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Lagrangian modelling of plankton motion: From deceptively simple random walks to Fokker–Planck and back again

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Abstract

The movement of plankton, either by turbulent mixing or their own inherent motility, can be simulated in a Lagrangian framework as a random walk. Validation of random walk simulations is essential. There is a continuum of mathematically valid stochastic integration schemes upon which random walk simulations depend, each of which lead to radically different macro-scale dynamics as expressed in their corresponding Fokker–Planck equations. In addition, diffusivity is not a unique parameter describing a random walk and its corresponding Fokker–Planck equation. Spatially varying translation speed and turn frequency have different effects on population distributions. Validation requires extra information either in the form of the well-mixed condition for physical diffusion, or in detailed information on the sensing ability, internal state modulation and swimming response for plankton motility.

Keywords: Organism aggregations; Plankton; Swimming; Turbulent diffusion; Stochastic process; Foraging behaviour

1. Introduction

Planktonic marine organisms are confronted by the need to search for patchy and scarce resources in a medium that is continually stirred by turbulence, and that lends itself to relatively poor transmission of spatial information. Two important components of their motion through space, their quasi-random swimming behaviour and their advection by turbulent motion, are both diffusive-like processes that can be simulated for individual plankters, at least in its simplest form, as a random walk. Simulations of the relative motion of planktonic organisms derived in this manner can lead for instance to a mechanistic understanding of their encounter rates with each other and patchy distributions of resources, as well as pointing to more complex descriptions such as Levy walks (e.g. Klafter et al., 1996, 2001; Viswanathan et al., 2001), fractional random walks (e.g. Metzler and Klafter, 2000; Schmitt and Seuront, 2001; Metzler and Klafter, 2004), or area-restricted searches (e.g. Grünbaum, 2000; Hill et al., 2000; Leising and Franks, 2002) that may better simulate observed behaviours.

Lagrangian simulations and individual based models (IBMs) are becoming increasingly widespread in investigating marine processes, and provide a natural platform upon which the interactions (oftentimes nonlinear) of plankton with each other and their environment can be modelled. The prevalence of affordable and powerful computing capacity has made this approach not only feasible, but readily accessible. One

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of the cornerstones of Lagrangian and individual based models is the use of random walks to simulate diffusive-like processes, and provide a transparent means of modelling both turbulent dispersion (e.g. Yamazaki and Kamykowski, 1991; Kamykowski et al., 1994; Franks and Marra, 1994; Visser, 1997; Hannah et al., 1998) as well as behavioural aspects of swimming (e.g. Davis et al., 1991; Turchin, 1998; Flierl et al., 1999; Leising, 2001).

While random walk models are useful tools in Lagrangian simulations, they also have a strong conceptual appeal. In particular, one of the most powerful aspects of random walks is that they connect the kinematics of individual organisms at the micro-scale with macro-scale dynamics of a population of like organisms. Properties of individual motion can be related directly to a continuum description of concentration fields in advection–diffusion-like equations (more properly Fokker–Planck equations), the currency of traditional Eulerian based models.

Random walks are *deceptively* simple. That is, there are any number of seemingly simple aspects of random walks that can lead to unexpected results. With respect to the implementation of random walk models in simulating the Lagrangian aspects of the movement of plankton, I will address the following points:

a) Random walk can be characterized by diffusivity.
b) Conversely, a diffusive process can be simulated by a random walk.
c) Random walks so characterized and realized, equate to a Fokker–Planck description of a probability density function.
d) The form of the corresponding Fokker–Planck description is determined by the axiomatic assumption of the stochastic integration of the random walk process.
e) Diffusivity is not a unique parameter governing all aspects of the Fokker–Planck description of a specific random walk process.
f) An area-restricted search predicated on changing rates of turning requires a memory, and can be formulated in terms of an encounter modulated random walk.

Points (a–c) are the simple aspects of random walks, while points (d–f) are deceptive.

2. Random walk to diffusion and back again

A simple random walk of discrete, straight-line segments in n dimensions, interrupted by instantaneous uniformly random reorientations (Fig. 1a), can be characterized by an equivalent diffusivity

$$D = \frac{1}{n} v^2 \tau = \frac{1}{n} \frac{\lambda^2}{\tau} \tag{1}$$

where v is the uniform speed at which the particle (organism) travels, and τ is the mean intensity of exponentially distributed reorientation events. That is, the probability of reorienting in the time interval $(t, t+\delta)$ is $P(t, t+\delta) = 1 - e^{-\delta/\tau}$. This diffusive limit is reached for time scales $t \gg \tau$, (i.e. after a large number of run-tumble cycles). There are a number of classic works that examine this relationship (Chandrasekhar, 1943; Berg, 1992; Okubo and Levin, 2001). While some planktonic organisms exhibit run-tumble motility patterns (e.g. bacterial, flagellates) others exhibit a more continuous and sinuous trajectory (Fig. 1b). Taylor's analysis of continuous

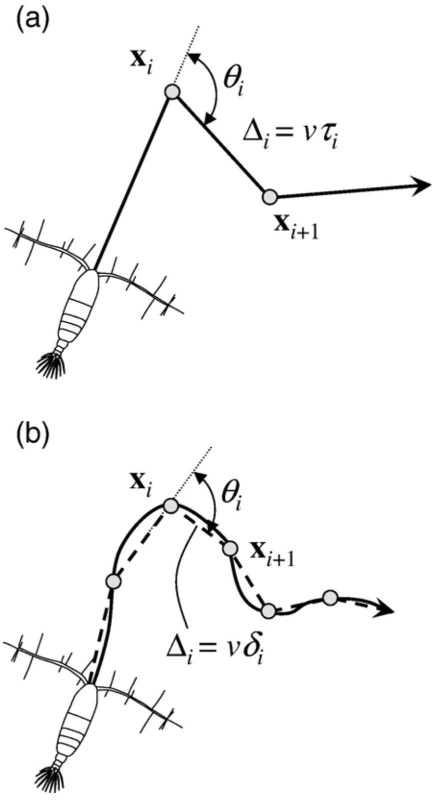

Fig. 1. Examples of the motility of a marine copepod. (a) Discrete run-tumble and (b) continuous random walk. In the discrete trajectory, the re-orientation angle θ_i is uniformly random in n dimensions, and run lengths Δ_i are exponentially distributed following the distribution of tumble intervals τ_i. The continuous case can be seen in a similar fashion where the trajectory is sampled at time intervals δ_i. This then looks like a discrete run-tumble trajectory with a degree of correlation between successive run directions.

random walk (Taylor, 1921) examines both the ballistic ($t<\tau$) and diffusive ($t\gg\tau$) regimes, and provides a reasonable model for a range of plankton motile behaviours (Jakobsen et al., 2005; Visser and Kiørboe, 2006), as well as physical stirring by turbulence. The analysis of a continuous random walk is similar to that of a discrete run-tumble random walk with the additional consideration of correlations between successive run directions. It can be arrived at by sampling the continuous trajectory at time intervals δ (Fig. 1b), and examining net displacement properties in the limit as $\delta\rightarrow 0$ (Taylor, 1921, see also Othmer et al., 1988). For the continuous random walk, τ in Eq. (1) is the correlation time scale, and can be related to the mean correlation between trajectory directions ($\hat{\vartheta}(t)$) at time offsets δ, i.e.

