

Telegraphic Dispersions in Biology

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The telegraphic process remedies the two drawbacks of Fickian diffusion in modeling certain biological systems: infinite propagation speed and lack of velocity correlation. In this paper we discuss the telegraphic process both through theoretical and modeling considerations. We present a general form of the telegraph equation that includes spatially dependent drift, and obtained a stationary state solution in analogy with the classic Ornstein-Uhlenbeck process. The resulting distribution tends to a Gaussian in the appropriate limits.

We also performed numerical simulations to compare the mean squared deviations and mean exit times of the telegraph process to the diffusion process. The simulation was also generalized to include mean reverting drifts and the results are found to be consistent with the theoretical distribution.

Keywords: Telegraph equation, hyperbolic differential equations, Ornstein-Uhlenbeck process, escape time, swarm dynamics

I. INTRODUCTION

Animal dispersion is of fundamental research interest in ecology. Diffusion is often used to study such behaviors [1, 2]. Fickian diffusion, however, allows for infinite velocities and does not consider velocity correlations, and is thus sometimes criticized in modeling animal movements [3-5]. Fickian diffusion is often described with the Fokker-Planck equation, which for probability distribution $P(x, t)$ has the following form in 1D

$$P_t = -(F_1 P)_x + \frac{1}{2}(F_2 P)_{xx}, \quad (1)$$

where as in the rest of this paper, position and time variables in subscripts denote differentiations, and

$$\begin{aligned} \langle \delta x(t) \rangle &= F_1 \delta t, \\ \langle \delta x(t)^2 \rangle &= F_2 \delta t. \end{aligned} \quad (2)$$

The second line in Eq. (2) indicates that $\delta x_{rms}/\delta t = F_2/\delta x_{rms} \rightarrow \infty$. The fact that particles travel at infinite velocity can also be readily seen from the solution of Gaussian diffusion. Letting $F_1 = U$, $F_2 = 2D$, the solution of Eq. (1)

$$P(x, t) = \frac{1}{\sqrt{4\pi Dt}} e^{-(x-Ut)^2/4Dt} \quad (3)$$

is positive for any x and t .

Diffusion also assumes that the direction of motion at each step is uncorrelated with the previous direction. However, on small enough time scales, the velocity of any system depends on its previous velocity within its correlation time. Diffusion should be considered an approximation to the underlying correlated process when

the measurement time in the experiment is large compared to the correlation time.

For many systems in physics, the time between measurements is large compared to other times involved in the microscopic motions of the system. This fact was the starting point for the development of stochastic models describing Brownian motion. However, the movement of biological systems occurs on a very different time scale and the correlation times are much longer [2]. For these systems, the diffusion approximation breaks down and the system should be modeled with the correlations included, such as with the telegraph equation.

This paper is organized as follows. In Sec. II we review the telegraph equation. In Sec. III-IV we derive the telegraph equation with drift and solve for a stationary solution. In Sec. V we give the backward equation and discuss some rough ideas of more general solutions. In Sec. VI, we compare the telegraphic and diffusion processes through modeling. Sec. VII shows some ideas of future work and Sec. VIII concludes.

II. THE TELEGRAPH EQUATION

An alternate formulation to the Fokker-Planck dispersion was proposed by [6]. The proposed telegraph equation remedies the infinite velocity and also includes velocity correlations. We formulate this idea as adapted from [7]:

Instead of specifying a jump rate in the way one usually derives a Fokker-Planck equation from a Master's equation, we let the probability that the particle (or animal) keep the same direction be p , and the probability of turning around be q . In small time s after the last turn, the animal has moved distance δ , and we consider

them to be of the same order so that their ratio, the velocity γ remains constant. We let λ be the rate of turning so that the turning probabilities are given by

$$\begin{aligned} p &= 1 - \lambda s, \\ q &= \lambda s. \end{aligned} \quad (4)$$

