Artificial Systems."
2. Mach, R., Ordemann, A., Schweitzer, F., 2003. "Modeling Vortex Swarming in Daphnia." Preprint.
3. Figure obtained at http://www.hawriverprogram.org.
4. Nielsen, R. "Why Sex?" *Science* **311**, 960 (2006).
5. Paland, S., Lynch, M. "Transitions to Asexuality Result in Excess Amino Acid Substitutions." *Science* **311**, 990 (2006).
6. Erdmann, U., Goller, S., Schimansky-Geier, L., Sokolov, I., Moss, F. "Theory of Optimal Foraging." Preprint submitted to *Mathematical Biosciences*.
7. Smith, K. C., Macagno, E. R. "UV Photoreceptors in the Compound Eye of Daphnia Magna (Crustacea, Branchiopoda). A Fourth Spectral Class in Single Ommatidia." *J. Comp. Physiol.,* A **166**, 597-606 (1990).
8. Moore, M. V., Pierce, S. M., Walsh, H. M., Kvalvik, S. K., Lim, J. D. "Urban Light Pollution Alters the Diel Vertical Migration of Daphnia." *Verh. Internat. Verein. Limnol.* **27:** 1-4 (2000).
9. Erdmann, U., Ebeling, W., Schimansky-Geier, L., Schweitzer, F. "Brownian Particles far from Equilibrium." *European Physical Journal B* 15(1), 105–113 (2000).
10. Ebeling, W., Schweitzer, F. "Self-Organization, Active Brownian Dynamics, and Biological Applications." *Nova Acta Leopoldina* NF 88(332), 169–188 (2003).
11. Tilch, B., Schweitzer, F., Ebeling, W. "Directed Motion of Brownian Particles with Internal Energy Depot." *Physica A* 273(3-4), 294–314 (1999).