$$\left\langle \hat{\vartheta}(t)\cdot\hat{\vartheta}(t+\delta)\right\rangle = \langle \cos\theta_i\rangle = \psi \tag{2}$$

as

$$\tau = \delta/(1-\psi) \tag{3}$$

so that diffusivity (or the random motility of organisms) may be written as

$$D = \frac{1}{n}\frac{v^2\delta}{1-\psi} \tag{4}$$

(Berg, 1992). In the above, as in what follows, $\langle\ldots\rangle$ indicates the expectation value or ensemble average of the enclosed expression — these are equivalent for an ergodic process (Monin and Yaglom, 1975). Eq. (4) links the micro-scale kinematics of the motion of individual particles to the dynamics of a population of like particles.

Conversely, a diffusive process can be simulated by a random walk. That is, given a diffusivity D, the trajectory of individual particles, $\mathbf{x}(t)$, can be simulated as

$$\mathbf{x}_{i+1} = \mathbf{x}_i + \mathbf{r}_i\sqrt{2nD\delta} \tag{5}$$

where $\mathbf{x}_i=\mathbf{x}(t=i\delta)$, δ is a short time interval, and $\mathbf{r}_i$ is a random vector in n space such that the expectation value of its moments satisfy $\langle\mathbf{r}_i\rangle=0$, $\langle\mathbf{r}_i\cdot\mathbf{r}_i\rangle=1$, and $\langle\mathbf{r}_i\cdot\mathbf{r}_j\rangle=0$ for $i\neq j$. From this, it can be readily shown that the evolution of the variance (2nd moment) of the particle distribution follows

$$\left\langle(\mathbf{x}_m-\mathbf{x}_0)^2\right\rangle = 2nDt \tag{6}$$

where $t=m\delta$. That is, variance increases linearly with time — a characteristic of a diffusive process. In fact, Eq. (6) can serve as a definition of diffusivity D, it is $1/(2n)$ times the rate of change of variance of a particle distribution (Taylor, 1921).

3. Relating a random walk to a Fokker–Planck equation

3.1. Random walk as a stochastic integral

A random walk characterized and realized in terms of diffusivity equates to the Fokker–Planck equation in the continuum. That is, if the position $\mathbf{x}$ of a particle executing a random walk is governed in n dimensions by

$$\mathbf{x}_{i+1} = \mathbf{x}_i + \mathbf{u}(\mathbf{x}_i)\delta + \mathbf{r}_i\sqrt{2nD(\mathbf{x}_i)\delta} \tag{7}$$

then in the long time limit ($t\gg\delta$), the evolution of the probability density function (or concentration) is described by

$$\frac{\partial p}{\partial t} = -\nabla\cdot(\mathbf{u}p) + \nabla^2(Dp) \tag{8}$$

For the 3 dimensional case, $p(x, y, z, t)\,\mathrm{d}x\,\mathrm{d}y\,\mathrm{d}z\,\mathrm{d}t$ is the probability of finding the particle within a small volume of space $[x+\mathrm{d}x, y\pm\mathrm{d}y, z\pm\mathrm{d}z]$ in a small time interval $[t, t+\mathrm{d}t]$, although p can also be interpreted as the concentration of a population of like random walkers, provided they do not interact with each other. For generality, an advection velocity $\mathbf{u}$ is included. This result, i.e. Eq. (7)⇒Eq. (8) is well known and its derivation can be found in a number of places (e.g. Chapman, 1928; Skellam, 1951; Patlak, 1953; Lapidus and Levandowsky, 1981; Turchin, 1998; Okubo and Levin, 2001).

An important point to note is that Eq. (8) is *not* the advection–diffusion equation. It contains an effective additional advective term, $\nabla\cdot(p\nabla D)$, transporting particles down gradients of diffusivity. A consequence of this is that at steady state, $p\propto D^{-1}$. That is, random walking particles following a trajectory defined by Eq. (7) will aggregate in regions where diffusivity is low. For physical diffusion, (e.g. turbulent diffusion) this is deemed non-physical, violating the well-mixed condition (Thomson, 1987; Sawford, 2001) and necessitating a "correction" term (Hunter et al., 1993; Visser, 1997). For behavioural diffusivity (motility), the well-mixed condition need not apply, as the organisms involved have internal energy reserves that can be utilized to decrease entropy. Indeed, one of the best studied motility mediated aggregative effects, the "chemotaxis" of bacteria (any directed motion towards or away from chemicals, regardless of underlying mechanism, Schnitzer et al., 1990), is often explained in terms of a kinetic response of an increased turn rate (klinokinesis) in regions of high chemical concentration (Berg and Brown, 1977). In this interpretation the macroscale phenomenon of chemotaxis (a movement along a chemical gradient) is achieved even though the organisms involved have no knowledge of the gradient itself (*cf* Lapidus and Levandowsky, 1981). For physical diffusion (i.e. molecular and turbulent), aggregation does not occur. For instance, salt does not accumulate in the thermocline where turbulent diffusivity is low and neither should passively drifting particles; at least not through this mechanism. Since Lagrangian simulation may very well rely on similar random walk descriptions for both behavioural and physical aspects of planktonic motion, it is of some concern to identify where and why a correction term should be used and where it shouldn't.

In the following, I will examine the origin of the "correction" term, and outline how it relates to the axiomatic conditions inherent in stochastic integration. While in general, the problem is 3 dimensional, for simplicity I examine only the 1 dimensional case in what follows, and note that results so obtained can be projected into 3 dimensions by considering the superposition of 1 dimensional solutions onto 3 independent coordinates.

Consider a 1 dimensional stochastic trajectory where particle positions, $x(t)$, evolve according to

$$x(t+\Delta t)-x(t)=u\Delta t+\lambda\Delta\eta \tag{9}$$

Here Δt is a small time step and $\Delta\eta$ is a Wiener process such that $\langle\Delta\eta\rangle=0$ and $\langle(\Delta\eta)^2\rangle=\Delta t$ (Gardiner, 1985) This is a discretization of the stochastic differential equation

$$\mathrm{d}x=u\ \mathrm{d}t+\lambda\mathrm{d}\eta \tag{10}$$

where u and λ are respectively the *drift* and *intensity* of the stochastic process. Given this process, it is easily shown that in terms of the ensemble average of position statistics, the drift parameter u is given by

$$u=\lim_{\Delta t\to 0}\frac{\langle x(t+\Delta t)-x(t)\rangle}{\Delta t} \tag{11}$$

That is, u is the time rate of change of the 1st moment of the evolving probability density function. Likewise, the intensity parameter λ is given by

$$\lambda^2=\lim_{\Delta t\to 0}\frac{\left\langle(x(t+\Delta t)-x(t))^2\right\rangle}{\Delta t} \tag{12}$$

corresponding to the time rate of change of the 2nd moment of the evolving probability density function. Thus, the intensity can be related to diffusivity D (*cf*. Eq. (6)) as

$$\lambda=\sqrt{2nD} \tag{13}$$

where we include n as the number of dimensions for generality, although herein we set $n=1$. It can be shown that the continuum equation – the Fokker Planck equation – describing the time evolution of the probability density function (or concentration) for particles following this general random walk process can be written as

$$\frac{\partial p}{\partial t}=-\frac{\partial}{\partial x}(up)+\frac{\partial^2}{\partial x^2}(Dp) \tag{14}$$

(cf Okubo, 1980 p145 to 147), and is examined further in what follows. This is quite general, and takes into account the possibility that u and/or D (and thus λ) can vary spatially.

