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by

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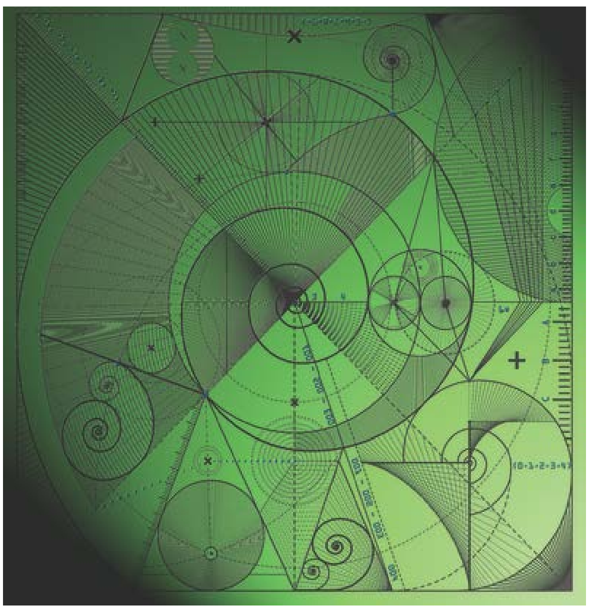

Moving finite element approximation of an aggregating population in two dimensions

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Abstract

The evolution of a species is modelled in two dimensions by a Lotka-Volterra equation system in which the random motion of individuals is biased so as to increase their expected rate of reproduction. The system is solved numerically in a fixed finite region using a moving mesh finite element method in which the mesh movement is driven by local conservation. With random seeding the population is seen to form clusters which depend on parameters representing diffusion and the size of a local survival region.

1 Introduction

In [3, 4] Grindrod noted that the derivation of many dispersion models rests on the assumption that the dispersal of individuals is due solely to random diffusive motion. However, it is readily apparent that in the real world individuals group together to improve their chances of survival, do not voluntarily overcrowd themselves to death, and deliberately avoid predators. Grindrod therefore proposed a dispersion model in which the random motion of individuals is biased by an optimal velocity in which the population is on average dispersing so as to increase an individual's expected rate of reproduction.

Results obtained in [4] from this model for a single population in one dimension demonstrated that from an initially random seeding of individuals local clusters are formed.

In this paper we demonstrate the clustering phemonenon numerically in two dimensions using a moving mesh finite element method based on conservation. The numerical approximation uses linear finite elements moving with a conservation velocity, for which weak forms of the balance equation and conservation laws are derived. The algorithm is implemented and results discussed for a number of two-dimensional scenarios.

1.1 A clustering model

Following [4] a standard population balance equation is augmented by a term describing the projected net rate of reproduction per individual, constructed in a manner comparable to the logistic term in a Lotka-Volterra equation. The crucial difference compared to the standard model is that it is assumed that individuals seek to maximise their chances of survival and so move towards a optimum.

The projected net rate of reproduction is defined as

$$E = \text{average birth rate - average death rate}$$

Overcrowding or loneliness means a death rate higher than birth rate and in between there is an optimum population density. As in [3, 4] it is assumed that E depends only on the population density $u(\mathbf{x}, t)$, and an optimal velocity $\boldsymbol{\nu}(\mathbf{x}, t)$ is constructed as a local average of $\nabla E(u)$. For convenience the optimal velocity is assumed to be derived from a potential $q(\mathbf{x}, t)$, that is $\boldsymbol{\nu} = \nabla q$. Following [3, 4] we define the relationship between $E(u)$ and q to be

$$E(u) = -\epsilon \nabla^2 q + q. \tag{1}$$

where ϵ is a parameter. Conceptually, in (1) the potential $q(\mathbf{x}, t)$ is a measure of the attractiveness of the location of an individual, taking into account not just survival chances at that point but also the local area. The size of the area defined as local is important and is controlled by the parameter ϵ.

