Movement

In the random flight case above (ignoring all the population dynamics to focus just on movement), the position and velocity evolve according to

$$
\begin{aligned}
d\mathbf{X} &= \mathbf{U}dt \\
d\mathbf{U} &= -r[\mathbf{U} - \tilde{\mathbf{u}}(\mathbf{X}, t)]dt + \beta(\mathbf{X}, t)d\mathbf{R}
\end{aligned}
$$

with $\tilde{\mathbf{u}}$ the preferred velocity.

We want to find the effective diffusivity

$$
\kappa_b = \int^t dt' \langle U_i(t)U_j(t')\rangle
$$

and the spread of a patch, showing that the latter aslo corresponds to diffusion.

From the velocity equation for constant $\tilde{\mathbf{u}}$

$$
\langle \mathbf{U}(t + dt)\rangle = (1 - rdt)\langle \mathbf{U}(t)\rangle + rdt\tilde{\mathbf{u}} \quad \Rightarrow \quad \mathbf{U} \to \tilde{\mathbf{u}}
$$

We can write $\mathbf{U}' = \mathbf{U} - \tilde{\mathbf{u}}$ then ignore $\tilde{\mathbf{u}}$, noting that it just gives translation of the whole pattern (not true when it's variable, of course). Then we can show that

$$
\begin{aligned}
\langle U_i'\rangle &\to 0 \\
\langle U_i'(t)U_j'(t)\rangle &\to \frac{\beta^2}{2r}\delta_{ij} \\
\langle U_i'(t)U_j'(t - dt)\rangle &= (1 - rdt)\langle U_i'(t - dt)U_j'(t - dt)\rangle \\
\langle U_i'(t)U_j'(t - \tau)\rangle &= (1 - rdt)^{\tau/dt}\frac{\beta^2}{2r}\delta_{ij} \\
&\simeq \exp(-r\,\tau)\,\frac{\beta^2}{2r}
\end{aligned}
$$

giving a diffusivity of

$$
\kappa_b = \frac{\beta^2}{2r^2}
$$

To see, the spread, we look at this example. The mean square displacement $\langle X^2 + Y^2\rangle$ grows linearly with time.

$$
\begin{aligned}
\langle X_i(t + dt)X_j(t + dt)\rangle &= \langle X_i(t)X_j(t)\rangle + \langle X_i(t)U_j(t) + X_j(t)U_i(t)\rangle dt \\
\langle X_i(t + dt)U_j(t + dt)\rangle &= \langle X_i(t)U_j(t)\rangle - rdt\langle X_i(t)U_j(t)\rangle + \langle U_i(t)U_j(t)\rangle dt \\
&\Rightarrow \\
\langle X_iU_j\rangle &\to \frac{1}{r}\langle U_i(t)U_j(t)\rangle = \frac{\beta^2}{2r^2}\delta_{ij} \\
&\Rightarrow \\
\langle X_i(t)X_j(t)\rangle &\to \langle X_i(0)X_j(0)\rangle + \frac{\beta^2}{r^2}\delta_{ij}t
\end{aligned}
$$

The latter corresponds to a diffusivity of $\kappa_b = \beta^2/2r^2$.

$$\frac{\partial}{\partial t} b = \kappa_b \nabla^2 b \quad \Rightarrow \quad \frac{\partial}{\partial t}\int b = 0 \quad , \quad \frac{\partial}{\partial t}\int x b = 0$$
$$\frac{\partial}{\partial t}\int x^2 b = 2\kappa_b \int b \quad \Rightarrow \quad \int x^2 b \Big/ \int b \to 2\kappa_b t$$

- Area grows like $4\kappa_b t$ ($6\kappa_b t$ in 3-D)
- Velocity variance is $r\kappa_b$

In the more general case when $\tilde{\mathbf{u}}$ and/or β vary, we can consider the probability distribution $\mathcal{P}(\mathbf{x}, \mathbf{U})$

$$\frac{\partial}{\partial t}\mathcal{P} = -\frac{\partial}{\partial x_i} U_i \mathcal{P} - \frac{\partial}{\partial U_i} r[\tilde{u}_i - U_i]\mathcal{P} + \frac{\partial^2}{\partial U_i^2} K_U \mathcal{P}$$

with $K_U = \beta^2/2$. From this, the biomass density $b(\mathbf{x}, t) = \int d\mathbf{U}\, \mathcal{P}(\mathbf{x}, \mathbf{U}, t)$ changes by the divergence of fluxes

$$\frac{\partial}{\partial t} b = -\frac{\partial}{\partial x_i} F_i \quad , \quad F_i = \int d\mathbf{U}\, U_i \mathcal{P}$$

