Invited Paper

Daphnia swarms: from single agent dynamics to collective vortex formation*

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ABSTRACT

Swarm theories have become fashionable in theoretical physics over the last decade. They span the range of interactions from individual agents moving in a mean field to coherent collective motions of large agent populations, such as vortex-swarming. But controlled laboratory tests of these theories using real biological agents have been problematic due primarily to poorly known agent-agent interactions (in the case of e.g. bacteria and slime molds) or the large swarm size (e.g. for flocks of birds and schools of fish). Moreover, the entire range of behaviors from single agent interactions to collective vortex motions of the swarm have here-to-fore not been observed with a single animal. We present the results of well defined experiments with the zooplankton *Daphnia* in light fields showing this range of behaviors. We interpret our results with a theory of the motions of self-propelled agents in a field.

Keywords: Swarming, vortex, biological agents, zooplankton

1. Introduction

Herding or, for animals that move in a three dimensional environment, swarming has been observed in certain mammals, fish, insects, and birds to enhance feeding, mating, and offspring rearing success as well as to avoid predators more successfully.[1,2] In the case of species that are highly exposed to the risk of becoming prey of visually hunting predators, the formation of swarms can serve as a predator-confusing mechanism. These swarms of self-propelled animals are observed to be self-organized systems, i.e. there is no leading animal and the global patterns are emerging properties of the local interactions.[3] The local interactions constitute of some form of alignment of neighboring animals, such as visual alignment which can be found in birds.[4] Some swarming animals can be observed to form fascinating vortex-swarms in the field, usually in connection with a central swarm marker. Unfortunately, not much is known about the biological and physical aspects of these formations, as it is difficult to carry out experiments under well defined lab conditions on this phenomenon, mainly because of the size of the animals or the difficulty of understanding the local interactions. For example bacterial and slime mold colonies move quite slowly under the influence of poorly understood chemotactic, thermal and viscous gradients,[5,6] while flocks of birds and schools of fish are too large for well controlled lab experiments. In our recent experiments with the zooplankton *Daphnia,*[7,8] which is intermediate in size and biological complexity (see Fig. 1), we observe both circling of individual animals as well as vortex formation in large swarms of *Daphnia*. These well defined lab experiments open up a wide field of research, part of which will be addressed in the following.

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1.1. *Self-propelled agent theories*

In the last decade, the modeling of the motion of so called self-propelled biological agents has become of considerable interest to theoretical physicists, leading to a wide range of variants of the two major models, the single-particle model of Active Brownian Particles (ABP)[9] and the many-particle model of Self-Propelled Interacting Particles (SPIP).[10] Despite the lack of experimental data on vortex-swarming animals until recently, two different two-dimensional models predicting circular motion of individual agents[11] as well as agent groups[12] without an external rotational force or special boundary conditions were developed. The minimum necessary ingredients for circling of the agents in both directions (clockwise and counterclockwise with same probability) to occur in these models was found to be a relatively constant non-zero agent velocity and a topological confinement of the agents to an accessible or preferred domain of motion, the latter being introduced either as an external force given by a parabolic potential[11] or as a mean field potential resulting from a long range attractive and a short range repulsive force between the agents.[12] Details of the mechanism, such as energy reservoirs to modulate the speed, were found to be of minor significance. For an agent vortex to emerge, i.e. circling of all agents in the same direction after some transition time, spontaneous symmetry breaking is necessary to occur. In the SPIP model this is achieved by introducing an alignment of the agents to the average velocity direction of neighboring agents.[12] The originally single-particle ABP model has been further developed to include the transition from external fields to mean fields generated by agent swarms[13] as well as a range of global and local interactions between particles: It was found that when incorporating an attraction to the center of mass of the swarm, clusters of agents circle in both directions and change their circling direction due to the implemented noise[14], whereas a global coupling to the mean angular momentum of the agents ('aligning') breaks the symmetry of the system leading to the circling of all agents in the same direction and thus forming a vortex state.[15] The introduction of a local hydrodynamic interaction between the *Daphnia* modeled by an Oseen-type tensorial force also breaks the symmetry and leads to a vortex state.[16] In addition, a vortex state of an agent swarm can also be achieved by implementing a local agent-agent voidance term[17] similar to the one developed for avoidance maneuvers in pedestrian dynamics.[18]