2 Model equations for a single species

In order to emphasise clustering effects we assume that births or deaths occur on a much longer time scale than clustering, so are neglected here.

The single species population balance equation for the population density $u(\mathbf{x}, t)$ in a region Ω is then

$$\frac{\partial u}{\partial t} = -\nabla \cdot (u\mathbf{v}) \tag{2}$$

where the velocity $\mathbf{v}$ is the sum of the optimal velocity $\boldsymbol{\nu} = \nabla q$ and a diffusive velocity $-\delta\,(\nabla u)/u$, leading to

$$\frac{\partial u}{\partial t} = \delta \nabla^2 u - \nabla \cdot (u \nabla q), \tag{3}$$

$\mathbf{x} \in \Omega, \quad t \geq 0$ where δ is a diffusion coefficient. Boundary conditions on u and q are the reflective conditions

$$\partial u/\partial n = 0, \qquad \partial q/\partial n = 0, \qquad \mathbf{x} \in \partial\Omega, \quad t \geq 0. \tag{4}$$

Note that a consequence of (3) and (4) is that the total population

$$\int u(\mathbf{x}, t) \mathrm{d}\mathbf{x} \tag{5}$$

is constant in time.

Given $E(u)$ and the population density $u(\mathbf{x}, t)$ at any given time, we can obtain $q(\mathbf{x}, t)$ from (1) and use (3) to determine the evolution of u. Following [3, 4] we take $E(u)$ to be of the form

$$E(u) = (1 - u)(u - a) \tag{6}$$

where $a = 0.2$.

3 Solution procedure on a moving domain

We follow a procedure in which the interior of the domain Ω is allowed to deform in time so as to preserve and track a distribution of the local population.

We write (2) as

$$\frac{\partial u}{\partial t} + \nabla \cdot (u\mathbf{v}) = 0, \tag{7}$$

an Eulerian conservation law equivalent to constancy in time of the (Lagrangian) local mass

$$\int_{\Omega(t)} u \, \mathrm{d}\mathbf{x} \tag{8}$$

when the points of the domain $\Omega(t)$ move with velocity $\mathbf{v}(\mathbf{x}, t)$.

We solve (3) numerically using the moving-mesh finite element procedure based on conservation described in [1, 2, 5], as follows. Comparing (7) with (3), the velocity $\mathbf{v}$ satisfies

$$-\delta\nabla^2 u + \nabla \cdot (u\boldsymbol{\nu}) = \nabla \cdot (u\mathbf{v}) \tag{9}$$

Having found $\mathbf{v}(\mathbf{x}, t)$ from (9), a deforming coordinate $\widehat{\mathbf{x}}(\mathbf{x}, t)$ is found by integrating the differential equation

$$\frac{\partial \widehat{\mathbf{x}}}{\partial t} = \widehat{\mathbf{v}}(\widehat{\mathbf{x}}, t) \tag{10}$$

where $\widehat{\mathbf{v}}(\widehat{\mathbf{x}}, t) = \mathbf{v}(\widehat{\mathbf{x}}(\mathbf{x}, t), t)$. The local population density $u(\widehat{\mathbf{x}}, t)$ at any time is then deduced from the constancy of the local population (8) in the form

$$\int_{\widehat{\Omega}(t)} u(\widehat{\mathbf{x}}, t) \, \mathrm{d}\mathbf{x} = \int_{\Omega(0)} u(\mathbf{x}, 0) \, \mathrm{d}\mathbf{x}$$

where the right hand side is calculated from the initial condition at $t = 0$.

