Passive particles Lévy walk through turbulence mirroring the diving patterns of marine predators

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Lagrangian stochastic models for the simulation particle trajectories in turbulent flows can be made to be consistent with Kolmogorov’s similarity theory and with prescribed Eulerian velocity statistics. Intermittency (i.e., large temporal fluctuations in the rate of dissipation of turbulent kinetic energy) can also be accounted for but is usually neglected because its impact on turbulent dispersion is typically negligible. Here I show both heuristically and with the aid of numerical simulations that intermittency results in Lévy (Cauchy) walk movement patterns. The novel predictions find strong support in an analysis of movement pattern data for inert (dead) copepods in turbulent flows. This is the first experimental account of single particle movements in turbulence having Lévy walks characteristics. The mechanism stands apart from the much-studied chaotic and multiplicative pathways to Lévy walking. Lévy walks have been observed in sharks, bony fishes and in other aquatic marine predators and these have been attributed to the execution of an evolved, advantageous searching strategy. The new finding suggests that going with the flow movements is sufficient to explain the occurrence of these Lévy walks.

Keywords: | Lévy walks | Turbulence | Passive advection | Intermittency | Marine predators
1. Introduction

Lagrangian stochastic (LS) models are routinely used to simulate the trajectories of tracer-particles in turbulence [1]. They can produce trajectories that are consistent with Kolmogorov’s similarity theory of turbulence [2] and with prescribed Eulerian velocity statistics (used as model inputs); incorporating all available velocity statistics even when non-stationary and inhomogeneous. In atmospheric and oceanic boundary layers, large-scale shear, driven by external factors, provides the energy source for the turbulence, as disturbances extract energy from the unstable shear flow. The smaller scale flows are themselves unstable and produce even smaller flows, leading to a cascade of energy from large to small scales of motion where turbulent kinetic energy is eventually dissipated as heat. The rate of transfer of energy exhibits large fluctuations over time. Nonetheless, such fluctuations, known as ‘intermittency’, are usually neglected in LS models because they typically make a negligible contribution to eddy-diffusion coefficients and to other long-time dispersal statistics [3]. Consequently, LS models are usually formulated in terms of the average rate of transfer of energy between the large and small scales of motion. Here I show both heuristically and with the aid of numerical simulations that intermittency results in Lévy walk (LW) movement patterns. The novel prediction finds strong support in an analysis of movement pattern data for inert (dead) copepods in turbulent flows [4]. LWs have previously been implicated in the relative movements of particle pairs in turbulence (Richardson’s law) and have been identified in single particle trajectories in laminar (non-turbulent) flows [5] but this is the first theoretical and experimental account of single particle movements in turbulence having LW characteristics. Nonetheless, the hallmarks of LWs have been identified in vertical diving patterns of a diverse range of aquatic marine predators, including sharks, sea turtles, penguins bony fish and jelly fish (horizontal movements have not been quantified) [6-8]. Seeds, spores, pollens and other tracer-like particles are therefore predicted to traverse the atmospheric boundary-layer in the same way that large aquatic marine predators traverse the water column. This congruence of movement patterns suggests that LWs in aquatic marine predators might be attributed to flow-following; a tentative hypothesis that awaits experimental verification.

2. The simplest Lagrangian stochastic particle-tracking models predict the emergence of Lévy walks

In the simplest of case of stationary, isotropic, homogeneous, Gaussian, high-Reynolds number turbulence, the LS model for the simulation of tracer-particle movements consists of 3 independent Uhlenbeck Ornstein processes for movements in the x-, y- and z-directions [9]. Modelled movements in the x-direction are described given by
\[
du = \frac{-u}{T} \, dt + \sqrt{\frac{2 \sigma_u^2}{T}} \, dW \\
\frac{dx}{dt} = u dt
\] (1)

where \( x \) and \( u \) are the position and velocity of the particle at time \( t \). \( T = 2 \sigma_u^2 / C_0 \bar{\varepsilon} \) is the Lagrangian velocity autocorrelation timescale, \( \bar{\varepsilon} \) is the average rate of dissipation of turbulent kinetic energy, \( C_0 \) is a universal constant (Kolmogorov’s constant) and \( dW \) is an incremental Wiener process with mean zero and variance \( dt \) [9].