The drift term, u, in the above can be any function. A particularly revealing case is when this term is set to

$$u=\alpha\frac{\partial D}{\partial x} \tag{15}$$

and where α is a factor between 0 and 1. In this case, the corresponding Fokker Planck equation becomes

$$\frac{\partial p}{\partial t}=(1-\alpha)\frac{\partial}{\partial x}\left(p\frac{\partial D}{\partial x}\right)+\frac{\partial}{\partial x}\left(D\frac{\partial p}{\partial x}\right) \tag{16}$$

Thus, when $\alpha=0$, we have

$$\frac{\partial p}{\partial t}=\frac{\partial}{\partial x}\left(p\frac{\partial D}{\partial x}\right)+\frac{\partial}{\partial x}\left(D\frac{\partial p}{\partial x}\right)=\frac{\partial^2}{\partial x^2}(pD) \tag{17}$$

which leads to aggregation in regions of low D, whereas when $\alpha=1$, we have

$$\frac{\partial p}{\partial t}=\frac{\partial}{\partial x}\left(D\frac{\partial p}{\partial x}\right) \tag{18}$$

which is pure diffusion, and leads to no aggregation.

The interpretation of α can be got by examining the relationship

$$x(t+\Delta t)-x(t)=\xi=\lambda(x+\alpha\xi)\Delta\eta$$

This is simply Eq. (9) where 1) the explicit drift term is dropped and 2) the intensity of the stochastic process is evaluated not at the start of each excursion, but at a point between the start and end locations. This is sketched in Fig. 2. A Taylor expansion about x thus leads to

$$\begin{aligned}x(t+\Delta t)-x(t)=\xi&=\lambda(x)\Delta\eta+\alpha\xi\frac{\partial\lambda}{\partial x}\Delta\eta\\&=\lambda(x)\Delta\eta+\alpha\lambda\frac{\partial\lambda}{\partial x}\Delta t\\&=\lambda(x)\Delta\eta+\alpha\frac{\partial D}{\partial x}\Delta t\end{aligned} \tag{19}$$

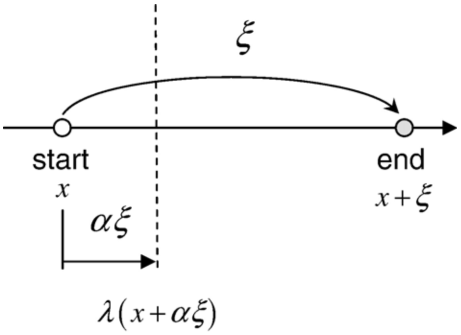

Fig. 2. Intensity λ of the stochastic integral (random walk) is evaluated at a fractional position a between the start and end of a run.

Thus, evaluating the intensity of the stochastic process at a position $x+\alpha\xi$ with no drift, is equivalent to evaluating the intensity at a position x (start position) and adding a drift velocity $u=\alpha\partial D/\partial x$. The corresponding Fokker Planck equation is Eq. (16) which leads to a pure diffusive process when $\alpha=1$, that is when the intensity of the stochastic process is approximated by that at the *end* point of each excursion.

At this stage, a couple of points should be noted. Firstly, on the sliding scale, $\alpha=0$ corresponds to Itô stochastic integration where as $\alpha=1/2$ corresponds to Stratonovich stochastic integration. There is no formal name for the integration scheme that arises out of $\alpha=1$, so we will term it Transport stochastic integration. Secondly, all integration schemes for $\alpha>0$ remain technically Markov processes as in practice they use only information at the start of each run.

In contrast to the above development, Okubo, 1986) (see also Skellam, 1973; Okubo and Levin, 2001) appears to derive a result that predicts that the pure diffusive case is given when the intensity is evaluated half way between start and end points — that is for the Stratonovich stochastic integration (Yamazaki et al., 2002). Thus there is an apparent inconsistency between the above analysis and that of Okubo. A closer examination however reveals that Okubo's derivation assumes *a priori* that all jump lengths have the same variance for equal time intervals, and that spatial variation of diffusivity arises only when the pause time (i.e. the probability of not moving) is a function of space. This is quite a different type of stochastic process from that described in Eq. (9). Here the probability of not moving is zero, and the variance of jump lengths changes in space for a given time step — depending on spatial gradients of the intensity $\lambda(x)$ for instance. In what follows, we will examine a derivation of the Fokker–Planck equation corresponding to Eq. (9) where explicit spatial variation or jump lengths are taken into account.

3.2. Fokker–Planck equation for spatially variable jump lengths: Itô integration

The Chapman–Kolmogorov master equation for a one dimensional stochastic jump process corresponding to Eq. (9) with $u=0$, can be written as

$$p(x,t+\Delta t)\mathrm{d}x = \frac{1}{2}p(x-\xi^-,t)\mathrm{d}x^- + \frac{1}{2}p(x+\xi^+,t)\mathrm{d}x^+ \tag{20}$$

where

$$\begin{aligned}\xi^- &= \lambda(x-\xi^-)|\Delta\eta|\\ \xi^+ &= \lambda(x+\xi^+)|\Delta\eta|\end{aligned} \tag{21}$$

This relates the probability of a particle being at x at time $t+\Delta t$ to where it must have come from at time t. Given equal probability of moving left or right, half must have arrived from $x-\xi^-$, and the other half from $x+\xi^+$ (cf. Fig. 3). Here, the jump length can vary in space as would arise when the intensity of the stochastic process is a spatial variable. $p(x,t)$ is the probability density function of finding particles in a small region $x\pm\mathrm{d}x$ in a time interval $t\pm\mathrm{d}t$. It should be noted that because the jump lengths are variable, particles arriving at $x\pm\mathrm{d}x$ will have originated from different spatial intervals depending on the local intensity at their point of departure. For instance, if intensity increases to the right, particles arriving in the interval $x\pm\mathrm{d}x$ from the left will have initially been in the interval $(x-\xi^-)\pm\mathrm{d}x^-$ where $\mathrm{d}x^- < \mathrm{d}x$. Thus the

