RANDOM WALK THEORY APPLIED TO DAPHNIA MOTION

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The zooplankton *Daphnia* or "water flea" - one of the most common crustacean to be found in freshwater - is subject to recent studies. It is known to perform vortex motions under certain light conditions as well as more complex navigational tasks. Experimental data show that *Daphnia* move with a preferred turning angle, what is of main interest in this paper. The above-mentioned experimental fact is taken in order to derive a Diffusion law for these types of motion. Deviations from the free diffusive behavior are investigated, based on random walk theory.

Keywords: self-driven particles, enhanced diffusion

1. Introduction

Applying mathematical models to organisms goes back to the beginning of the 20th century. Experimental investigation of animal dispersion started in the 1940s with observing insects [1, 2]. Recent observations of animal motion include *Daphnia* [3] (so called "water flea"), *Copepods* [4, 5] (the salt water analog), *Desert Isopods* [6] and many other animals (e.g. in [7]).

Complex movement features like aggregation in groups or periodic behavior can be modeled using Active Brownian particles – particles in a space dependent potential with an energy depot, which can be converted into kinetic energy [8, 9] – or self-propelled particles [10, 11], which are individually driven by a force with fixed magnitude and an interaction potential. Both include friction. What has been found in these type of models that diffusive behavior of the driven particles is different from the normal one [9, 12, 13]. Observing single *Daphnia* in darkness [14], thus reducing the potentials, reveal a nonuniform distribution of angles between two successive steps (Fig. 1). In this work we want to neglect any interaction with neighbors or external fields and focus on the influence of non uniformly distributed turning angles. We will derive diffusion coefficients for Gaussian distribution of turning angles and characterize between short time and long time behavior using a
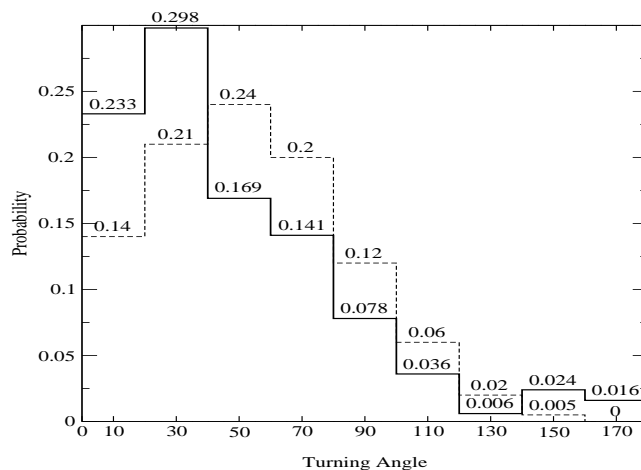
persistent random walker.

Fig 1. Experimental data for (single) *Daphnia* moving in darkness (taken from [14]). Rotational direction wasn't distinguished, thus we presume a left-right symmetrical distribution. A fit to a Gaussian approximation has the mean $\langle \eta \rangle = 48°$ and variance $\sigma = 36°$ and is shown as dashed histogram.

2. The *Daphnia* as a Random Walker

About three short straight swim strokes per second give the *Daphnia* a velocity of $\approx 4 - 16 \frac{\text{mm}}{\text{s}}$. For having negative buoyancy their hops are directed slightly upwards so we reduce the *Daphnia* to a (discrete) Random Walker in two dimensions with $\lambda \approx \frac{10}{3}$mm and $\tau \approx \frac{1}{3}$s (fixed step length and time interval). The ith displacement vector can be given by:

$$\vec{r_i} = \begin{pmatrix} \lambda \cos \theta_i \\ \lambda \sin \theta_i \end{pmatrix} \tag{1}$$

$$\theta_i = \theta_{i-1} + \eta_i \tag{2}$$

where θ_i is the angle between a fixed axis and the direction of motion. As mentioned above, the turning angles η_i are not distributed uniformly but bell like with one maximum at $30°$ and a very small local maximum at $150°$ (Fig. 1). The latter might vanish in experimental uncertainty but interestingly enough the *Copepods* show the same feature [5]. After $n = \frac{t}{\tau}$ steps the walker has a squared distance from the point of start of:

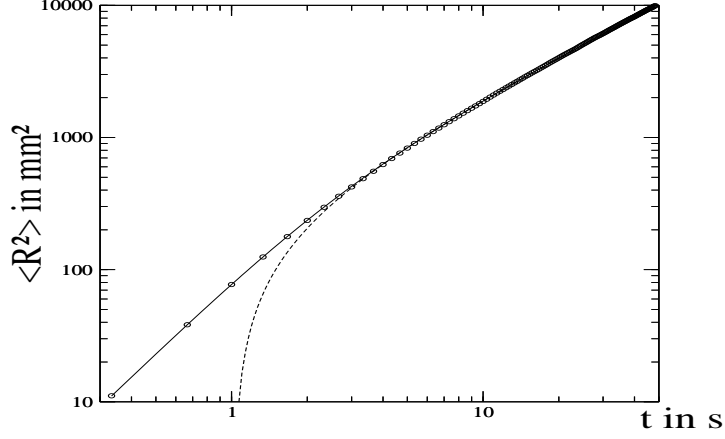$$\vec{R}_n^2 = \left(\sum_{i=1}^{n} \vec{r_i} \right)^2 . \tag{3}$$

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Fig 2. Simulation for 10^4 *Daphnia* with Gaussian angular distribution ($\langle \eta \rangle = 20°$,$\sigma = 36°$). Straight line represents the theoretical prediction by (8), the dashed line represents the asymptote (9) and the circles show the simulated data.

Averaging over an ensemble of walkers we have:

$$
\begin{aligned}
\left\langle \vec{R}_n^2 \right\rangle &= \left\langle \sum_{i=1}^{n} \vec{r}_i \sum_{j=1}^{n} \vec{r}_j \right\rangle = \sum_{i=1}^{n} \langle \vec{r}_i \rangle + 2 \sum_{i=1}^{n-1} \sum_{j=1}^{n} \langle \vec{r}_i * \vec{r}_j \rangle \\
&= n\lambda^2 + 2\lambda^2 \sum_{i=1}^{n-1} \sum_{j>1}^{n} \langle cos(\theta_i - \theta_j) \rangle .
\end{aligned}
\tag{4}
$$

With the angular correlation γ ($f(\eta)$ as distribution function for η):

$$
\gamma = \langle \cos(\theta_i - \theta_{i+1}) \rangle = \langle \cos \eta \rangle = \int_{-\pi}^{\pi} f(\eta) \cos \eta \, d\eta
\tag{5}
$$

and presuming correlation only between successive steps we get

$$
\begin{aligned}
\langle \cos(\theta_i - \theta_{i+2}) \rangle &= \int_{-\pi}^{\pi} f(\eta) \int_{-\pi}^{\pi} f(\eta') \cos(\eta + \eta') d\eta' \, d\eta \\
&= \int_{-\pi}^{\pi} f(\eta) \int_{-\pi}^{\pi} f(\eta') \cos \eta \cos \eta' d\eta' \, d\eta \\
&= \gamma^2 \,,
\end{aligned}
\tag{6}
$$

since sine is an asymmetrical function. It can be shown as well, that

$$
\langle \cos(\theta_i - \theta_{i+s}) \rangle = \gamma^s .
\tag{7}
$$

3

So we can solve the sum in (4) and get a formula for the mean squared displacement of a 2D correlated random walk like in [2] and [15] which was derived first by KAREIVA and SHIGESADA:

$$\left\langle \vec{R}_n^2 \right\rangle = \lambda^2 \left(n\frac{1+\gamma}{1-\gamma} - 2\gamma\frac{1-\gamma^n}{(1-\gamma)^2} \right) . \tag{8}$$

Values for a simulation of 10^4 walkers are presented in Fig. 2.

3. Diffusion

Since $|\gamma| < 1$ the second term on the right hand side of (8) is time independent for large n:

$$\lim_{n\to\infty} \left\langle \vec{R}_n^2 \right\rangle = \lambda^2 \left(n\frac{1+\gamma}{1-\gamma} - \frac{2\gamma}{(1-\gamma)^2} \right) . \tag{9}$$

Therefore the diffusion in long times is normal, for short times anomalous. The simulation (Fig. 2) shows a quick approach to the asymptotic limit. The diffusion coefficient is (in real time and two spatial dimensions):

$$4\,D = \frac{1+\gamma}{1-\gamma}\frac{\lambda^2}{\tau} . \tag{10}$$

To check the validity of (8) and (9) a population of 10^4 random walkers with a Gaussian angular distribution was simulated. Angular correlation for this type of distributions will be evaluated in a later chapter. Fig. 2 shows the results. After only a few steps the data approach the asymptote.