Pope and Chen [10] were the first to incorporate intermittency into LS models, i.e., were the first to replace the average rate of dissipation of turbulent kinetic energy, \( \bar{\varepsilon} \), by the instantaneous rate of dissipation of turbulent kinetic energy, \( \varepsilon \). They did this by noting that dissipation rates are approximately log-normally distributed (i.e., \( \chi = \ln(\varepsilon / \bar{\varepsilon}) \) is Gaussian distributed with \( \bar{\chi} = -\frac{1}{2} \sigma_{\chi}^2 \) [10]) and have exponential autocorrelation, as evidenced by data from DNS [11]. Consequently, Eqn. 1 can be supplemented by a stochastic equation,

\[
d\chi = -\left(\frac{\chi - \bar{\chi}}{T_x}\right) dt + \sqrt{\frac{2 \sigma_{\chi}^2}{T_x}} dW' \] (2)

where \( T_x \) is the autocorrelation timescale. Taken together, Eqns. 1 and 2 are equivalent to the long-time limit (i.e., \( t >> \) Kolmogorov’s dissipation timescale) of the model of Reynolds [12,13] which is in close agreement with data from carefully controlled, high-precision laboratory experiments [14].

A simple heuristic argument suggests that together, Eqns. 1 and 2, result in “Cauchy walks” [15], i.e., in LWs with Lévy exponent \( \mu=2 \). The argument is premised on the expectation that the long-time dynamics will be governed by the ratio of two Gaussian noises which can closely approximate Cauchy noise. In the long-time limit with \( \varepsilon \) effectively held constant, Eqn. 1 reduces to a random walk model

\[
dx = \sqrt{2K} dW \] (3)
with diffusivity \( K = 2\sigma_v^2 / C_0 \varepsilon^{*} \) that describes tracer-particle movements over time intervals with durations \( \Delta t \gg T \) [9]. This model is driven by the ratio of two noises, \( dW / \varepsilon^{*1/2} \) where \( \varepsilon^{*1/2} \) are averages of \( \varepsilon^{1/2} \) over the time intervals of duration \( \Delta t \). The central limit theorem dictates that these averages will tend to be Gaussian distributed because \( \varepsilon \) has finite mean and variance. It follows from this that displacements, \( dx \), will, to good approximation and up to a constant, be Cauchy distributed. This is simply because the ratio of the two Gaussian noises, \( y \) and \( z \), i.e. \( dW \) and \( \varepsilon^{1/2} \), is, to good approximation and up to a constant, Cauchy distributed

\[
P(s = y / z) = \frac{1}{2\pi \sigma_y \sigma_z} \int_{-\infty}^{\infty} dy dz \exp \left(-\frac{y^2}{2\sigma_y^2}\right) \exp \left(-\frac{(z-y)^2}{2\sigma_z^2}\right) \delta(s - y / z)
\]

\[
\approx \exp \left(-\frac{z^2}{2\sigma_z^2}\right) \frac{1}{\pi} \frac{\gamma}{\gamma^2 + s^2} \text{ when } s \gg \gamma = \frac{\sigma_y}{\sigma_z}
\]

The random walk, Eqn. 3, may therefore be a “Cauchy walk”. If so then Cauchy walks could, by virtue of the generalized central limit theorem, also arise at short times. These speculations are supported by the results of numerical simulations (Fig. 1) using Eqn. 1 and 2. Step-lengths, i.e., distances travelled between consecutive changes in the direction of travel, are seen to be Cauchy distributed. This is the hallmark of a Cauchy walk [15]. Moreover, the averages of \( \varepsilon^{1/2} \) are seen to be Gaussian distributed.

Similar results are expected whenever the LS models reduce to random walk models in the long-time limit, e.g., whenever turbulence is weakly inhomogeneous so that the timescale on which conditions change as viewed by a tracer-particle (due to inhomogeneity or unsteadiness in the turbulence) is much longer than \( T \) [9]. By way of contrast, if \( \varepsilon \) is constant then the LS model, Eqn. 1, produces exponentially-truncated LWs with \( \mu = 4 / 3 \) [16].

This finding suggests that going with the flow in the presence of turbulence results in \( \mu=2 \) LWs.

This possibility was examined in a re-analysis of telemetry data for inert (dead) and active (living) copepods in an aquarium. [4]. Even when inertial effects are negligible, LWs in copepods are not inevitable because their non-spherical shape will cause them to turn in response to the local fluid velocity gradients, making their trajectories deviate from those of tracer-particles [17].
3. Inert and active copepods Cauchy walk in turbulence

The aquarium was a 27 cm (W) x 18 cm (D) x 17 cm (H) glass tank. Quasi-homogeneous, isotropic turbulence was produced by two arrays of four counter rotating, 4 cm diameter, discs located on the lateral sides of the aquarium [18]. The intensity of the turbulence produced was comparable to that found in coastal zones and tidal estuaries. At this intensity living copepods can accelerate much more strongly than the flow. Three-dimensional Lagrangian particle tracking measurements were made using four synchronized cameras recording at 100 Hz. These measurements were made within a 10 cm x 10 cm x 10 cm volume in the middle of the aquarium. Copepod movements were recorded for 5 minutes in still water and in turbulent water. Michalec et al. [4] reported that copepods swimming in still water display intermittent behaviour characterised by a high probability of small velocity increments associated with steady cruising through the water, and by stretched exponential tails associated with frequent relocation jumps. Somewhat surprisingly they also found that velocity differences of living and dead copepods in turbulence collapse when normalized by their variance. This suggests that relocation jumps and strong fluid acceleration produce a similar intermittency. This intermittency can be modelled very well by a log-stable model with a non-analytical cumulant generating function (details given in the Supplementary Material).