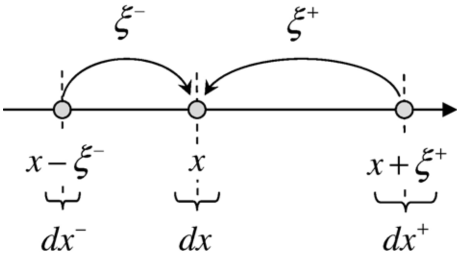

Fig. 3. Sketch of Chapman–Kolmogorov arrivals for spatially varying jump lengths. Arrival of random walkers at $x\pm\mathrm{d}x$ is determined by the Itô stochastic integral. Departure intervals $\mathrm{d}x^{\pm}$ scale with jump lengths $\xi^{\pm}$.

distinction between dx, dx^- and dx^+ in Eq. (20). A Taylor expansion of Eq. (21) about x leads to:

$$\begin{aligned}\xi^- &= \lambda(x)|\Delta\eta| - \frac{1}{2}\frac{\partial\lambda^2}{\partial x}|\Delta\eta|^2 + O\left(|\Delta\eta|^3\right) = \lambda(x)|\Delta\eta| - \frac{\partial D}{\partial x}\Delta t + O\left(|\Delta\eta|^3\right)\\ \xi^+ &= \lambda(x)|\Delta\eta| + \frac{1}{2}\frac{\partial\lambda^2}{\partial x}|\Delta\eta|^2 + O\left(|\Delta\eta|^3\right) = \lambda(x)|\Delta\eta| + \frac{\partial D}{\partial x}\Delta t + O\left(|\Delta\eta|^3\right)\end{aligned} \tag{22}$$

from which we can derive

$$\begin{aligned}\mathrm{d}x^- &= \mathrm{d}(x-\xi^-) = \mathrm{d}x\left(1 - \frac{\partial\lambda}{\partial x}|\Delta\eta| + \frac{\partial^2 D}{\partial x^2}\Delta t\right) + O\left(|\Delta\eta|^3\right)\\ \mathrm{d}x^+ &= \mathrm{d}(x+\xi^+) = \mathrm{d}x\left(1 + \frac{\partial\lambda}{\partial x}|\Delta\eta| + \frac{\partial^2 D}{\partial x^2}\Delta t\right) + O\left(|\Delta\eta|^3\right)\end{aligned} \tag{23}$$

Thus, to $O(|\Delta\eta|^3)$,

$$\begin{aligned}p(x,t+\Delta t) &= p(x,t) + \Delta t\frac{\partial p}{\partial t}\\ &= \frac{1}{2}\left(p(x,t) - \xi^-\frac{\partial p}{\partial x} + \frac{(\xi^-)^2}{2}\frac{\partial^2 p}{\partial x^2}\right)\left(1 - \frac{\partial\lambda}{\partial x}|\Delta\eta| + \frac{\partial^2 D}{\partial x^2}\Delta t\right)\\ &\quad + \frac{1}{2}\left(p(x,t) + \xi^+\frac{\partial p}{\partial x} + \frac{(\xi^+)^2}{2}\frac{\partial^2 p}{\partial x^2}\right)\left(1 + \frac{\partial\lambda}{\partial x}|\Delta\eta| + \frac{\partial^2 D}{\partial x^2}\Delta t\right)\\ &= p(x,t)\left(1 + \frac{\partial^2 D}{\partial x^2}\Delta t\right) + \frac{\xi^+ - \xi^-}{2}\frac{\partial p}{\partial x}\\ &\quad + \frac{\xi^+ + \xi^-}{2}\frac{\partial\lambda}{\partial x}|\Delta\eta|\frac{\partial p}{\partial x} + \frac{(\xi^+)^2 + (\xi^-)^2}{4}\frac{\partial^2 p}{\partial x^2}\end{aligned} \tag{24}$$

Noting the following identities derived from Eq. (22):

$$\begin{aligned}&\frac{\xi^+ - \xi^-}{2} = \frac{\partial D}{\partial x}\Delta t\\ &\frac{\xi^+ + \xi^-}{2}\frac{\partial\lambda}{\partial x}|\Delta\eta| = \lambda\frac{\partial\lambda}{\partial x}\Delta t = \frac{\partial D}{\partial x}\Delta t\\ &\frac{(\xi^+)^2 + (\xi^-)^2}{4} = \frac{1}{2}\lambda^2\Delta t = D\Delta t\end{aligned} \tag{25}$$

Eq. (24) reduces to

$$\frac{\partial p}{\partial t} = p\frac{\partial^2 D}{\partial x^2} + 2\frac{\partial D}{\partial x}\frac{\partial p}{\partial x} + D\frac{\partial^2 p}{\partial x^2} \tag{26}$$

or in simplified form

$$\frac{\partial p}{\partial t} = \frac{\partial^2}{\partial x^2}(Dp) \tag{27}$$

This is the same as Eq. (16) for $\alpha=0$.

3.3. Fokker–Planck equation for spatially variable jump lengths: General stochastic integration

We can go through the whole exercise again, this time evaluating the displacements not at the point of departure, but at a location somewhere between the start point and the end point (Fig. 4). If we take α as the ratio of the position of evaluation to the total displacement, then we can write

$$\begin{aligned}\xi^- &= \lambda(x - (1-\alpha)\xi^-)|\Delta\eta|\\ \xi^+ &= \lambda(x + (1-\alpha)\xi^+)|\Delta\eta|\end{aligned} \tag{28}$$

which can be evaluated via a Taylor expansion as

$$\begin{aligned}\xi^- &= \lambda(x)|\Delta\eta| - (1-\alpha)\frac{\partial D}{\partial x}\Delta t + O\left(|\Delta\eta|^3\right)\\ \xi^+ &= \lambda(x)|\Delta\eta| + (1-\alpha)\frac{\partial D}{\partial x}\Delta t + O\left(|\Delta\eta|^3\right)\end{aligned} \tag{29}$$

and lead to

$$\begin{aligned}\mathrm{d}x^- &= \mathrm{d}x\left(1 - \frac{\partial\lambda}{\partial x}|\Delta\eta| + (1-\alpha)\frac{\partial^2 D}{\partial x^2}\Delta t\right) + O\left(|\Delta\eta|^3\right)\\ \mathrm{d}x^+ &= \mathrm{d}x\left(1 + \frac{\partial\lambda}{\partial x}|\Delta\eta| + (1-\alpha)\frac{\partial^2 D}{\partial x^2}\Delta t\right) + O\left(|\Delta\eta|^3\right)\end{aligned} \tag{30}$$