3.1 A distributed conservation principle

In order to construct a finite element method we define a distributed conservation principle and weak forms. For any positive weight function $w(\mathbf{x}, t)$ the distributed population,

$$\int_{\Omega} w(\mathbf{x}, t) \, u(\mathbf{x}, t) \, \mathrm{d}\Omega, \tag{11}$$

is constant in time (consistent with (5)), inducing a distributed velocity $\mathbf{v}(\mathbf{x}, t)$. Differentiating the constant mass (11) with respect to time using the Reynolds Transport Theorem,

$$\frac{\mathrm{d}}{\mathrm{d}t} \int_{\Omega(t)} w(\mathbf{x}, t) \, u(\mathbf{x}, t) \, \mathrm{d}\Omega = 0$$

$$= \int_{\Omega(t)} \frac{\partial}{\partial t}(wu)\,\mathrm{d}\Omega + \oint_{\partial\Omega} w(\mathbf{x},t)u(\mathbf{x},t)\mathbf{v}(\mathbf{x},t)\cdot\hat{\mathbf{n}}\mathrm{d}S,$$

yielding

$$\int_{\Omega(t)} \left[w(\mathbf{x},t)\frac{\partial u}{\partial t} + u(\mathbf{x},t)\frac{\partial w}{\partial t} + w(\mathbf{x},t)\nabla\cdot(u\mathbf{v}) + u(\mathbf{x},t)\mathbf{v}(\mathbf{x},t)\cdot\nabla w \right] d\Omega = 0. \tag{12}$$

Assuming that the weight functions $w(\mathbf{x},t)$ move with the velocity $\mathbf{v}(\mathbf{x},t)$ of the points of the domain,

$$\frac{\partial w}{\partial t} + \mathbf{v}(\mathbf{x},t)\cdot\nabla w = 0,$$

so that equation (12) reduces to

$$\int_{\Omega(t(} \left[w(\mathbf{x},t)\frac{\partial u}{\partial t} - u(\mathbf{x},t)\mathbf{v}(\mathbf{x},t)\cdot\nabla w \right] d\Omega = 0$$

After integration by parts using the boundary condition (4) we obtain the weak form

$$-\int_{\Omega(t)} w(\mathbf{x},t)\nabla\cdot(u\mathbf{v})\,\mathrm{d}\Omega = \int_{\Omega(t)} w(\mathbf{x},t)\frac{\partial u}{\partial t}\,\mathrm{d}\Omega, \tag{13}$$

Then, substituting the weak form of the driving PDE (3) into (13),

$$-\int_{\Omega(t)} w(\mathbf{x},t)\nabla\cdot(u\mathbf{v})\,d\Omega = \int_{\Omega(t)} w(\mathbf{x},t)(\delta\nabla^2 u - \nabla\cdot(u\nabla q))\,\mathrm{d}\Omega$$

After integration by parts using the boundary conditions (4), we obtain the weak form

$$-\int_{\Omega(t)} \nabla w\cdot(u\mathbf{v})\ \mathrm{d}\Omega = \delta\int_{\Omega(t)} \nabla w\cdot\nabla u\ \mathrm{d}\Omega - \int_{\Omega} u(\mathbf{x},t)\nabla w\cdot\nabla q\,\mathrm{d}\Omega$$

for the velocity $\mathbf{v}(\mathbf{x},t)$.

For a unique $\mathbf{v}(\mathbf{x},t)$ we introduce a velocity potential $\phi(\mathbf{x},t)$ such that $\mathbf{v}(\mathbf{x},t) = \nabla\phi$, leading to the weak form

$$\int_{\Omega(t)} u(\mathbf{x},t)\nabla w\cdot\nabla\phi\,\mathrm{d}\Omega = -\delta\int_{\Omega(t)} \nabla w\cdot\nabla u\ \mathrm{d}\Omega + \int_{\Omega(t)} u(\mathbf{x},t)\nabla q\cdot\nabla w\,\mathrm{d}\Omega, \tag{14}$$

for $\phi(\mathbf{x},t)$, given $u(\mathbf{x},t)$ and $q(\mathbf{x},t)$. Equation (14) has a unique solution for $\phi(\mathbf{x},t)$ given the boundary conditions (4), apart from a constant which differentiates out.

