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Pattern formation and stochastic motion of the zooplankton *Daphnia* in a light field

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Abstract

We extend our study of single and collective motions of the zooplankton *Daphnia* both in experiment and computer simulation. *Daphnia*, as well as many other prey animals, can be observed to swarm under certain circumstances as a protective behavior against predators. *Daphnia* swarms can be induced by an optical marker such as a vertical shaft of light, to which they are attracted. For low *Daphnia* densities we observe that individual *Daphnia* develop a circular motion around the optical marker, whereas for high densities we can reproducibly induce swarming *Daphnia* to carry out a vortex motion. To learn more about this circular pattern and the associated spontaneous symmetry breaking, the motion of single *Daphnia*, as well as swarms, is characterized with respect to the light shaft. A stochastic model based on experimental data is compared with the observed *Daphnia* behavior as well as with existing models for single agents and agent swarms performing a circular motion to reveal the essential ingredients for vortex motion to occur.
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1. Introduction

Certain mammals, fish, insects, and birds form swarms or herds for various reasons such as enhanced feeding, caring and mating as well as predator avoidance [1]. Many species that are at high risk of becoming prey of visually hunting predators

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and that move in a three-dimensional environment are commonly known to form self-organized swarms as a predator-confusing mechanism [2,3]. In rare events in the field, some predator-confusing animal swarms have been observed to perform a fascinating vortex-like motion. As it is difficult to perform well-defined experiments on this phenomenon, mainly because of the large size of the animals in the case of fish and birds or the difficulty of understanding the local interactions in the case of bacterial [4] and slime mold colonies [5], not much is known about the biological and physical aspects of these vortex-swarms. Our recent detailed experimental observation of circling and vortex-swarming events of the cladoceran *Daphnia*, intermediate in size and biological complexity between bacteria and birds, obviates many of these difficulties [6,7], and opens up a wide field of research, part of which will be addressed in the following.

Swarm theories of so-called self-propelled agents attracted much attention in theoretical physics lately [8], spanning the range of interactions from single agents moving in a mean field to coherent collective motions of large populations. Despite the lack of experimental data on vortex-swarming animals until recently, two different two-dimensional models showing circular motion of the agents without an external rotational force or special boundary conditions were developed. However, the question remains what are the essential ingredients for circling as well as vortex-swarming to occur: (a) In the single-particle model of active Brownian motion by Schweitzer et al. [9] the agent experiences friction, an external force given by a parabolic potential, noise and a self-propelling force which is connected to an energy storage depot. For certain parameter settings a Hopf bifurcation is found where the agent moves from Brownian motion to a stochastic limit cycle. In addition, many-particle models with various interactions among the active Brownian particles (ABP) were investigated by them [10,11]. 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 noise, whereas a global coupling to the mean angular momentum of the agents (aligning) breaks the symmetry of the system leading to circling of all agents in the same direction and thus forming a vortex state. (b) In the many-particle model of Levine et al. [12] (self-propelled interacting particles, SPIP) each particle experiences a self-propelling force, friction, as well as attractive and repulsive forces between the particles. Using two different rules for the determination of the self-propelling force, (i) without or (ii) with alignment to the average velocity direction of the neighboring particles, Levine et al. find stable states with circular motion of the agents, where, depending on the implementation of the self-propelling force, the agents either (i) circle both clockwise and counterclockwise randomly or (ii) circle all in the same direction after a certain transition time, leading to a vortex state.

2. Experiments with *Daphnia*

Triggered by several chance observations of zooplankton performing a horizontal circular motion under lab conditions [13] and of one vortex-swarming incidence of the oceanic zooplankton *Anchylomera blossevilli* in the field [14], a successful experimental
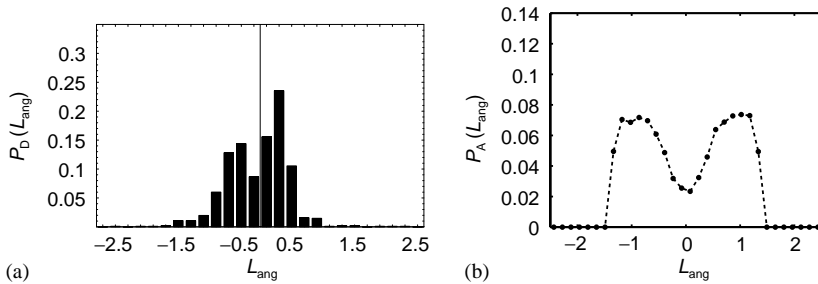
Fig. 1. (a) Probability distribution $P_D(L_{ang})$ of the angular momentum L_{ang} of *Daphnia* motion with respect to the center of the light shaft, determined from data of four different individual *Daphnia*, observed circling around the light shaft (total recorded time $t_{rec} = 624$ s, time resolution $t_{res} = 1$ frames/s). The average speed of these four *Daphnia* is $\bar{v} = 5.71 \pm 1.35$ mm/s. (b) Probability distribution $P_A(L_{ang})$ of the angular momentum L_{ang} of the agent motion with respect to the center of attraction, determined from simulated data of 40,000 agent time steps with attraction strength $L = 0.4$. The experimental observation and the simulation show the bimodal symmetric distribution expected for circular motion in both directions.