Looking at Eqs. (8) and (9) it can be seen that the second term in the sum can be interpreted as the square of a characteristic length scale. If this length scale is much smaller than the length scale of the process itself, Diffusion approximation holds.

As can be seen from Eq. (5) γ vanishes if η is equally distributed. This corresponds to the motion of a freely diffusing particle without any orientational preferences. Diffusion is enhanced if γ is in the range between 0 and 1. For example, this is the case if η is Gaussian with a mean turning between 0 and Pi.

4. Crossing Over Time

Now, let's find out, when the asymptote is reached or, to be more precise, when does the graph of equation (8) cut a straight line parallel to (9)? The distance of the two straight lines will be a fraction p of the absolute member e: With $D_n := \frac{1+\gamma}{1-\gamma}$ and $e := \frac{2\gamma}{(1-\gamma)^2}$ we can rewrite (8) and require:

$$D_n n - e + e\gamma^n \doteq D_n n - e + ep$$
$$\Rightarrow n_{\text{crossover}} = \frac{\ln p}{\ln \gamma} \tag{11}$$

To prove the formula a *Daphnia* population (of N individuals) is simulated S times starting from the origin. Every simulation yields a crossover time (when $\left\langle R_n^2 \right\rangle_N$ reaches the asymptote) to average over all simulations in the end. This has

to be done for different γ, i.e. different angle distributions. Here again we use a Gaussian distribution with a fixed variance ($\sigma = 36°$) and the mean between 0 and 90°. The consistency between theory and simulation (Fig. 3) is quite good, the step like appearance comes from averaging over discrete time steps.
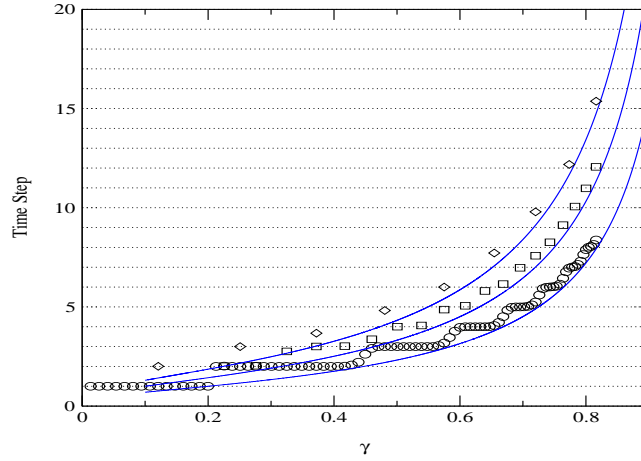

Fig 3. Time of crossing over dependent on the angular correlation γ. Simulations done with Gaussian distribution (variance $= 36°$). The lines represent the prediction according to (3). (Circles: $p=0.2$, N=1000, S=500; Squares: $p=0.1$, N=5000, S=1000; Diamonds: $p=0.05$, N=10^6, S=50000)

5. The angular Correlation

As we see, the angular correlation γ is crucial to calculate the time dependency of $\left\langle \vec{R}_n^2 \right\rangle$ as well as other movement features. We'll have a look at two different classes of distributions, a set of two delta peaks and a Gaussian distribution.

5.1. *Two Delta Peaks*

A (left-right symmetrical) distribution of two delta functions on both sides is a very simple representation of the two maxima observed in the biological experiment. Calculation of γ is trivial:

$$
\begin{aligned}
f(\eta) &= \frac{1}{2}\left[a\,\delta(|\eta| - \eta_1) + (1-a)\,\delta(|\eta| - \eta_2)\right] \\
\gamma &= \int_{-\pi}^{\pi} f(\eta)\cos\eta\,d\eta \\
&= a\cos\eta_1 + (1-a)\cos\eta_2 .
\end{aligned}
\tag{12}
$$

Here a controls the weight of the peaks at η_1 and η_2. Angular correlation and diffusion coefficient for a ratio of 10:1 ($a = \frac{10}{11}$) are shown in Fig. 4. This ratio