If $\tilde{\mathbf{u}}$ is steady and uniform and K_U is constant, the probability distribution will be Maxwellian:

$$\mathcal{P} = b(\mathbf{x}, t)\mathcal{P}_M(\mathbf{U} - \tilde{\mathbf{u}}, K_U/r)$$
$$\mathcal{P}_M(\mathbf{U}', s) = (2\pi)^{-3/2} s^{-3/4} \exp\left(-|\mathbf{U}'|^2/2s\right)$$

For this form, the flux is just

$$F_i = \int (U_i - \tilde{u}_i) b \mathcal{P}_M + \tilde{u}_i b \int \mathcal{P}_M = \tilde{u}_i b$$

The basic idea is that this distribution is a good local approximation, but that spatial variations will generate deviations because of the ∇ term, and, in turn, these deviations will give non-zero flux divergences. If r is large, the distribution is narrow, and the dominant terms are

$$\mathcal{L}(\mathcal{P}) \equiv r\frac{\partial}{\partial U_i}(U_i - \tilde{u}_i)\mathcal{P} + \frac{\partial^2}{\partial U_i^2} K_U \mathcal{P}$$

and

$$\mathcal{L}(\mathcal{P}) = \frac{\partial}{\partial t}\mathcal{P} + \frac{\partial}{\partial x_i} U_i \mathcal{P}$$

The lowest order gives $\mathcal{P} = b\mathcal{P}_M(\mathbf{U}', K_U/r)$ with $\mathbf{U}' = \mathbf{U} - \tilde{\mathbf{u}}$. At the next iteration,

$$\mathcal{L}(\mathcal{P}) = \mathcal{P}\left[\frac{\partial}{\partial t}b + \frac{\partial}{\partial x_i}\tilde{u}_i b\right] + U_j'\mathcal{P}_M\frac{\partial}{\partial x_j}b$$

Multiplying by U_i' and integrating over $\mathbf{U}$ gives

$$-rF_i + r\tilde{u}_i b = \frac{\partial}{\partial x_j}\int U_i'U_j'\mathcal{P}_M b = \frac{\partial}{\partial x_j}\delta_{ij}\frac{K_U}{r}b$$

so that

$$F_i = \tilde{u}_i b - \frac{1}{r}\frac{\partial}{\partial x_i}\frac{K_U}{r}b$$

or

$$\mathbf{F} = (\tilde{\mathbf{u}} - \frac{1}{r}\nabla r\kappa_b)b - \kappa_b\nabla b$$

with the diffusivity κ_b being K_U/r^2.

$$\boxed{\frac{\partial}{\partial t}b = -\nabla\cdot(\mathbf{u}_b b - \kappa_b\nabla b) \quad , \quad \mathbf{u}_b = \tilde{\mathbf{u}} - \frac{1}{r}\nabla r\kappa_b}$$

The velocity includes the fluid velocity and directed swimming (both in $\tilde{\mathbf{u}}$) as well as movement from regions with higher random accelerations into areas where it's lower. Note that turbulent diffusion will come from the $\mathbf{u}b$ term: if the damping rate is fixed, there's no swimming, and κ is constant, the advecting velocity is just $\mathbf{u}$. Both purposeful biological movement (e.g., a tendency to swim upwards) and variability in the random motion in response to environmental cues can give a $\mathbf{u}_b$ which is convergent and tends to increase the concentration.

Taxis and Kinesis

Organisms can respond in various ways depending on environmental cues. We represent the latter by $C(\mathbf{x},t)$ and distinguish

- taxis: $\mathbf{u}_b$ depends on gradients of cue fields $\nabla C(\mathbf{x},t)$. Gradients may be sensed directly or by using memory of past conditions. (The grass is greener over there so let's go that way.)
- kinesis: β (and therefore κ_b) depends only on the local cue field $\exp(-C/C_0)$. (The grass is lousy here so let's move.)

Cues may be environmental (food, light, depth,...) or social (positions of neighbors,...)