The corresponding equation governing the evolution of the probability density function is then given by

$$\begin{aligned}p(x,t+\Delta t) &= p(x,t) + \Delta t\frac{\partial p}{\partial t}\\ &= \frac{1}{2}\left(p(x,t) - \xi^-\frac{\partial p}{\partial x} + \frac{(\xi^-)^2}{2}\frac{\partial^2 p}{\partial x^2}\right)\left(1 - \frac{\partial\lambda}{\partial x}|\Delta\eta| + (1-\alpha)\frac{\partial^2 D}{\partial x^2}\Delta t\right)\\ &\quad + \frac{1}{2}\left(p(x,t) + \xi^+\frac{\partial p}{\partial x} + \frac{(\xi^+)^2}{2}\frac{\partial^2 p}{\partial x^2}\right)\left(1 + \frac{\partial\lambda}{\partial x}|\Delta\eta| + (1-\alpha)\frac{\partial^2 D}{\partial x^2}\Delta t\right)\\ &= p(x,t)\left(1 + (1-\alpha)\frac{\partial^2 D}{\partial x^2}\Delta t\right) + \left(\frac{\xi^+ - \xi^-}{2} + \frac{\xi^+ + \xi^-}{2}\frac{\partial\lambda}{\partial x}|\Delta\eta|\right)\\ &\quad \times\frac{\partial p}{\partial x} + \frac{(\xi^+)^2 + (\xi^-)^2}{4}\frac{\partial^2 p}{\partial x^2}\end{aligned} \tag{31}$$

where from Eq. (29) the identities involving ξ^- and ξ^+ are given by

$$\begin{aligned}&\frac{\xi^+ - \xi^-}{2} = (1-\alpha)\frac{\partial D}{\partial x}\Delta t\\ &\frac{\xi^+ + \xi^-}{2}\frac{\partial\lambda}{\partial x}|\Delta\eta| = \lambda\frac{\partial\lambda}{\partial x}\Delta t = \frac{\partial D}{\partial x}\Delta t\\ &\frac{(\xi^+)^2 + (\xi^-)^2}{4} = \frac{1}{2}\lambda^2\Delta t = D\Delta t\end{aligned} \tag{32}$$

Thus, substituting and arranging terms

$$\frac{\partial p}{\partial t} = (1-\alpha)p\frac{\partial^2 D}{\partial x^2} + (2-\alpha)\frac{\partial D}{\partial x}\frac{\partial p}{\partial x} + D\frac{\partial^2 p}{\partial x^2} \tag{33}$$

This can be recast as

$$\frac{\partial p}{\partial t} = \frac{\partial}{\partial x}\left(D\frac{\partial p}{\partial x}\right) + (1-\alpha)\frac{\partial}{\partial x}\left(p\frac{\partial D}{\partial x}\right) \tag{34}$$

which is equivalent to Eq. (16).

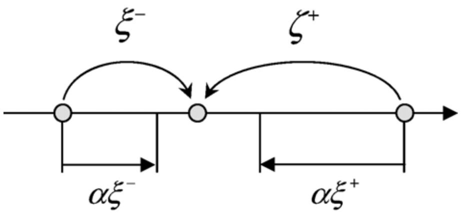

Fig. 4. Sketch of Chapman–Kolmogorov arrivals for variable jump lengths. Arrival of random walkers at a location are determined by the general α stochastic integral.

These results are verified numerically in Fig. 5. Specifically, a spatially varying diffusivity of the form $D=a_0+a_1\,x^2$ is chosen ($a_0=10^{-3}$ cm^2/s, $a_1=10^{-3}$ s^{-1}), similar in form to that used by Yamazaki and Nagai (2005), and a random walk of the form

$$x_{i+1}=x_i+r_{i+1}\sqrt{6D\delta}+\alpha\frac{\partial D}{\partial x}\delta \tag{35}$$

implemented, and where α is assigned the values 1, 1/2 and 0 respectively. r_i is a random variable, uniformly distributed between −1 and 1, thus with variance 1/3. The simulation time step is $\delta=1$ s. The distribution of random walking particles is plotted for each of these cases after 4 h of simulated time, and compare favourably with the theoretical distributions predicted by the steady state solution of Eq. (34) *viz.* $p\propto D^{-(1-\alpha)}$. That is, $\alpha=1$ maintains a uniform distribution, while aggregation becomes progressively more pronounced for $\alpha=1/2$ and $\alpha=0$, and is consistent with the model of Yamazaki and Nagai (2005).

There is something quite remarkable about these results; namely that the evaluation of the stochastic integral is strongly dependent on where the integrand is evaluated within a small interval — even in the limit as the interval tends to zero!! This is a phenomenon not encountered in ordinary integration and arises because of the nature of the stochastic process: a small change in interval Δt corresponds to a change in integrand proportional to $(\Delta t)^{1/2}$ becoming comparatively more important as $\Delta t\rightarrow 0$. From a practical point of view, this means that whenever a stochastic integration is preformed (e.g. a random walk implementation) the axiomatic assumption of the integration scheme, whether Itô, Stratonovich or any one of the α-integration scheme continuum, pre-determines the nature of the solution. There is nothing in the mathematical formalism that promotes one specific α-integration scheme over another.

In this interpretation, the correction term introduced to maintain the well-mixed condition in random walk simulations of physical diffusion (Hunter et al., 1993; Visser, 1997) is simply transforming from the Itô stochastic integral ($\alpha=0$) to the Transport integral ($\alpha=1$); that is, transforming to a stochastic integration scheme that is consistent with physical diffusion. Mathematical rigour cannot be used to distinguish one form the other. Model validation can only come from additional information such as the macroscopic distribution of particles (e.g. is the well-mixed condition met?) or

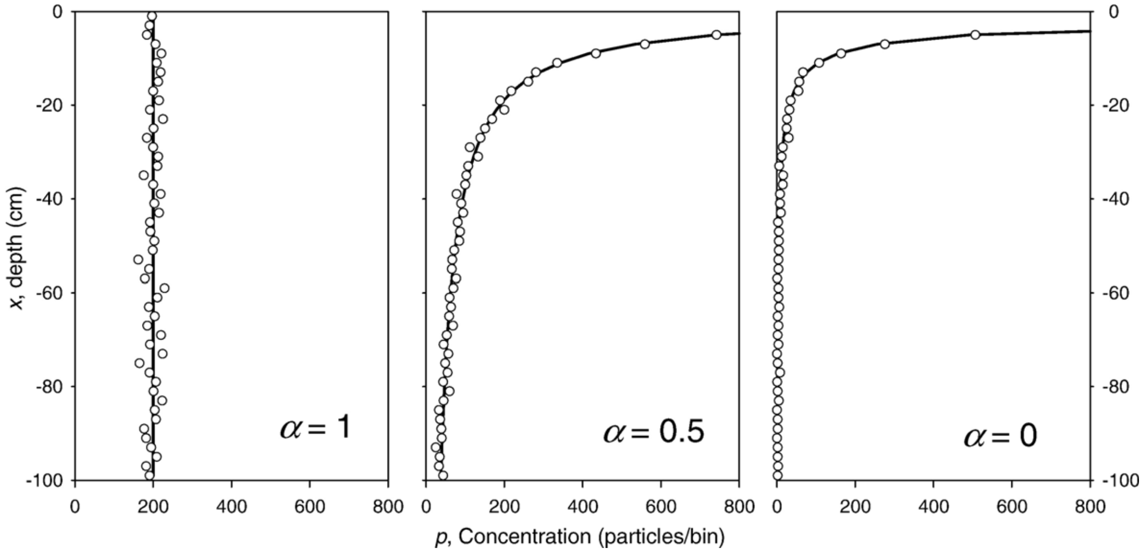

Fig. 5. Numerical experiment results for random walking particles following Eq. (35) for $\alpha=1$, 1/2 and 0 respectively. 10,000 particles are tracked at 3 s time steps and the particle concentration after 4 h plotted (symbols). The theoretical distribution predicted by the steady state solution of Eq. (34) is indicated by the line.

a microscopic analysis of organisms' behaviour (e.g. does translocation exhibit a directional bias?).