2. Experimental observations

p to now, well defined experimental observations of circling behavior in biological systems comparable to the above tlined theoretical models have only been reported for disc-shaped aggregates of the bacteria *Paenibacillus vortex*[5] and gregated cells of the mold amoeba *Dictyostelium*.[6] As these systems are on a low evolutionary level compared with ds and fish, the physical and behavioral aspects of the observed motions are difficult to compare. Triggered by a nce observation of vortex-swarming oceanic zooplankton *Anchylomera blossevilli* close to Hawaii,[19] a successful perimental set-up was developed to induce the common fresh-water zooplankton *Daphnia* to circle horizontally und a vertical optical marker in the shape of a light shaft to which *Daphnia* are known to be attracted. For the ailed set-up see Fig. 2 in Ref. 7. When comparing the specific circumstances and environmental conditions for this ling behavior to take place in zooplankton in general and in *Daphnia* in particular, it occurs that the existence of lator smell, so-called kairomones, is necessary for circling to develop.[8,20,21] For swarming in general to take place, ven light distribution[22] and high food density[23] seem to be of importance. By using a manual tracking software ckIt from IguanaGurus, at two frames per second) we analyzed the projection to the horizontal plane of the path of *hnia* under varying animal densities in the observation vessel.

Individual *Daphnia*

n placing individual *Daphnia* or a very small number of *Daphnia* in the vessel, we surprisingly observed some of ndividual *Daphnia* to circle in both directions around the light shaft and to frequently change their rotational tion, while others performed a motion of frequently jumping against the light shaft and back (see Fig. 2). The fact ingle *Daphnia* circle eliminates the possibility that the circular motion is a self-organized pattern occurring only in *Daphnia* populations. Due to several recent experiments showing that *Daphnia* can detect the plane of polarization ht and prefer to swim perpendicular to it,[24-26] it seems feasible that individual *Daphnia* are led on a circular track ertain radius by the polarization of the light. When comparing the tracks of several circling *Daphnia*, it occurs that every animal seems to have its own preferred radius of circling. This can account for the observation that some *Daphnia* circle and others keep hitting the solid light shaft as their individual preferred circling radius might be smaller than the radius of the light shaft.

2.2. Swarm of *Daphnia*

Having an intermediate *Daphnia* density in the observation vessel results in an animal swarm distributed around the light shaft with, besides random fluctuations, half of the circling *Daphnia* can be observed to move clockwise and the other half counterclockwise, frequently changing their individual circling direction (see Fig. 3). This indicates that the 'alignment' necessary for the symmetry breaking to take place, and therefore the vortex-swarm to form, is a very short ranged interaction. The local interactions between the *Daphnia* are too weak to induce a collective global motion for intermediate animal densities. In all experiments with this environmental condition a small proportion of *Daphnia* have been observed not to be circling but jumping against the light shaft and back.

2.3. Vortex-swarm of *Daphnia*

For high *Daphnia* densities we observe the formation of a fascinating vortex-swarm where all animals close to the center of the light turn in the same direction, either clockwise or counterclockwise (see Fig. 4). The actual turning direction of the vortex appears to be at random and the water inside the vortex rotates in the same direction as the animals themselves. These vortex-swarms can be explained as a self-organization phenomenon occurring for high enough *Daphnia* density: Due to random fluctuations, one circling direction can get sufficiently more pronounced, then the positive feedback of the water drag compels more and more closely packed *Daphnia* to circle in this direction and thereby the symmetry of the system is broken. The local interactions that causes the *Daphnia* vortex are not direct *Daphnia-Daphnia* interactions as it is the case e.g. for visually aligning birds and fish, but indirect interactions via the water drag.

As mentioned above, a recent variation of the ABP model follows these experimental observations and includes a hydrodynamic force to model the agent-agent interactions via the medium.[16] In addition to this, another possible reason for the symmetry breaking to occur in the high density case is that due to close range avoidance maneuvers of neighboring *Daphnia* and random fluctuations of the hopping direction, spontaneous formation of a preferred moving direction occurs,[17] similar to the findings in pedestrian dynamics. Well defined behavioral experiments characterizing avoidance maneuvers in *Daphnia* need to be performed to test this hypothesis.