- schooling: $\mathbf{u}_b$ depends on neighbors' $\mathbf{U}$ with $|\tilde{\mathbf{u}}|$ having a fixed value.

We define **taxis** as a preference for moving up the gradient of the cue field

$$\mathbf{u}_b = \alpha \nabla C$$

As an example, we consider $C = C_0[1-\cos(kx)]/2$ so that $\tilde{\mathbf{u}} = V_0 \sin(kx)\hat{\mathbf{x}}$ and

$$\mathbf{A} = -r[\mathbf{U} - \tilde{\mathbf{u}} - V_0 \sin(kx)\hat{\mathbf{x}}]$$

The u=0;beta=0.7 case shows aggregation in the favored region; mean flows u=0.5 shift the center downstream; smaller K beta=0.35 gives a tighter pattern.

- Taxis on a spatially and temporally fixed cue field causes aggregation where $\nabla \cdot \tilde{\mathbf{u}}$ [or $\nabla^2 C$] is most negative
- Advection can shift this downstream and decrease the strength of aggregation.
- κ_b controls the width of the aggregation.

As a standard prompple, consider swimmming towards a fixed target depth (taken to be $z=0$)

$$\tilde{w} = -w_0 \tanh(z/h)$$

This is a divergent flow, which can, in general be represented as flow down a potential gradient

$$\tilde{\mathbf{u}} = -\nabla \phi$$

with $\phi = -\alpha C$ for taxis. A steady state solution to

$$\frac{\partial}{\partial t} b = \nabla \cdot [b \nabla \phi + \kappa_b \nabla b]$$

is just

$$b = b_0 \exp(-\phi/\kappa_b)$$

For the $\tilde{w}$ above,

$$\phi = -w_0 h \ln \cosh(z/h)$$

and

$$b = b_0 [\mathrm{sech}(z/h)]^{w_0 h/\kappa_b}$$

Numericsshow this solution is approached rapidly if we start with a uniform distribution over a finite area.

Social taxis

Social behavior can be represented as a cue which epends on the density of neighbors. For example,

$$C(\mathbf{X}) = \sum_{\mathbf{X}'} \left[\frac{1}{4}|\mathbf{X}' - \mathbf{X}|^4 - \frac{1}{2}|\mathbf{X}' - \mathbf{X}|^2\right] \left[|\mathbf{X} - \mathbf{X}'| < 1\right]$$

gives attraction to neighbors.

Kinesis is a more primitive response in which the random accelerations increase or decrease depending on the cue field:

$$\beta = \beta(C)$$

For a first example, we let $\beta = \beta_0 - \beta_1 C/C_0$

u=0;beta0=2.7;beta1=2.4.

- Kinesis can produce aggregation
- Groups tend to be looser, depending on β_{max}/β_{min}

This behavior could arise from pausing for feeding, leading to aggregation in regions of high food concentration.

For an analytical example, we note that if r is constant, the equation is equivalent to

$$\frac{\partial}{\partial t} b = \nabla^2 \frac{K_U}{r^2} b$$

which has steady solutions

$$b = const. \frac{1}{K_U}$$

The net flux from high K_U regions (high β) to low K_U regions produces convergence into the latter. Comparison with taxis suggests the results will look rather similar if $K_U \sim \exp(-C/C_0)$. The comparison of the stochastic model with the PDE versions quite good.

Social kinesis

$$C(\mathbf{X}) = \sum_{\mathbf{X}'} \left[1 - |\mathbf{X}' - \mathbf{X}|^2\right] \left[|\mathbf{X}' - \mathbf{X}| < 1\right]$$

less randomness Another example assumes organisms turn more frequently in the presence of many neighbors $\Rightarrow$ small mean free path.avoidance

Schooling can be represented as

$$\tilde{\mathbf{u}} = V_0 \tilde{\mathbf{u}}_1 / |\tilde{\mathbf{u}}_1|$$

$$\tilde{\mathbf{u}}_1 = \alpha \sum_{\mathbf{X}'} (\mathbf{X}' - \mathbf{X}) w(|\mathbf{X}' - \mathbf{X}) + \sum_{\mathbf{X}'} \mathbf{U}' w(|\mathbf{X}' - \mathbf{X}|)$$

alpha = 0.3 alpha = 0.7