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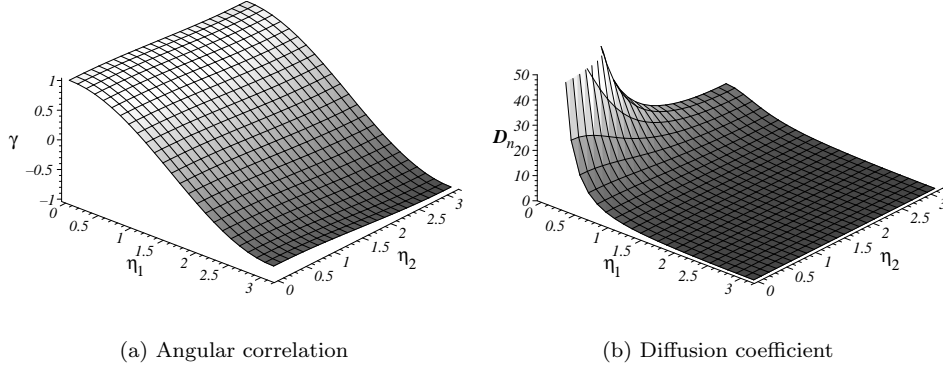(a) Angular correlation

(b) Diffusion coefficient

Fig 4. Angular correlation (a) and diffusion coefficient (b) versus the position of two different turning angles

reflects the values for the two peaks in the original experiment (Fig. 1). With the larger peak fixed at 48° (as observed in the experiments) the position of the second peak is crucial to the diffusion coefficient. With increasing $\eta_2 > \eta_1$ the enhanced diffusive behavior is damped up to 40% in term s of the diffusion coefficient and up to 30% in terms of the angular correlation.

5.2. Gaussian Distributions

Supposing again a symmetrical $f(\eta)$ integration of (5) can be done over $[0, \pi]$ with a factor 2. So the distribution consists of a Gaussian with probability $\frac{1}{2}$ on either side of the ordinate.

$$
\begin{aligned}
\| f(\eta) \|_{[-\pi, \pi]} &= 2 \| f(\eta) \|_{[0, \pi]} \\
&= 2 \int_0^\pi \exp\left(\frac{-(\eta - \langle\eta\rangle)^2}{2\sigma^2} \right) d\eta \\
&= 2 \sqrt{\frac{\pi}{2}}\, \sigma \left[\operatorname{erf}\left(\frac{\pi - \langle\eta\rangle}{\sqrt{2}\sigma} \right) + \operatorname{erf}\left(\frac{\langle\eta\rangle}{\sqrt{2}\sigma} \right) \right]
\end{aligned}
\tag{13}
$$

So we calculate

$$
\begin{aligned}
\gamma &= 2 \| f(\eta) \|_{[-\pi, \pi]}^{-1} \int_0^\pi \exp\left(\frac{-(\eta - \langle\eta\rangle)^2}{2\,\sigma^2} \right) \cos(\eta)\, d\eta \\
&= 2 \| f(\eta) \|_{[-\pi, \pi]}^{-1} \frac{1}{2}\, i\, e^{-i\langle\eta\rangle - \frac{\sigma^2}{2}} \sqrt{\frac{\pi}{2}}\, \sigma \\
&\quad \left[e^{2\,i\,\langle\eta\rangle} \operatorname{erfi}\left(\frac{-i\,\langle\eta\rangle + \sigma^2}{\sqrt{2}\,\sigma} \right) - e^{2\,i\,\langle\eta\rangle} \operatorname{erfi}\left(\frac{i\,\pi - i\,\langle\eta\rangle + \sigma^2}{\sqrt{2}\,\sigma} \right) - \right. \\
&\quad \left. - \operatorname{erfi}\left(\frac{i\,\langle\eta\rangle + \sigma^2}{\sqrt{2}\,\sigma} \right) + \operatorname{erfi}\left(\frac{i\,\pi + i\,\langle\eta\rangle + \sigma^2}{\sqrt{2}\,\sigma} \right) \right],
\end{aligned}
\tag{14}
$$