We shall first quote the result for no drift and generalize to arbitrary drift field in the next section. Consider $\alpha(x, t)$ and $\beta(x, t)$ the probability density at coordinate x and time t arriving from the left and right, respectively. Then we can write

$$\begin{aligned} \alpha(x, t + s) &= p\alpha(x - \delta, t) + q\beta(x - \delta, t), \\ \beta(x, t + s) &= p\beta(x + \delta, t) + q\alpha(x + \delta, t). \end{aligned} \quad (5)$$

Expand to first order in s and λ and get

$$\begin{aligned} \alpha + s\alpha_t &= p(\alpha - \delta\alpha_x) + q(\beta - \delta\beta_x), \\ \beta + s\beta_t &= p(\beta + \delta\beta_x) + q(\alpha + \delta\alpha_x). \end{aligned} \quad (6)$$

Use Eq. (4) so that we get

$$\begin{aligned} \alpha_t + \gamma\alpha_x &= -\lambda(\alpha - \beta), \\ \beta_t - \gamma\beta_x &= \lambda(\alpha - \beta), \end{aligned} \quad (7)$$

where $\gamma = \delta/s$ is the finite velocity of the particle. After some straightforward manipulations, we arrive at the telegraph equation for the total probability density $P(x, t) = \alpha(x, t) + \beta(x, t)$:

$$P_{tt} - \gamma^2 P_{xx} + 2\lambda P_t = 0. \quad (8)$$

Notice in particular if the rate of turning $\lambda = 0$, the probability satisfies the linear wave equation, with the wave packet solution

$$P(x, t) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{\infty} A(k) \exp[ik(x \pm \gamma t)]. \quad (9)$$

For $\lambda \neq 0$, there is no normalizable solution of this form.

The solution to the telegraph equation for general lambda when the initial conditions are $P(x, 0) = \delta(x)$ and $P_t(x, 0) = 0$ is given by Morse and Feshbach [8] as

$$\begin{aligned} P(x, t) &= \begin{cases} \frac{e^{-\lambda t}}{2} (\delta(x - \gamma t) + \delta(x + \gamma t)) + \frac{\lambda}{\gamma} [I_0(Z) + \frac{\lambda t}{Z} I_1(Z)] & \text{for } |x| < \gamma t \\ 0 & \text{for } |x| \geq \gamma t \end{cases} \\ &\text{with } Z = \lambda \sqrt{t^2 - \frac{x^2}{\gamma^2}} \end{aligned} \quad (10)$$

where I_0 and I_1 are the zeroth and first order modified Bessel functions of the first kind. We can also find a differential equation for the second moment of this distribution directly from Eq. (8) by multiplying the equation by x^2 and integrating over all x . This yields the following equation

$$\frac{\partial^2 \langle x^2 \rangle}{\partial t^2} + 2\lambda \frac{\partial \langle x^2 \rangle}{\partial t} = 2v^2 \quad (11)$$

whose solution, subject to the desired initial conditions that $\langle x^2 \rangle|_{t=0}$ and $\frac{d}{dt} \langle x^2 \rangle|_{t=0}$, is

$$\langle x^2 \rangle = \frac{v^2}{\lambda} \left(t - \frac{1}{2\lambda} (1 - e^{-2\lambda t}) \right) \quad (12)$$

Notice that, in the long time limit, the term with the exponential goes to 0 and then the mean square deviations are linear in time. This is in agreement with the behavior of Fickian diffusion where $\langle x^2 \rangle = 2Dt$. Therefore, we can construct a Gaussian distribution that agrees with the telegraph solution in the long time limit by selecting $D = \frac{v^2}{2\lambda}$. By comparing the telegraph

solution to its corresponding Gaussian, we can model the convergence of the telegraph equation to the diffusion equation as the value of λt increases, i.e. as the ratio of the time elapsed to the correlation time increases. This convergence is depicted in Fig. 1.

III. TELEGRAPHIC DISPERSION IN DRIFT FIELD

Consider now the system in a drift field $U(x)$. In biology this scenario could represent for example the dispersion of plankton in a current, or the process of evolution: random genetic drift with natural selection. Though in the latter case there is little motivation to favor the telegraphic dispersal over Fickian diffusion. (Alternatively one may consider letting the turning rate depend on position. This approach is explored in [9].)