set-up was developed to induce *Daphnia* to circle horizontally around a vertical optical marker in the shape of a light shaft to which they are attracted. For the detailed set-up see Fig. 2 in Ref. [6]. Surprisingly, single *Daphnia* were also found to circle in both directions and to frequently change the rotational direction. Therefore, for *Daphnia* the circular motion cannot be a collective motion emerging in a swarm of animals, e.g. due to alignment of neighboring animals as observed for fish and birds, but it is instead an individual reaction to a certain light pattern. By using a manual tracking software (TrackIt from IguanaGurus) and calculating the angular momentum L_{ang} of the *Daphnia* motion with respect to the center of the light shaft, we analyzed the projection to the horizontal plane of the path of several recorded Daphnia that circle individually around the light shaft and confirmed the rotational character of the movement (see Fig. 1a, cf. Fig. 8 in Ref. [10]). Further on, we determine the distribution $P(N_{avg})$ of the number of moves circling in one direction N_{avg} (i.e., either clockwise or counterclockwise), before reversing the direction (see Fig. 2a). Note that besides many very short sequences of hopping in one rotational direction, there are a few very long (up to seven complete rotations) continuous circling sequences. Investigating the specific circumstances for this circling behavior to occur in *Daphnia* and the effects of certain environmental changes on their swimming behavior suggests that the existence of predator kairomones is important for circling to occur [7]. The presence of predator kairomones was also observed to enhance the swarming tendency in zooplankton [15]. Further on, it is believed that uneven light distribution [13,16] and high food density [16,17] are necessary for swarming to occur in general in zooplankton. Guided by these observations, we could reproducibly induce vortex swarms in a tank with high *Daphnia* densities [6]. As the water inside the *Daphnia* vortex circles in the same direction as the *Daphnia* themselves, the formation of this vortex-swarm can be explained as a self-organization phenomenon occurring for high enough *Daphnia* density. If, due to random fluctuations, one circling direction is sufficiently more pronounced, the positive feedback of the water drag compels more and more *Daphnia* to circle in the
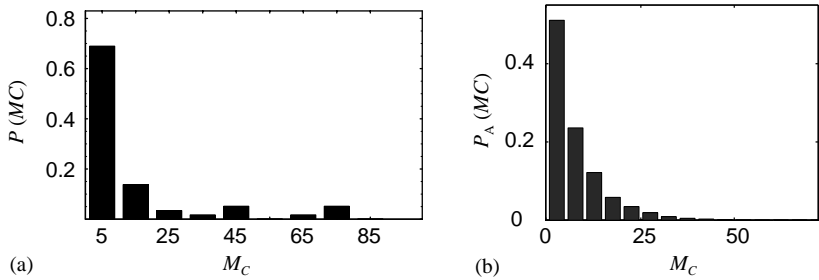
Fig. 2. (a) Distribution $P(M_C)$ of the number of successive moves M_C of *Daphnia* heading clockwise/counterclockwise before changing the circling direction, determined from the same data as in Fig. 1a. (b) Distribution $P_A(M_C)$ of the number of successive moves M_C of the agent heading clockwise/counterclockwise before changing the circling direction, determined from the same data as in Fig. 1b. Without the short-range correlation inducing the preference of the agent to move forward included into the random walker model, no circling sequences of a full turn or more occur. The experimental observation and simulation are in good qualitative agreement.

same direction thereby breaks the symmetry of the system. A recent generalization of the ABP model follows these observations and includes hydrodynamic interactions to model the interaction of the agents through the medium [18]. Another possible explanation for the symmetry breaking to occur is that due to observed avoidance maneuvers of *Daphnia* and random fluctuations of hopping direction, spontaneous formation of a preferred moving direction occurs, similar to the findings in pedestrian dynamics [19]. Sophisticated behavioral experiments concerning the characterization of these avoidance maneuvers are needed to test this hypothesis.