6

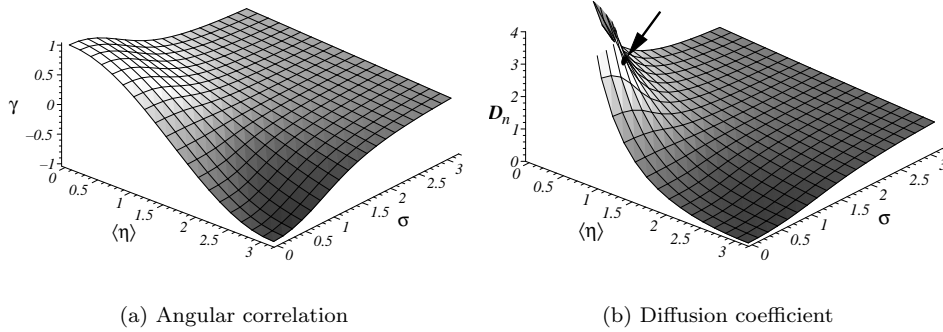(a) Angular correlation   (b) Diffusion coefficient

Fig 5. (a): Angular correlation versus mean ($\langle\eta\rangle$) and variance (σ) of a Gaussian distribution. (b): Diffusion coefficient calculated from (10) and (15). The experimental values for the *Daphnia* are indicated with an arrow at the following values: $\langle\eta\rangle = 0.84$, $\sigma = 0.63$ and $D_n = 3.1$.

where erfi is the complex error function which relates to the normal error function erf like $\text{erfi}(z) = \frac{\text{erf}(iz)}{i}$. With this, Eq. (13) and the substitutions $b := \frac{\langle\eta\rangle + i\,\sigma^2}{\sqrt{2}\,\sigma}$ and $c := \frac{-\pi + \langle\eta\rangle + i\,\sigma^2}{\sqrt{2}\,\sigma}$ equation (14) can be rewritten to:

$$\gamma\left(\langle\eta\rangle, \sigma\right) \;=\; \frac{\cos\langle\eta\rangle \cdot \Re\left[\text{erf}(b) - \text{erf}(c)\right] - \sin\langle\eta\rangle \cdot \Im\left[\text{erf}(b) - \text{erf}(c)\right]}{e^{\frac{\sigma^2}{2}}\left[\text{erf}\left(\frac{\pi - \langle\eta\rangle}{\sqrt{2}\sigma}\right) + \text{erf}\left(\frac{\langle\eta\rangle}{\sqrt{2}\sigma}\right)\right]} \quad (15)$$

$\Re$ and $\Im$ denote the real and imaginary part and we have a real function for all $\langle\eta\rangle$ and σ. In Fig. 5(a) γ is drawn versus the parameters of a Gaussian distribution and Fig. 5(b) shows the diffusion coefficient $D_n = \frac{1+\gamma}{1-\gamma}$. For $\langle\eta\rangle = \pi/2$ we have a $\gamma = 0$ and therefore $D_n = 1$, what is equivalent to free diffusion, and does not depend on the standard deviation of the turning angle anymore.

6. Conclusion

In this paper the random motions of *Daphnia* have been investigated. These motions were described by a random walk theory as in [3]. Due to the fact that the species described above prefer motions into a certain direction (preferred turning angle) the overall motion of a single *Daphnia* should deviate from the free diffusive behavior. With the help of the approach of KAREIVA and SHIGESADA [2] a Diffusion law for species moving with preferred turning angle has been developed. It has been found that the preference of an angle to turn in-between 0 and 90 degrees allows the individuals to cover a certain area faster than with a normal/free random walk. The effectiveness of searching for food is higher in this case compared to a search strategy based on pure random motion. With the help of the derived diffusion law the time which would be needed to be at every point of a given area could be calculated. Let us give a short example here: This work is dedicated to Frank Moss and his stimulating work on this field. That is why we would apply the formula especially to something what he is related to. Let us assume that Franks office is

about 30m^2. Thinking that Frank is going to become a even bigger fan of *Daphnia* he probably could fill his office with water to give more space to his lovely animals. The question what occurs then, is: How long will a single Daphnia take to travel over an area as big as Franks office is. The law given in this paper tells us it would take about 40 hours to be with the same probability at every position of this office.

Furthermore the existence of a second peak in the angular distribution was considered. Even, if this second peak is very small compared to the main peak it has a crucial influence to the enhancement of the diffusion. The bigger the peak the less is the deviation from the free diffusive behavior of the animals.

Acknowledgments

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