3. Random Walk Model

We have recently developed a simple two-dimensional, stochastic model (here called *Daphnia* Random Walk model, DRW) for discretely moving self-propelled agents based on a random walk with a short-range, temporal correlation taken from experimental observation of *Daphnia* moving in darkness and an attraction to a central point, which is of strength L and proportional to the agent's distance from the center of attraction.[7] This model successfully simulates the general features of the experimentally observed moving behavior of individual *Daphnia* in darkness and in a central light field. For an intermediate attraction strength L=0.4, individual agents circle in both directions around the center of attraction and frequently change their circling direction. Characterizing the movement of the agents with the same measures that were used for the *Daphnia* movements shows very good agreement between experiment and simulation.[7] The DRW model turned out to be closely related to the original single-particle ABP model, but fulfills its aim to be as simple as possible and based on experimentally observed *Daphnia* movements.

3.1. Vortex-swarm of biological agents

To simulate the experimentally observed vortex-swarm including the hydrodynamic interactions that lead to the symmetry breaking, we generalize the DRW model to be an N-particle model where the indirect interactions between the agents via the water drag is incorporated by a simple 'alignment' or 'water drag' kick which is added to the direction of motion of the single agents given by the original DRW. The kick is proportional to the ratio $R = (N_{CCW} - N_{CW}) / N_N$, where N_{CW} is the number of neighboring agents circling clockwise, N_{CCW} is the number of neighboring agents circling counterclockwise, and N_N is the number of all neighboring agents. Here an agent being defined as 'circling' if the absolute angle between the direction of motion and the direction to the center of attraction is between 80° and 100°. The direction of the kick is either clockwise for negative R or counterclockwise for positive R. Depending on the strength of the 'water drag' kick and the range of the interaction, a vortex-swarm forms after an average transition time. A typical example for the evolution in time of the ratio $V = (A_{CCW} - A_{CW}) / N$, where A_{CCW} is the number of all clockwise circling agents and A_{CCW} for all counterclockwise circling agents, is shown in Fig. 5 for intermediate kick strength and interaction range with $N = 30$. Note that for $V = 1$, a counterclockwise vortex has formed, while for $V = -1$ the agents in the vortex turn clockwise.

4. Conclusion

In conclusion, we shed more light on the general physical, chemical and biological aspects of vortex-swarming in prey animals with both, a self-propelled agent model leading from single agent circular motion to vortex-swarming as well as laboratory experiments on circling and vortex-swarming *Daphnia*. With this zooplankton species it is possible for the first time to observe the entire range of behaviors from single agent interactions to collective motions of the vortex-swarm in a single species in well defined conditions. This facilitates the detailed investigations of the different local interactions and environmental circumstances that lead to vortex formation in prey animals. In contrary to the observations in fish and birds, the local interaction between *Daphnia* is an indirect one via the hydrodynamic coupling due to the water drag. The schooling of prey fish seems to indicate that the preferred motion of a swarm is linear and not circular, as long as there exists no center of attraction such as a central light field or a visible object in the water, e.g. a vertical water plant or debris floating on the water surface.

Further experiments with *Daphnia* have to include systematical investigations of close range avoidance maneuvres, the light perception of *Daphnia*, in particular the polarization orientation, as well as the physical aspects of the fluid dynamic vortex. In addition it might prove intriguing to try a similar experimental set-up using other zooplankton species.

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REFERENCES

1. A. Okubo and S. A. Levin, *Diffusion and Ecological Problems*, Springer-Verlag, New York, 2002.
2. J. K. Parrish and L. Edelstein-Keshet, "Complexity, Pattern, and Evolutionary Trade-Offs in Animal Aggregation", *Science* **284**, 99-101, 1999.