Here the movement pattern data of Michalec et al. [4] is re-analysed. The re-analysis is based on the distances travelled in the vertical direction between consecutive turns which facilitates the detection of LW “diving” patterns that can be compared directly with the vertical diving patterns of large aquatic marine predators [7-8]. Michelec [4], on the other hand, presented results for displacements made across fixed-time durations. Re-analysis provides strong support for Cauchy walk movements in the vertical (Fig 2 and 3), and especially so when turbulence is relatively strong. Cauchy movement patterns are also evident to some extent in active copepods in still water. This is not surprising given that copepods swimming in still and turbulent flow belong to the same intermittency class [4]. In still waters the copepods self-induced motion consists of a succession of intermittent periods of slow swimming with strong relocation jumps that mimic the effects of turbulence. Nonetheless, such active behaviours are not required for the emergence of LW in turbulence and would be energetically costly because they would require that organisms frequently swim against the flow. Further analyses are presented in the Supplementary Material where it is shown that the velocity statistics of the model, Eqns. 1 and 2, like those of the copepods, are characterized by non-analytic cumulants (Figs. S1 and S2) and where evidence is presented for the copepods having 3-dimensional movement patterns resembling Lévy walks (Fig. S3).
4. Discussion

It was shown heuristically and with aid of numerical simulations that intermittency results in tracer particles in turbulence having LW (Cauchy walk) movement patterns (Fig. 1). These predictions found strong support in pre-existing data for dead (inert) and living (active) copepods in turbulence (Figs. 2 and 3). The result illustrates that generative mechanisms for LWs are often hiding in plain, as evidenced here by the cited literature pertaining to Eqns. 1 and 2 which comes from the 1980’s and 1990’s.

Tracer particles therefore move through turbulence in the same way as large aquatic marine predators traverse the water column [6-8]. Nonetheless, it remains to be seen whether the similarities between tracer particles and large aquatic marine predators encompass not only patterns of movement but also underlying generative processes. The LW diving patterns of large aquatic marine predators could be the result of their following the vertical flow movements. For marine predators, this free-ride or flow-assisted-ride would be an energetically favourable way of exploring the water column. Resisting such movements would incur energetic costs. In this regard, it is interesting to note that intermittency in oceanic turbulence is not confined to the smallest turbulence scales, as widely thought, but occurs across all scales [19]. Unlike many other organisms, aquatic marine predators may therefore be predisposed to have LW diving patterns. In other words, aquatic marine predators may have complex behaviours that are triggered both intrinsically by internal drivers and extrinsically by environmental cues but these are not required for the emergence of LW movement patterns which could occur freely, as a kind of null template. If so then their occurrence in marine predators would mirror those in other organisms which seem to have emerged accidentally from innocuous, banal organism-specific behaviours [20,21]. This challenges the widely-held view that LWs in marine predators are intrinsic and the result of selection for advantageous searching [6-8].

Data Accessibility. The datasets and computer codes supporting this article can be obtained from the author.

Competing interests. I have no competing interests.

Author contributions. AMR conceived the mathematical models, performed the numerical simulations, analysed the experimental data, interpreted the results, and wrote the paper.
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Figure 1 Simulation data supporting the heuristic argument for the emergence of LW movement patterns in intermittent turbulence. Simulation data for the step-lengths (distances travelled between consecutive changes in the direction of travel) produced by Eqns. 1 and 2 with $\sigma_u^2 = 1$, $\sigma_x^2 = 4$, $C_0 = 3$, $T_x = 1$ and $\bar{\varepsilon} = 50$ (o) together with the best-fit Cauchy distribution (red line) (left panel). Simulation data for the distribution of step-average values of $\varepsilon^{1/2}$ (o) together with the best Gaussian distribution (red line) (right panel). The simulation
data have skewness 0.19, flatness 3.02 and hyperflatness 15.01. Gaussian variables have skewness 0, flatness 3 and hyperflatness 15.
Figure 2 Inert (dead) copepods have LW movement patterns. Distributions of distances travelled in the vertical direction between consecutive changes in the direction of travel up and down the aquarium for inert copepods for different stirring rates (●) together with the best fit Cauchy distributions (red lines). Comparable results (not shown) were obtained for movements in the horizontal directions.
Figure 3. Active (living) copepods have LW movement patterns. Distributions of distances travelled in the vertical direction between consecutive changes in the direction of travel up and down the aquarium for active copepods for different stirring rates together with the best fit Cauchy distributions (red lines). Comparable results (not shown) were obtained for movements in the horizontal directions.