The Fickian dispersal is given by the Fokker-Planck Eq. (1), with $F_1(x) = U(x)$ and $F_2(x) = 2D$. To derive the corresponding result for telegraphic dispersion, we consider again Eq. (5), except now α and β represents the probability density of particles arriving from the left

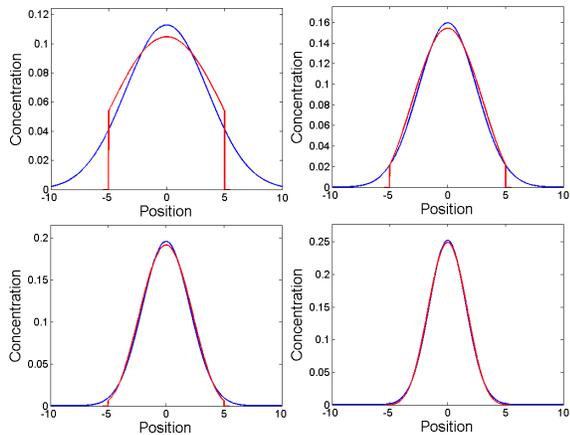


FIG. 1. **Telegraph versus Gaussian solutions.** Depicts the differences between the solution of the telegraph equation and its corresponding Gaussian distribution ($D = \frac{v^2}{2\lambda}$), depicted in red and blue respectively, as a function of the reversal rate λ . As λ increases the distribution approaches a Gaussian for the fixed time interval. From left to right, top to bottom $\lambda = 2, 4, 6, 10$. Notice that the solution to the telegraph equation has a cut-off since there is a finite maximum velocity. Other parameters: $v = 5, t = 1$.

and right in the frame that's locally at rest with the fluid (i.e. Lagrangian description). Then to transfer to the lab frame we realize that the drift introduces a flux $U(x)P(x, t)$, so that

$$\begin{aligned}\alpha_t &\rightarrow \alpha_t + (U\alpha)_x, \\ \beta_t &\rightarrow \beta_t + (U\beta)_x,\end{aligned}\quad (13)$$

where α and β still refer to the fluid's frame. Effecting this change in Eq. (6) and following through the rest of the derivation, we arrive at the following equation for telegraphic dispersion in field $U(x)$:

$$P_{tt} - \gamma^2 P_{xx} + 2(UP)_{xt} + [U(UP)_x]_x + 2\lambda [P_t + (UP)_x] = 0. \quad (14)$$

As a simple exercise, we shall compute the traveling wave solutions in the simple case $\lambda = 0$ and U is constant. Consider solution of the form $P(x, t) = f(x - ct)$, then Eq. (14) gives

$$(c^2 - 2Uc + U^2 - \gamma^2)\partial_x^2 f = 0. \quad (15)$$

Since a linear f is not normalizable, $\partial_x^2 f \neq 0$. Hence we get

$$c = U \pm \gamma, \quad (16)$$

i.e. the wave can travel in either direction in the medium with Galilean velocity addition, just as expected. To derive traveling wave solutions for $\lambda \neq 0$, it is necessary to diagonalize the differentiation, in the manner briefly described in Section V.

IV. STATIONARY SOLUTION

A. Stationary Equation

To obtain a stationary solution, we let all time derivatives go to zero in Eq. (14), arriving at

$$\partial_x J = 0, \quad (17)$$

where the current

$$J = -\gamma^2 P_x + U(UP)_x + 2\lambda UP \quad (18)$$

must thus be constant.

B. Telegraphic Ornstein-Uhlenbeck Process

Consider the Ornstein-Uhlenbeck field

$$U(x) = -\kappa x. \quad (19)$$

This scenario for Fickian diffusion is sometimes used to model a group of animals [1], where the diffusive force is countered with attraction to the swarm center or, in this simple model, the origin. For Fickian diffusion, the probability density is defined on the entire real line, and hence for normalization's sake the current in Eq. (18) must vanish. Since the velocity of the animals is now finite, the equilibrium distribution must be bounded on the interval

$$x \in \left[-\frac{\gamma}{\kappa}, \frac{\gamma}{\kappa} \right], \quad (20)$$

where $X = \gamma/\kappa$ represents a horizon of no escape. The current must vanish at the horizon, and consequently, on the entire interval. We thus have from Eq. (18) and Eq. (19)

$$(\kappa^2 x^2 - \gamma^2)P + (\kappa^2 x - 2\kappa\lambda x)P_x = 0 \quad (21)$$

or

$$\frac{P_x}{P} = -\frac{\kappa x}{\kappa^2 x^2 - \gamma^2}(\kappa - 2\lambda). \quad (22)$$