Before (14) is solved for $\phi(\mathbf{x},t)$ we obtain the function $q(\mathbf{x},t)$ from a weak form of equation (1),

$$\int_{\Omega(t)} w(\mathbf{x},t)E(u)\,\mathrm{d}\Omega = -\epsilon\int_{\Omega} w(\mathbf{x},t)\nabla^2 q\,\mathrm{d}\Omega + \int_{\Omega(t)} w(\mathbf{x},t)q(\mathbf{x},t)\,\mathrm{d}\Omega.$$

Integrating the right hand side by parts using the boundary condition (4), we obtain the weak form

$$\epsilon\int_{\Omega(t)} \nabla w\cdot\nabla q\,\mathrm{d}\Omega + \int_{\Omega(t)} w(\mathbf{x},t)q(\mathbf{x},t)\,\mathrm{d}\Omega = \int_{\Omega(t)} w(\mathbf{x},t)E(u)\,\mathrm{d}\Omega, \tag{15}$$

for $q(\mathbf{x},t)$, given $u(\mathbf{x},t)$.

The solution procedure for the velocity $\mathbf{v}(\mathbf{x},t)$ is therefore to obtain $q(\mathbf{x},t)$ from (15) and (1), deduce $\phi(\mathbf{x},t)$ from (14) and hence the velocity $\mathbf{v}(\mathbf{x},t)$ from a weak form of the relation $\mathbf{v}-\nabla\phi=0$.

3.2 Finite elements

Finite elements are applied on a mesh of triangles within a 2-D polygonal region. Let w be a standard piecewise-linear finite element basis function $W_i(\widehat{\mathbf{x}})$, $(1\le i\le N)$, on the mesh (the full set forming a partition of unity). The total distributed mass is constant in time through the imposition of zero Neumann natural boundary conditions (4).

A piecewise-linear population density $\widehat{u}(\widehat{\mathbf{x}},t)$ is given by the expansion

$$U(\widehat{\mathbf{x}},t) = \sum_j U_j(t)W_j(\widehat{\mathbf{x}}) \tag{16}$$

The distributed conservation principle (11) then becomes

$$\int_{\Omega(t)} W_i(\mathbf{x},t)\,U(\mathbf{x},t)\,\mathrm{d}\Omega = C(W_i), \tag{17}$$

constant in time, where

$$C(W_i) = \int_{\Omega(0)} W_i(\mathbf{x},0)U(\mathbf{x},0)\,\mathrm{d}\Omega$$

is obtained from the initial conditions (at $t = 0$)

We take q and $E(u)$ to be the piecewise-linear finite element functions Q and $\mathcal{E}$ having expansions

$$Q = \sum_j Q_j(t) W_j(\mathbf{x}, t), \qquad \mathcal{E} = \sum_j \mathcal{E}_j(t) W_j(\mathbf{x}, t),$$

respectively. Note that although $E(u)$ is a nonlinear function of u we calculate discrete values of $\mathcal{E}$ at the nodes and accept a linear approximation between nodes. The weak form (15) then becomes

$$\sum_{j=1}^{N} \left[\int_{\Omega(t)} W_i W_j \, \mathrm{d}\Omega \right] \mathcal{E}_j(t)$$

$$= \epsilon \sum_{j=1}^{N} \left[\int_{\Omega(t)} \nabla W_i \cdot \nabla W_j \, \mathrm{d}\Omega \right] Q_j(t) + \sum_{j=1}^{N} \left[\int_{\Omega(t)} W_i W_j \, \mathrm{d}\Omega \right] Q_j(t). \tag{18}$$

In terms of mass and stiffness matrices $\mathcal{M}$ and $\mathcal{K}$ we can write equation (18) as

$$\epsilon \mathcal{K} \underline{Q} + \mathcal{M} \underline{Q} = \mathcal{M} \underline{\mathcal{E}}$$

for the vector $\underline{Q}$ with entries Q_i, where the vector $\underline{\mathcal{E}}$ has entries $\mathcal{E}_i$. Rearranging, we find

$$\underline{Q} = (\epsilon \mathcal{K} + \mathcal{M})^{-1} \mathcal{M} \underline{\mathcal{E}} \tag{19}$$