3. Modeling of self-propelled agents

When comparing the two above-mentioned models for the circular motion of self-organizing groups of self-propelled agents, the following general question arises: which ingredients are essential for circular motion to occur. To answer this question and to simulate the observed behavior in single *Daphnia* we developed a self-propelled agent model based on random walks (RW) with the aim of being as simple as possible and closely related to natural *Daphnia* movement [6]. The model consists of two ingredients, (i) a short-range temporal correlation (SRTC) taken from experimental observation, [1] and (ii) an attraction to a central point, of strength L and proportional to the agent's distance from the center of attraction. These two ingredients are sufficient to reproduce the circular motion in the light field. The SRTC causes the random walker to move ballistically for short times. To characterize this feature of the motion, we use the end-to-end distance exponent v, defined as $\langle R^2 \rangle^{1/2} \propto t^v$, where R is the end-to-end

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[1] Instead of choosing the direction of the next agent step randomly from a uniform distribution as in the basic random walk model, the direction is chosen according to the distribution of turning angles between two successive steps which were measured for *Daphnia* moving in darkness (see Fig. 5b in Ref. [6]).
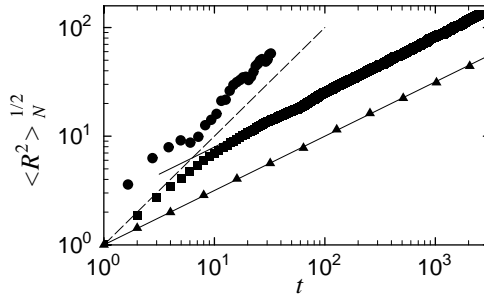
Fig. 3. The rms end-to-end distance $\langle R^2 \rangle_N^{1/2}$ versus time t of the agent averaged over N realizations for (triangle) $N = 500$ random walkers, (square) $N = 500$ random walkers with SRTC, and (circle) experimental data from $N = 8$ *Daphnia* hopping in darkness (distance in mm, time in s). The lines are guides for the eye: (straight line) slope $v = \frac{1}{2}$, (dashed line) slope $v = 1$.

distance of the walk trajectory and t is the time or step number (see e.g. Ref. [20]). For classical Brownian random walkers, $v = \frac{1}{2}$, whereas for Brownian walkers with SRTC v first briefly increases to $v = 1$ before asymptotically approaching $v = \frac{1}{2}$ (see Fig. 3). When comparing the results for *Daphnia* moving in darkness with the results for the simulated Brownian random walkers, we observe an exponent $v \approx 1$ for $t \leqslant 30$ s (see Fig. 3). Although it is widely assumed that for asymptotically long times (and asymptotically large water reservoir) the tracks of zooplankton resemble Brownian motion, in small time scales *Daphnia* do not move completely randomly. Instead, they try to cover much territory inside their radius of perception [21], in agreement with our experimental data. In addition, for very short time scales *Daphnia* are biased to move in a forward direction due to the shape of their body and their swimming and feeding appendages. Therefore, the incorporation of a memory of one step into our RW model taken from experimental observation of the turning angle distribution is reasonable. One could argue that the memory introduced into our agent most likely is considerably shorter than the memory of a *Daphnia*, but, following our aim to keep the model simple and based on measurable experimental observation, this SRTC provides us with a sufficient approximation of the overall short time moving behavior.

   When adding the point attraction to the RW model with SRTC, to model the attraction to light, this results in circling motions of the agent in both directions with frequently changing the direction for intermediate attraction strength $L \approx 0.4$ (see Fig. 6 in Ref. [6]). In addition to previously reported measurements of agent movement in simulations of this model (i.e., turning angle between successive agent moves, angle between agent heading and direction to light, agent distance to light in Ref. [6]), both the probability distribution $P_A(L_{ang})$ of the angular momentum L_{ang} of the agent motion with respect to the center of attraction (see Fig. 1b) and the distribution $P_A(M_C)$ of the number of successive moves M_C before changing the circling direction (see Fig. 2b), show good qualitative agreement between experiment and simulation.

   Comparing the observed behavior of *Daphnia* and the present RW model with the ABP and SPIP models reveals the essential ingredients for circular motion to occur:

(i) self-propelled agents with a preference to move forward (e.g. inherently as in the ABP and SPIP models or due to the SRTC in the present model) and a certain agent velocity range (e.g. constant velocity as in the present and in the SPIP model, or self-regulated velocity due to the energy depot as in the ABP model) and (ii) a point attraction, either directly in form of an external parabolic potential as in the ABP models and the present model or indirectly in form of an effective mean field potential resulting from the particle–particle interaction as in the SPIP model. For spontaneous symmetry breaking, leading to vortex formation, alignment is necessary, either directly as in the ABP and SPIP models or indirectly via the water drag as observed for vortex-swarming *Daphnia* and modeled in the ABP model with hydrodynamic interaction.

4. Conclusion

Although vortex-swarming *Daphnia* seem not to communicate or interact directly as birds and fish are observed to do, zooplankton can be considered as a promising genus of animals for well-defined lab experiments. Such experiments can be expected to shed more light on the general physical, chemical and biological aspects of vortex-swarming in prey animals, especially as the entire range of behaviors from single agent interactions to collective motions of the swarm can be observed with a single animal. Further, experiments with zooplankton should include systematic investigations of the light perception of the animals to understand the individual reaction to a certain light pattern that causes the circling motions, as well as investigations of the physical aspects of the fluid dynamic vortex.

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