Eq. (22) is readily integrable and the result is

$$P(x) = A(\gamma^2 - \kappa^2 x^2)^{\frac{\lambda}{\kappa} - \frac{1}{2}}, \quad (23)$$

where the normalization constant is determined by integrating over the domain Eq. (20)

$$A = \frac{\kappa\Gamma(1 + \lambda/\kappa)}{\sqrt{\pi}\gamma^{2\lambda/\kappa}\Gamma(\frac{1}{2} + \frac{\lambda}{\kappa})}. \quad (24)$$

Throughout the entire problem, one can rescale x to rid of γ . (In fact, the entire model depends on the only non-dimensional parameter κ/λ .) Notice

$$\lim_{\kappa \rightarrow 0} (1 - \kappa^2 x^2)^{\frac{\lambda}{\kappa} - \frac{1}{2}} = \lim_{n \rightarrow \infty} (1 + \frac{1}{n})^{-n\lambda\kappa x^2 - \frac{1}{2}} = e^{-\lambda\kappa x^2}. \quad (25)$$

In other words, in the limit of low attraction, or equivalently high rate of turning, the result approaches the Fickian Ornstein-Uhlenbeck process. For $\kappa \ll \lambda$, we have a wide swarm. The swarm tightens as $\kappa \rightarrow 2\lambda$, when the distribution becomes constant. When $\kappa > 2\lambda$, the rate of turning is not big enough to exhibit swarming in the given field, and the particles are concentrated towards the horizon. In reality, only small κ corresponds to swarm and we plot a few results in Fig. 2, where we have taken $\lambda = 50$.

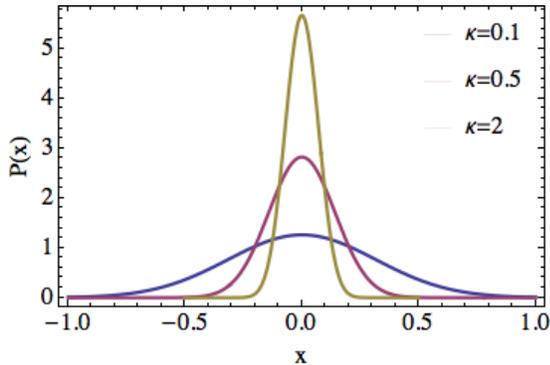


FIG. 2. **Stationary telegraphic swarms.** x axis is scaled so that $\gamma = 1$. λ is taken to be 50.

V. BACKWARD EQUATIONS AND DIAGONALIZATION

The conditional probability $P(x, t|x_0, t_0)$ satisfies the forward telegraph equation in x, t . One can similarly derive a backward equation for x_0 and t_0 by modifying Eq. (5) into backwards in time

$$\begin{aligned}\alpha(x, t) &= p\alpha(x + \delta, t + s) + q\beta(x - \delta, t + s), \\ \beta(x, t) &= p\beta(x - \delta, t + s) + q\alpha(x + \delta, t + s).\end{aligned}\quad (26)$$

Expanding again for first order and using Eq. (4)

$$\begin{aligned}\alpha_t + \gamma\alpha_x &= \lambda(\alpha - \beta) \\ \beta_t - \gamma\beta_x &= -\lambda(\alpha - \beta)\end{aligned}\quad (27)$$

which is the same as Eq. (6), except with λ changed sign. Thus

$$\partial_s^2 P(x, t|y, s) - \gamma^2 \partial_y^2 P(x, t|y, s) - 2\lambda \partial_s P(x, t|y, s) = 0. \quad (28)$$