3.3 The velocity potential

We now take the velocity potential ϕ in $\mathbf{v} = \nabla \phi$ to be the piecewise-linear function with expansion

$$\Phi(\mathbf{x}, t) = \sum_j \Phi_j(t) W_j(\mathbf{x}, t)$$

so that, from equation (14),

$$\sum_{j=1}^{N} \left[\int_{\Omega(t)} U(\mathbf{x}, t) \nabla W_i \cdot \nabla W_j \, \mathrm{d}\Omega \right] \Phi_j(t)$$

$$= -\delta \sum_{j=1}^{N} \left[\int_{\Omega(t)} \nabla W_i \cdot \nabla W_j \, \mathrm{d}\Omega \right] U_j(t) + \sum_{j=1}^{N} \left[\int_{\Omega(t)} \nabla W_i \cdot (U \nabla W_j) \, \mathrm{d}\Omega \right] Q_j(t),$$

in matrix form
$$\mathcal{K}(\underline{U})\underline{\Phi} = -\delta\,\mathcal{K}\underline{U} + \mathcal{K}(\underline{U})\underline{Q} \tag{20}$$
where $\underline{\Phi}$ is a vector with entries $\Phi_i(t)$ and $\mathcal{K}(\underline{U})$ is the weighted stiffness matrix with entries
$$\int_{\Omega(t)} U(\mathbf{x},t)\nabla W_i \cdot \nabla W_j \;\mathrm{d}\Omega.$$
with U given by (16).

3.4 The velocity

Once $\underline{\Phi}$ has been determined we obtain a piecewise linear-velocity from the expansion
$$\mathbf{V}(\mathbf{x},t) = \sum_j \mathbf{V}_j(t) W_j(\mathbf{x},t)$$
using the projection
$$\int_{\Omega(t)} W_i(\mathbf{x},t)\mathbf{V}(\mathbf{x},t)\,\mathrm{d}\Omega = \int_{\Omega(t)} W_i(\mathbf{x},t)\nabla\Phi\,\mathrm{d}\Omega$$
of $\mathbf{v} = \nabla\phi$, giving
$$\sum_{j=1}^{N}\left[\int_{\Omega(t)} W_i W_j \;\mathrm{d}\Omega\right]\mathbf{V}_j(t) = \sum_{j=1}^{N}\left[\int_{\Omega(t)} W_i \nabla W_j\,\mathrm{d}\Omega\right]\Phi_j(t)$$
or in matrix form,
$$\mathcal{M}\underline{\mathbf{V}} = \mathcal{B}\underline{\Phi}_j \tag{21}$$
where $\underline{\mathbf{V}}$ is the vector containing the entries $\mathbf{V}_j(t)$. The matrix $\mathcal{B}$ is an asymmetric matrix with entries
$$\int_{\Omega(t)} W_i\,\nabla W_j\,\mathrm{d}\Omega$$

3.5 The moving nodes

In order to advance the nodes in time we approximate the differential equation (10), in the form
$$\frac{\mathrm{d}\widehat{\mathbf{X}}_i}{\mathrm{d}t} = \widehat{\mathbf{V}}_i(\widehat{\mathbf{X}},t),$$

where $\widehat{\mathbf{V}}_i(\widehat{\mathbf{X}}, t) = \mathbf{V}_i(\widehat{\mathbf{X}}(\mathbf{x}, t), t)$ by the explicit Euler scheme

$$\widehat{\mathbf{X}}_{\mathbf{i}}^{n+1} = \widehat{\mathbf{X}}_i^n + \Delta t \, \widehat{\mathbf{V}}_i^n \tag{22}$$

where Δt is the time step. The time step is chosen sufficiently small to avoid instability.