4. Decomposition of diffusivity

Thus, it appears to be a straightforward chain of reasoning from a random walk to diffusivity to the corresponding Fokker–Planck equation and so to advection–diffusion–reaction, and population level descriptions of spatial and temporal distribution patterns. However, D is a compound parameter, depending on 2 microscale variables; speed and correlation time scale (or correlation length scale). The same spatial variation of diffusivity can be achieved by varying either speed, or timescale, or both. Despite seemingly flawless arguments outlined above (i.e. points (a) to (c) from the introduction), these do *not* yield the same macroscopic, Fokker–Planck description (Schnitzer, 1993; Visser and Thygesen, 2003). Indeed, we can simulate the random walk not *via* Eq. (5) or Eq. (7), but at a more fundamental level as:

- At each time step δ, an angle θ_i is select from a normal distribution with mean $\langle\theta(x)\rangle=0$ and variance $\langle\theta(x)^2\rangle=\sigma(x)$. Note that the variance may be a function of position.
- The angle of motion ϕ is updated; $\phi_{i+1}=\phi_i+\theta_i$
- The particle position is updated; $x_{i+1}=x_i+v\,(x_i)\,\delta\hat{\varphi}_{i+1}$ where $\hat{\varphi}_{i+1}$ is the unit vector in the direction defined by ϕ_{i+1}.

For a normal distribution of angles, the probability of a specific angle laying in the interval $[\theta,\theta+\mathrm{d}\theta]$ is

$$P(\theta,\theta+\mathrm{d}\theta)=\frac{\mathrm{d}\theta}{\sigma\sqrt{2\pi}}e^{-\theta^2/(2\sigma)}$$

and $\langle\cos\theta\rangle=e^{-\sigma/2}=\psi$ (*cf* Eq. (2)). Thus the correlation time scale (*cf* Eq. (3)) can be related to the variance of the turn angle at time lag δ as

$$\sigma(x)=2\ln\left(\frac{\tau(x)}{\tau(x)-\delta}\right)$$

In regions where the correlation time scale is large, the angular variance is small; particles tend to travel in long straight paths. Conversely, where this time scale is small, the angular variance is large; particles tend to travel in convoluted paths. Within the above formulation, the correlation time scale (klinokinesis), and the speed of swimming (orthokinesis) can be adjusted independently, in response to an environmental cue.

While this problem can be approached analytically, it is extremely useful to model such processes numerically. Such models can be written in a couple of lines of code, run quickly, and can be used to verify the macro-scale effects of particular random walk implementations — effects that may be hidden in rigorous but impenetrable mathematical analysis. In Fig. 6 the results of such a model are presented. This represents, for instance, a vertical slice through a thin layer, wherein motile organisms change their local diffusivity by changing either (a) their correlation time scale (klinokinesis), or (b) their swimming speed (orthokinesis). 10,000 particles execute a vertical random walk with speed $v(z)$ and correlation time scale $\tau(z)$. The simulation covers a 2 m vertical section of the water column with a 20 cm thin layer wherein organisms (i.e. particles) change their turning frequency or swimming speed. For (a), $\tau(z)=15$ s outside and 1.5 s inside the thin layer while $v(z)=1$ cm/s throughout the whole simulated region. For (b), $v(z)=1$ cm/s outside and 0.316 cm/s inside the thin layer, while $\tau(z)=15$ s throughout the whole simulation. In both cases, diffusivity (i.e. that due to motility, Fig. 6c) has the same variation across the thin layer. The simulation time is 1 hour, after which the klinokinesis case (a) is still homogeneous while the orthokinesis case (b) displays a significant increase in concentration within the thin layer. It is apparent is that the effect of variable swimming speed leads to aggregation while variable turn frequency does not — even though their contribution to variable diffusivity, $D(z)=v(z)^2\,\tau(z)/n$ is equivalent.

By carefully considering the transition probabilities and the Chapman–Kolmogorov master equation, the corresponding Fokker–Planck continuum description is

$$\frac{\partial p}{\partial t}=\frac{1}{n}\nabla(v\tau\cdot\nabla(vp)) \tag{36}$$

(Visser and Thygesen, 2003). Thus, at steady state, $p\propto 1/v\propto D^{-1/2}$, and is independent of correlation time scale. Note that in the example in Fig. 5b the mean concentration ratio $(C_i/C_o)=3.19$ compares favourably with the diffusivity ratio $(D_i/D_o)^{-1/2}=3.16$. While this example is for a continuous random walk parameterized in terms of correlation time scale, an identical result is found for continuous run-tumble random walks parameterized in terms of turn frequency (Visser and Thygesen, 2003).

This result is somewhat surprising as klinokinesis is most often identified as the mechanism responsible for chemotaxis in bacteria (Keller and Segel, 1971) and prey-taxis in insects (Kareiva and Odell, 1987). The above is for a random walk where information is continually collected by the organism, and acted on immediately. That is, the organism's behaviour and the cue that triggered it are exactly spatially correlated. On the other hand, if the organism acts only on information at the start of each run