And similarly for the equation with drift, now with additional flux

$$\begin{aligned}\alpha_t &\rightarrow \alpha_t - U\alpha_x, \\ \beta_t &\rightarrow \beta_t - U\beta_x.\end{aligned}\quad (29)$$

The drift does not get differentiated because now we are evaluating at current time. Omitting the argument of

P , we have the forward and backward equations:

$$\begin{aligned}P_{tt} + 2(UP)_{xt} + 2\lambda P_t &= \\ -[U(UP)_x]_x + \gamma^2 P_{xx} - 2\lambda(UP)_x, \\ P_{ss} - 2UP_{ys} - 2\lambda P_s &= \\ -[U^2 P_y]_y + \gamma^2 P_{yy} - 2\lambda UP_y.\end{aligned}\quad (30)$$

In comparison to the Fokker-Planck equation, these equations are called hyperbolic. For constant U , this means $(2U)^2 - 4(U^2 - \gamma^2) = 4\gamma^2 > 0$. To discuss the equation further, it is convenient to diagonalize the differentiation in the following manner.

Consider constant drift. Let

$$M = \begin{bmatrix} 1 & -U \\ -U & -\gamma^2 \end{bmatrix} \quad (31)$$

and

$$d = \begin{bmatrix} \partial_t \\ \partial_x \end{bmatrix}. \quad (32)$$

Then

$$R^T M R = D, \quad (33)$$

where D is diagonal. The expressions for R and D turn out to be complicated and will be omitted here. However, we shall note that the resulting equations can be cast in the form

$$P_{z_1 z_1} + aP_{z_1} + bP_{z_2 z_2} + cP_{z_2} = 0, \quad (34)$$

where a, b, c are constants and $z_1 = x - ct$ and z_2 are linear combinations of x and t .

The fact that the equation is hyperbolic means $b < 0$. Wavefront solutions of equations of the form Eq. (34) are considered in [10, 11]. Here we shall only make a simple comment. Letting $P_{z_2} = 0$, we get $P_{z_1 z_1} + aP_{z_1} = 0$. If a is imaginary then we have traveling wave solution

$$P(z_1) = A \exp[iz_1] = A \exp[i(x - ct)]. \quad (35)$$

VI. A SIMULATION OF THE TELEGRAPH PROCESS

For a very simple model of correlated velocities we consider a situation analogous to that of a random walker on a 1D lattice. However, instead of stepping left with probability l or stepping right with probability r , consider a process where the walker continues moving forward with probability p or turns around and takes a step with probability $q = 1 - p$. Notice that, regardless of the value of the persistence probability p , the process will be unbiased. Hence we compare results of the simulation of this telegraph process to the canonical random walk with $r = l = 0.5$. When $p = 0.5$ in the telegraph process, the two processes are equivalent. Five sample paths for the telegraph process with $p = 0.5, 0.8$ are plotted in Fig. 3.

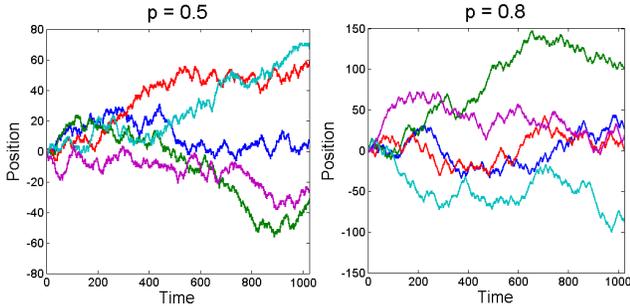


FIG. 3. **Example paths for a 1D telegraph process.** Simulated paths of the simple 1D telegraph process for two values of the persistence probability p . For $p = 0.5$ the sample paths are indistinguishable from those of a normal random walker. However, when $p = 0.8$ periods of repeated movement in the same direction become more frequent. Also notice that the deviations from the starting point tends to be greater for $p = 0.8$.

A. Comparisons between the telegraphic and random walk processes

In this section, we present some quantitative metrics to describe the differences between the 1D telegraph and random walk processes. The results lead to the same conclusion that can be seen in Fig. 3. Higher values of the persistence probability cause greater deviations from the starting point. Hence, movement according to the telegraph process is advantageous to animals because it means that they explore their environment faster, which aids them in the search of food and other resources.