3. S. Camazine, J.-L. Deneubourg, N.R. Franks, J. Sneyd, G. Theraulaz, and E. Bonabeau, *Self-Organization in Biological Systems*, Princeton University Press, Princeton and Oxford, 2001.
4. T.S. Caraco, S. Martindale, and H.R. Pulliam, "Avian flocking in the presence of a predato", *Nature* **285**, 400-401, 1980.
5. A. Czirok, E. Ben-Jacob, I. Cohen, T. and Vicsek, "Formation of complex bacterial patterns via self-generated vortices", *Phys. Rev. E* **54**, 1791-1801, 1996.
6. W.-J. Rappel, A. Nicol, A. Sarkissian, H. Levine, and W.F. Loomis, "Self-organized Vortex State in Two-Dimensional Dictyosetelium Dynamics", *Phys. Rev. Lett.* **83**, 1247-1250, 1999.
7. A. Ordemann, G. Balazsi, and F. Moss, "Motions of Daphnia in a Light Field: Random Walks with a Zooplankton", *Nova Acta Leopoldina NF* **87**, 2003, in press.
8. A. Nihongi, A. Ordemann, and R. Strickler, "*Daphnia pulex* reacting to a vertical attractor and kairomones", in preparation.
9. F. Schweitzer and L. Schimansky-Geier, "Clustering of 'active' walkers in a two-component system", *Physica A* **206**, 359-379,1994.
10. T. Vicsek, *Fluctuations and scaling in biology*, Oxford University Press, Oxford, 2001.
11. F. Schweitzer, W. Ebeling, and B. Tilch, "Complex Motion of Brownian Particles with Energy Depots", *Phys. Rev. Lett.* **80**, 5044-5047, 1998.
12. H. Levine, W.-J. Rappel, and I. Cohen, "Self-organization in systems of self-propelled particles", *Phys. Rev. E* **63**, 017101, 2001.
13. U. Erdmann, W. Ebeling, and V.S. Anishchenko, "Excitation of rotational modes in two-dimensional systems of driven Brownian particles", *Phys. Rev. E* **65**, 061106, 2002.
14. W. Ebeling and F. Schweitzer, "Swarms of Particle Agents with Harmonic Interactions", *Theory Biosci.* **120**, 207-224, 2001.
15. F. Schweitzer, W. Ebeling, and B. Tilch, "Statistical mechanics of canonical-dissipative systems and applications to swarm dynamics", *Phys. Rev. E* **64**, 021110, 2001.
16. U. Erdmann and W. Ebeling, "Collective Motion of Brownian Particles with Hydrodynamic Interactions", *Fluctuation and Noise Letters*, 2003 (to be published).
17. R. Mach and F. Schweitzer, (in preparation).
18. D. Helbing, P. Molnar, and F. Schweitzer, "Computer Simulations of Pedestrian Dynamics and Trail Formation", cond-mat/9805074, 1998.
19. P.S. Lobel and J.E. Randall, "Swarming behavior of the hyperiid amphipod Anchylomera blossevilli", *J. Plankton Res.* **8**, 253-262, 1986.
20. J. Pijanowska and A. Kowalczewski, "Predators can induce swarming behaviour and locomotory responses in Daphnia", *Freshwater Biology* **37**, 649-656, 1997.
21. K.H. Jensen, P.J. Jakobsen, and O.T. Kleiven, "Fish kairomone regulation of internal swarm structure in *Daphnia pulex* (Cladocera: Crustacea)", *Hydrobiol.* **368**, 123-127, 1998.
22. S. Young and C. Getty, "Visually guided feeding behaviour in the filter feeding cladoceran, *Daphnia magna*", *Anim. Behav.* **35**, 541-548, 1987.
23. P.J. Jakobsen and G.H. Johnsen, "The influence of food limitation on swarming behaviour in the waterflea *Bosmina longispina*", *Anim. Behav.* **36**, 991-995, 1988.
24. S. Young and V.A. Taylor, "Swimming tracks in two cladoceran species", *Anim. Behav.* **39**, 10-16, 1990.
25. R. Schwind, "*Daphnia pulex* swims towards the most strongly polarized light - A response that leads to 'shore flight'". *J. Exp. Biol.* **202**, 3631-3635, 1999.
26. I.N. Flamarique and H.I. Browman, " Wavelength-dependent polarization orientation in *Daphnia*", *J. Comp. Physiol. A* **186**, 1073-1087, 2000.

Fig. 1: Lateral view of the cladoceran *Daphnia pulex*, the head with the compound eye and the swimming antennae facing to the right, a juvenile can be seen in the brood chamber. The typical body length of this zooplankton species is 2-4mm. Picture by D. Russell with permission.