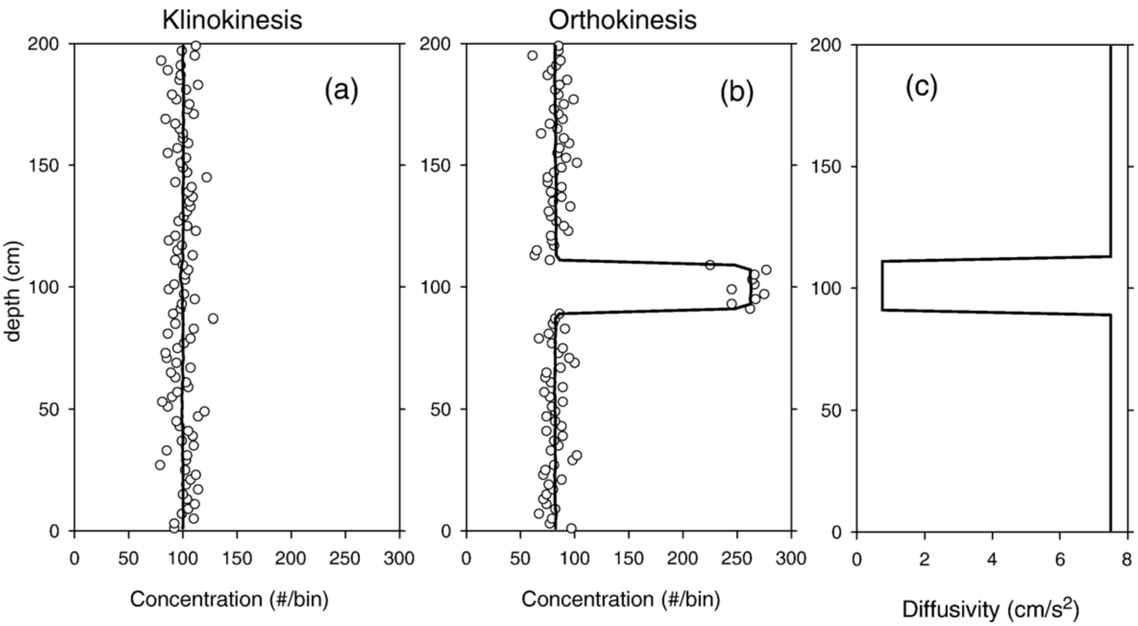

Fig. 6. Numerical experiment results. Spatially variable random walk where diffusivity (c) has the same profile, but where variable correlation time scale (a: klinokinesis) and translational speed (b: orthokinesis) are examined separately. 10,000 particles are tracked at 1 s time steps. Reflecting boundary conditions are applied at the surface and bottom while periodic boundaries are applied at the sides. The frequency distribution is calculated in 2 cm bins; the symbols giving the distribution at the last time step (after 1 h simulated time), and the solid line giving mean distribution per bin over the previous 1/2 h.

(i.e. when a tumble occurs), the governing Fokker–Planck equation becomes

$$\frac{\partial p}{\partial t} = \frac{1}{n}\nabla^2(v^2\tau\, p) \tag{37}$$

(Visser and Thygesen, 2003). This corresponds to the commonly used random walk Eq. (7) and its associated continuum description Eq. (8), and leads to aggregation for both ortho- and klinokinesis. In this case, the organism's behaviour and the cue that triggers it become uncorrelated. That is, at a fixed location, organisms that are observed there can exhibit behaviours that have been triggered by non-local cues.

There are 2 points to be made here. Firstly, diffusivity is a single parameter describing how the local variance of a random walk increases with time. However, it is a composite parameter and in itself does not uniquely describe all relevant aspects of the macro-scale properties of the random walk. Whether there is a spatial change in speed or tumble rate makes a difference, even if the spatial variation of diffusivity is the same. Secondly, how spatial information is acted upon also matters. For the behavioural factors governing random walk motility, instantaneous and continual responses to spatial information are apparently less efficient in aggregating organisms than responding periodically or with a time delay.

5. Area-restricted search

For planktonic organisms, the rate at which they encounter other organisms (prey, predators, and mates) is a key determinant in governing the rates of fundamental life processes (growth, mortality, and reproduction). Moreover, the distribution of resources (e.g. food organisms) is patchy. Area-restricted search is a foraging strategy characterized by a time dependent reduction in the turning frequency after the last resource has been located (e.g. Tinbergen et al., 1967; Leising and Franks, 2002). This strategy prolongs the time spent in areas of high resource abundance, and extends the search in regions where resources are scarce.

The criterion of a *time dependent* reduction in turn rate is important. As we saw in the previous section an *immediate* reduction in turn rate yields no aggregation. Inherent in the idea of an area-restricted search is the supposition that organisms have some memory of their recently sampled environment (e.g. Berg and Brown, 1977; Grünbaum, 1999, 2000). For instance, a bacterium travelling along a chemical gradient can compare the local chemical concentration to that sampled some time before.

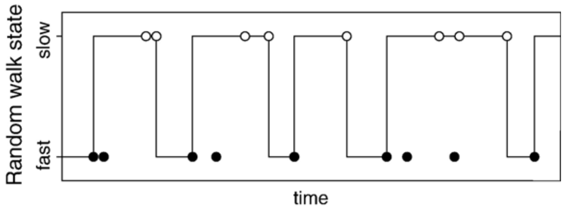

Fig. 7. Encounter modulated random walk. The transition from fast to slow is initiated by an encounter. The transition form slow to fast is a constant time interval T after the most recent encounter. Encounter times t_e are shown as filled circles, while t_e+T are shown a blank circles.

In this way, the bacterium can tell if its present motion is in a favourable direction or not. In other instances, organisms may not have a continuum cue, but rather rely on episodic events such as the encounter with a prey organism. In this case the pertinent parameter may be how long it has been since the last food particle was encountered. Any number of biochemical processes could provide a "clock" by which the time elapsed since an event can be measured (*e.g.* the decay of a chemical impulse initiated by an encounter).

An area-restricted search can be achieved via an encounter modulated random walk. That is, an organism remains in a slow-diffusion state for a period T following an encounter, before transiting to a fast-diffusion state. This transition from fast to slow diffusion and back again is illustrated in Fig. 7. We would expect that the relative proportion of time spent in one state versus the other depends on the ratio of the switching time T, to the mean time between encounters.

An encounter modulated random walk shares some characteristics of Levy walks, in that convoluted trajectories are interspersed periodically with long runs (Schmitt and Seuront, 2001; Schmitt et al., 2006). Fig. 8 shows an example path in 2 dimensions, where increased turning is initiated by contact with a prey item. The encounter modulated random walk has a conceptual advantage over a Levy walk proper in that a relatively simple biological mechanism can used to model the transition from one state to another — a mechanism that does not rely a long term "memory" integrating all past events.

Observational evidence at the macroscopic scale indicates that organisms can react to prey or solutes (Buskey and Stoecker, 1988; Fenchel and Blackburn, 1999; Bartumeus et al., 2003) and aggregate on thin layers — an ability observed for both copepods (Tiselius, 1992; Woodson et al., 2005) and ciliates (Menden-Deuer and Grünbaum, 2006). In many instances, behavioural shifts appear to be associated with direct prey contact. The behavioural shifts themselves take the form of either orthokinesis or klinokinesis. In some cases where aggregation is documented, organisms speed up in thin layers, a behaviour that acts against aggregation. It is therefore of some interest to explore whether an encounter modulated random walk expressed in terms of klinokinesis only, can lead to aggregation of organisms in favoured regions, supporting an area restricted foraging strategy.

The probability of encountering prey in a short time interval δ is

$$P_{\mathrm{enc}}(t,t+\delta)=1-e^{-Z\delta} \tag{38}$$

where $Z(\mathbf{x})$ is the encounter rate of the predator (j) on the prey (i), and can be formulated as

$$Z=\pi C_i R_{ij}^2\left(u_i^2+u_j^2+2w^2\right)^{1/2} \tag{39}$$

(Evans, 1989)Here, C_i is the prey concentration, R_{ij} is the distance at which the organism can detect a prey, u_i and u_j are the swimming velocities of the predator and prey respectively, and w is the turbulent velocity scale at the detection distance R_{ij} (Visser and MacKenzie, 1998). For a given situation, encounter rate increases with prey concentration, and it is this that we will primarily focus on here. However, it should be noted that encounter rate can also vary due to different levels of turbulence, or changes in prey swimming behaviour.