1. Mean squared deviations

It is easy to see from Fig.3 that deviations from the initial position increase as the persistence probability increases. To make this trend quantitative the mean square deviations for the telegraph process as a function of time are shown in Fig.4 for $p = 0.5, 0.8$. The deviations are linear in time on large scales with the slope increasing with the persistence probability as expected. Though, on short time scales, the relation is non-linear (except for $p = 0.5$ when we have the basic random walk). This result matches the theory of the telegraph equation with a non-linear solution Eq. (12).

2. First passage problem

Another approach to analyze the differences between the models is to consider a first passage problem. We model a situation where there are two absorbing boundaries placed symmetrically about the origin. How many steps does it take for the particle to find its way to one of these positions? We would expect that this time would decrease as the persistence probability increases and this

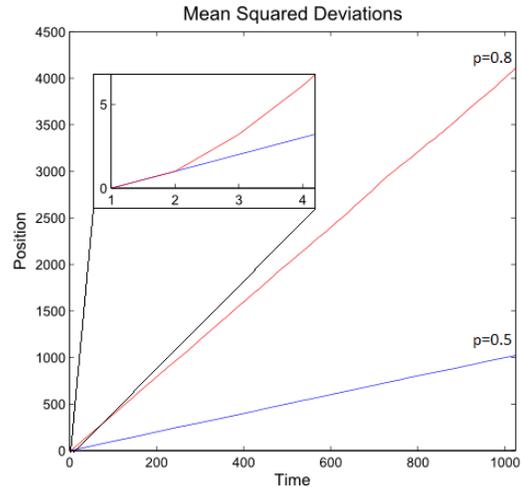


FIG. 4. **Mean square deviations.** Shows the dependence of the mean square deviations on time for the simulated telegraph process. The inset shows the behavior of the deviations for a small number of steps. For $p = 0.5$ the solution is precisely that of the random walk and the deviations are proportional to t everywhere. For $p = 0.8$ we see a higher slope and a deviation from the random walk linearity as expected.

dependence is precisely what we see in Fig.5. Therefore, an organism that tends to keep moving forward before turning around would find distant resources faster than one that walks randomly.

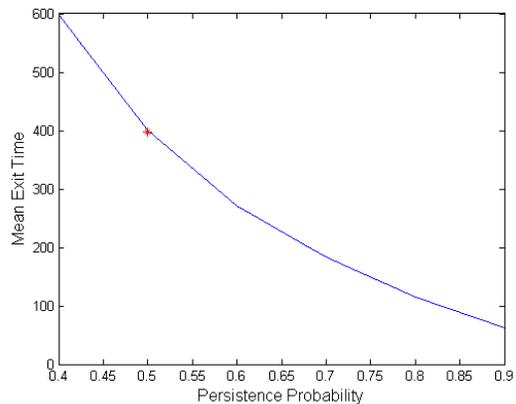


FIG. 5. **Mean exit times for the 1D telegraph process.** The mean time to exit a symmetric region about the initial position is seen to decrease as the persistence probability increases. The red asterisk shows the exit time for a normal random walker and is close to the exit time for $p = 0.5$ when the two processes are equivalent as expected. This result comes from the simulation of 2^{11} runs for each probability. The positions of the absorbing boundaries for this simulation were at ± 20 .

B. Simulation of a Telegraphic Ornstein-Uhlenbeck Process

We also considered a modified version of the telegraph process described above to include a mean reverting drift. The mean reverting drift is added into the process at each step, so now the step size varies with time. The amount of drift is assumed to increase linearly with the distance from the origin. Hence, there is a position on either side of the origin where the drift term would be equal to the maximum velocity of the particle so that it is forced back towards the origin. We simulated this process over many runs to determine the equilibrium distribution of the positions of the particles. The results of this simulation are shown in Fig. 6. It is easy to see the similarities between the results for this simulation and the results from the theory in section IV.