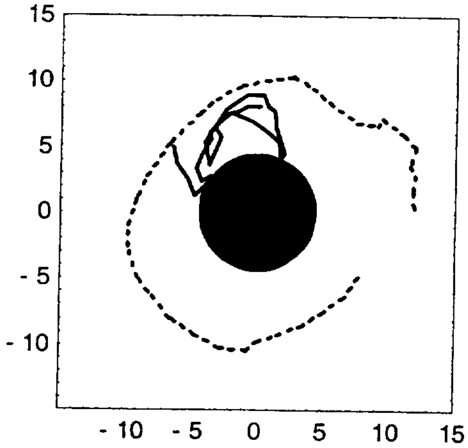

Fig.2: Two-dimensional projection (top view) of the track of individual *Daphnia* in a central light field, showing the two observed motions: (a) circling around the light, and (b) jumping against the light and back (light shaft shown as black circle, track of 20 sec, coordinates in mm).

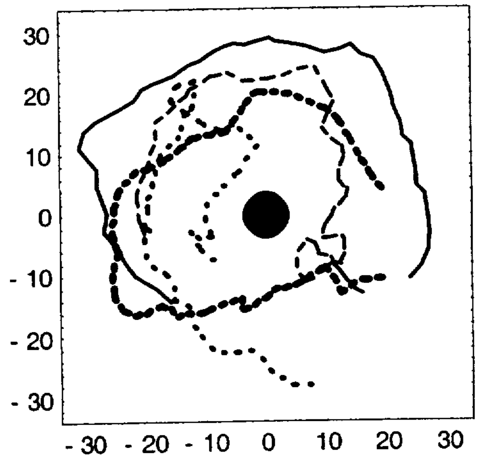

Fig.3: Two-dimensional projection (top view) of the tracks of four *Daphnia* inside a swarm in a central light field, showing the observed circling in clockwise and counterclockwise directions around the light (light shaft shown as black circle, track of 20 sec, coordinates in mm).

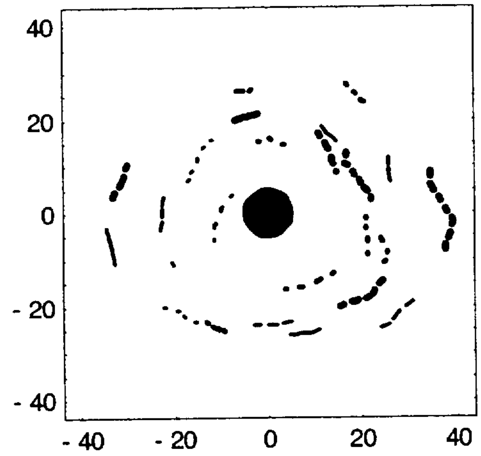

Fig.4: Two-dimensional projection (top view) of the tracks of many *Daphnia* inside a vortex swarm in a central light field, here circling counterclockwise (coordinates in mm).

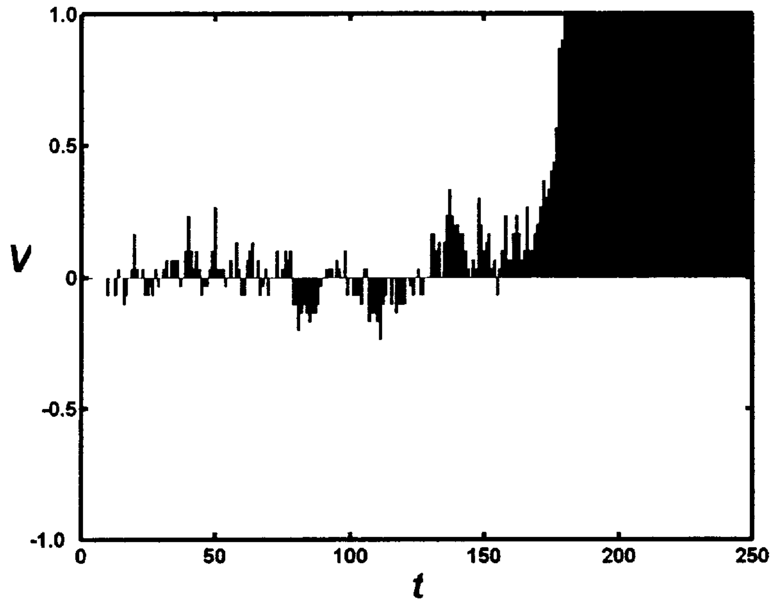

Fig.5: Evolution in time t of the ratio $V = (A_{CCW} - A_{CW}) / N$, for $N = 30$. After about 180 time steps a counterclockwise vortex has formed.