To illustrate the macro-scale effects of encounter modulated random walks, a numerical simulation is presented

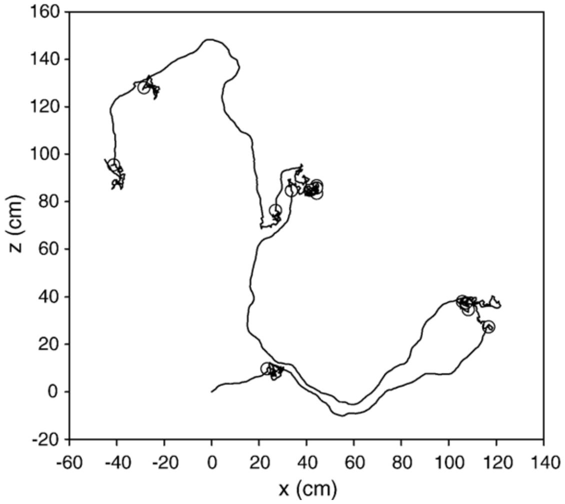

Fig. 8. Trajectory of an encounter modulated random walk. Particle starts at (0,0), and encounters are indicated by open circles. The correlation time scale for the fast and slow state are 10 and 2 s respectively, while the transition time is 50 s. Encounter rate is 0.01 s^{-1}.

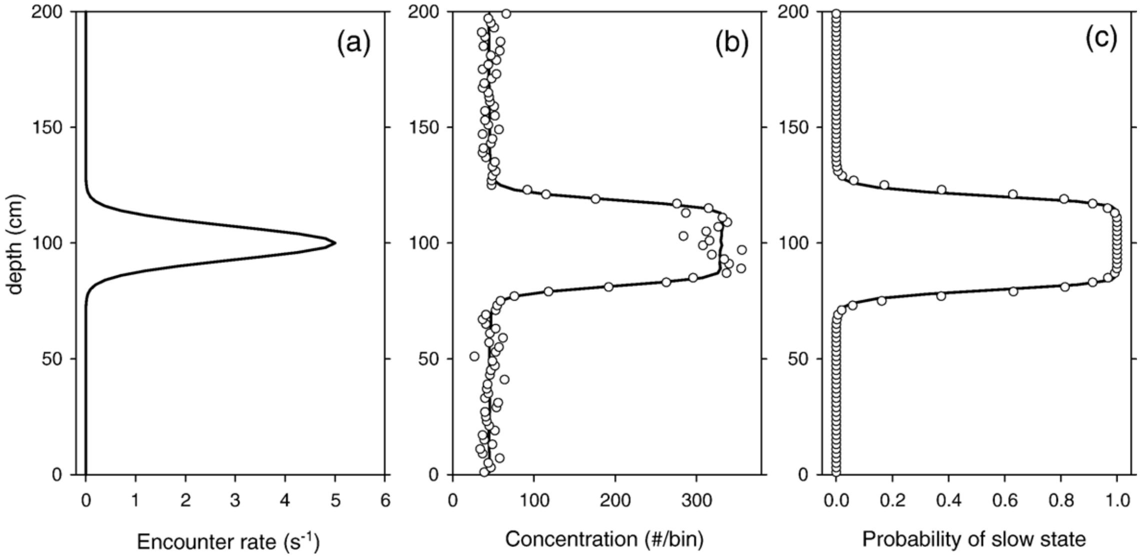

Fig. 9. Encounter modulated klinokinesis in a thin layer. (a) Profile of encounter rate, Z. (b) Vertical profile of particle concentration; symbols show concentration after 1 h of simulation time, while the solid line is the mean concentration over the last 1/2 h of simulation. (c) The probability of a particle being in the slow state as a function of depth; symbols show mean probability over the last 1/2 h of simulation while solid line gives theoretical curve; $p(\mathrm{slow})=1-e^{-ZT}$.

in Fig. 9. The rate at which organisms encounter prey (Fig. 9.a) is proportional to the prey concentration distributed in a thin layer. Motility parameters are the same as for the klinokinesis case in the previous section (*i.e.* $\tau(z)=15$ s outside, 1.5 s inside the thin layer and $v(z)=$ 1 cm/s uniform throughout). The switching time is $T=10$ s. An initially uniform distribution of 10^5 particles is tracked at 1 sec intervals for 1 hour. It appears that an encounter modulated klinokinesis can lead to aggregation of organisms in regions of high encounter rate (Fig. 9b). This is in contrast with a spatially varying klinokinesis with no memory (Fig. 6a) which leads to no aggregation and presumably does not increase foraging efficiency. Although a full analysis of the encounter modulated random walk is beyond the scope of this work, it appears that the steady state particle distribution (Fig. 9b) appears to follow the profile of the probability that the particle is in the slow diffusion state (Fig. 9c).

6. Conclusions

Random walk simulations and their associated Fokker–Planck equations provide a well founded path coupling micro-scale, individual-based, Lagrangian aspects of plankton motion to their macro-scale, Eulerian descriptions of population-level distributions. This approach can be used to examine both physical aspects of turbulent diffusion, and well as the quasi-random aspects of plankton's motility behaviour. There are however important and subtle validation issues that must be addressed.

The integration of a stochastic process – random walks and random flights being examples – requires an axiomatic decision. That is, for a specific stochastic process continuous in time, the choice of integration scheme used – whether Itô, Stratonovich or any of the continuum of α-integration schemes – directly effects the outcome of the integration. The choice of integration scheme must be validated. This requires extra information over and above the statistical properties of the random walk (e.g. diffusivity).

The recommendation for physical diffusion comes from thermodynamics — that a diffusive process cannot unmix a uniformly random particle distribution. This is the well mixed condition (Thomson, 1987). Any random walk simulation of physical diffusion that violates this condition cannot be validated. The stochastic integration scheme that is consistent with this criterion is the Transport stochastic integral ($\alpha=1$).

For behavioural motility, the choice of integration scheme is more complex. The well mixed condition need not apply. What is required is a detailed – or at least credible – understanding of how the organism senses its immediate environment, the internal processes through which this information is modulated, and the behavioural responses these trigger. The recommended integration scheme for a biologically mediated random walk, in the absence of other information, is the Itô stochastic integral

($\alpha=0$). There is, however a strong rider on this recommendation, namely, that organisms can "choose" their speed and turning rate depending not only on local conditions, but also their internal state. That is, the history of the organism also plays a role in its random walk characteristics and hence its spatial distribution. It is highly recommended that when detailed behavioural responses are known, simple numerical experiments should be conducted to verify that the appropriate Fokker–Planck equation is used to describe the distribution dynamics at the population level.

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