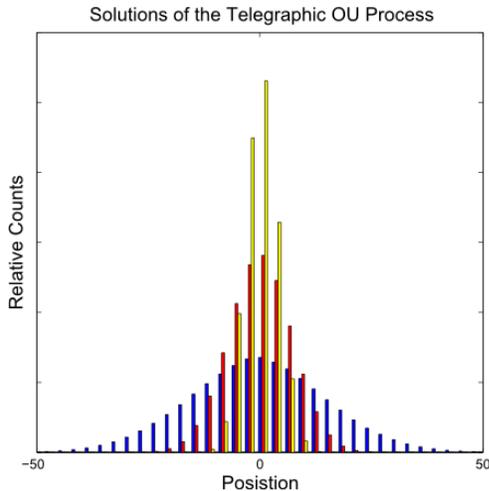


FIG. 6. **Simulated solution to the Telegraphic-OU process.** Distribution of positions for a simulated population subject to the Telegraphic Process with an OU mean reverting drift for three different values of the drift strength. The values were chosen to correspond to the three analytical solutions shown in Fig. 2. Good agreement can be seen between the analytical solutions and simulation results. Histograms contain values from 2^{12} simulations of 2^{12} steps for each of the sets of parameters.

VII. FUTURE WORK

A. Applications to Swarming

An introductory summary of the mathematical models of swarming can be found in [12]. Above we discussed the insect swarm attracted to the origin by an Ornstein-Uhlenbeck type force, and found the result to be a slight modification of Fickian dispersion. Fickian diffusion has been used to describe particle, insect swarms, such as bees [13], and animal dispersion through a landscape [7].

In such cases each individual in the swarm reacts in a simple way to its surroundings so that complex behaviors emerge from the collective group. Instead of assuming the swarm center to be fixed at the origin as we did above, a mean field theory can be developed with either Fickian or telegraphic diffusion, where animals react to local population density.

However, one realizes that in swarm of larger animals such as fish school or starling flock, the animals respond more to local direction of motion than population density, leading to strongly correlated velocity within the swarm. The fish on the boundary are subject to external forcing and as they react to an outside predator. In such cases the change of direction travels through the swarm as a wave, so that the fish in the middle of the swarm would react to the predator much earlier than it would if it were alone. The Fickian dispersion would thus be inappropriate to describe the behavior of such swarms. This type of swarming would be a natural generalization of the telegraph dispersion paradigm, where turning probability distribution is a function of local average velocities. Such a model can be conceptualized with ease in one dimension. This mean field generalization we leave to future work. One may consider higher dimensional cases as Cartesian products of one dimensional processes, but the full generalization to higher dimensions is non-trivial, as we now discuss.



FIG. 7. **Example of a fish school.** A school of bigeye trevally in Malaysia (photo credit [14]). Each individual aligns with local velocity average, so that complex swarming behavior emerge. Such collective behavior help protect the swarm against predators, for the reason that wave speed is larger than the speed of individual fish.

B. Generalization to Higher Dimensions

The derivation that leads to the telegraph equation in 1D does not directly generalize to higher dimensions. The result is a system of differential equations for the partial populations moving in different directions that cannot be combined into a single equation. A generalizable description considers the correlated random walk as a Poisson process with rate λ that gives the rate of reorientations per unit time. At each event in the Poisson process, the organism stops moving and chooses a new relative direction. This description of movement is very accurate for flagellated organisms such as *E. Coli* [2]. In general, the angular distribution of the reorien-

tations is organism specific and the step size may be directionally dependent as well. For example, an organism is likely to move further if it senses food in that direction. The interested reader is referred to the thesis by Edward Colding[15] for more details on the so called velocity jump process as applied to biological systems.

VIII. CONCLUSION

The telegraph equation is a fruitful alternative to the Fickian diffusion equation in modeling animal movements. In this paper, we considered the telegraph process in spatially dependent drift field and discussed the analogy to the Ornstein-Uhlenbeck process. We further

compared the mean square deviation and mean exit time with Fickian diffusion through numerical modeling. As expected, the processes considered do not produce significant differences between the two processes for wide range of parameters. However, the telegraphic approach can be more readily generalized to study certain behaviors not suitable for Fickian diffusions, such as fish schools.

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