3.6 The moved solution

Having found the mesh points $\widehat{\mathbf{X}}_i$ at time t^{n+1} we recover the population density $U(\widehat{\mathbf{x}}, t)$ at time t^{n+1} at the new time step from (16) expanded in terms of $W_j(\widehat{\mathbf{x}})$ as

$$U(\widehat{\mathbf{x}}, t^{n+1}) = \sum_{j=1}^{N} U_j^{n+1} W_j(\widehat{\mathbf{x}}),$$

using the weak form of the conservation principle (17), obtaining

$$\sum_{j=1}^{N} \left[\int_{\Omega(t)} W_i^{n+1} W_j{}^{n+1} \, \mathrm{d}\Omega \right], U_j^{n+1} = C(W_i) \tag{23}$$

where $C(W_i)$ is given from the initial conditions by

$$C(W_i) = \int_{\Omega(0)} W_i(\mathbf{x}, 0) \, U(\mathbf{x}, 0) \, \mathrm{d}\Omega \tag{24}$$

Equation (23) is equivalent to the matrix system

$$\mathcal{M}(\widehat{\mathbf{x}}) \underline{U}^{n+1} = \underline{C} \tag{25}$$

where $\underline{U}^{n+1}$ is the vector having entries U_i^{n+1}, $\underline{C}$ is the vector having entries $C(W_i)$, and $\mathcal{M}(\widehat{\mathbf{x}})$ is the mass matrix evaluated at $\widehat{\mathbf{x}}$.

4 Algorithm

Summarising, the algorithm for the moving mesh finite element solution of the single species aggregation model defined by equations (3), (1) and (6) on a mesh in 2-D in a region with fixed boundaries and with internal nodes moved by conservation is as follows.

From the initial mesh $\mathbf{X}_i(\mathbf{x}, 0)$ and initial conditions $U(\mathbf{x}, 0)$ obtain the constant-in-time values of $C(W_i)$ from (24). Then, at each time step,

1. Calculate the nodal values of the piecewise-linear function $\mathcal{E}(\mathbf{x}, t)$ from equation (18),

2. Obtain $Q(\mathbf{x}, t)$ from equation (19),

3. Find the velocity potential $\Phi(\mathbf{x}, t)$ from equation (20),

4. Deduce the node velocities $\mathbf{V}(\mathbf{x}, t)$ from equation (21),

5. Determine the moving coordinates $\widehat{\mathbf{X}}_i(\mathbf{x}, t)$ at the next time-step from (22),

6. Recover the solution $U(\widehat{\mathbf{x}}, t)$ on the moved mesh at the next time step from equation (25).

5 Results

We use a random seeding to provide the initial conditions for the model, selected from a normal distribution with a mean of 0.3 and a standard deviation of 0.01. We are able to run the model sometimes to a blow up and sometimes to a solution where population growth and decline become approximately balanced, depending on the initial values of u, and also on the parameters δ and ϵ. The parameter δ controlling the rate of diffusion has a smoothing effect while from the definition contained within (1) it is apparent that ϵ defines the scale of the clusters that are expected to form. We can see this scaling effect in the results, with the number and size of clusters reduced as ϵ increases.

An example solution is given in figure 1, for parameters $\epsilon = 0.005$ and $\delta = 0.01$. This choice produces four clusters from the initially random seeding. The clusters are under development in this snapshot and the calculation has not yet reached an approximately balanced population. We can see the difference that an alternative choice of ϵ produces in figure (2). With $\epsilon = 0.001$ and $\delta = 0.01$ we observe six clusters forming. If the model is allowed to continue we reach an approximately steady-state solution (figure 3). We observe that the reproductive potential $E(u)$ is very low in the centre of the clusters, due to overcrowding. This low $E(u)$ tends to disperse individuals away from the centre of the cluster. However, the population densities at the edges of the cluster are low enough to draw individuals in, and so eventually the two effects become balanced and the approximately balanced solution is observed.

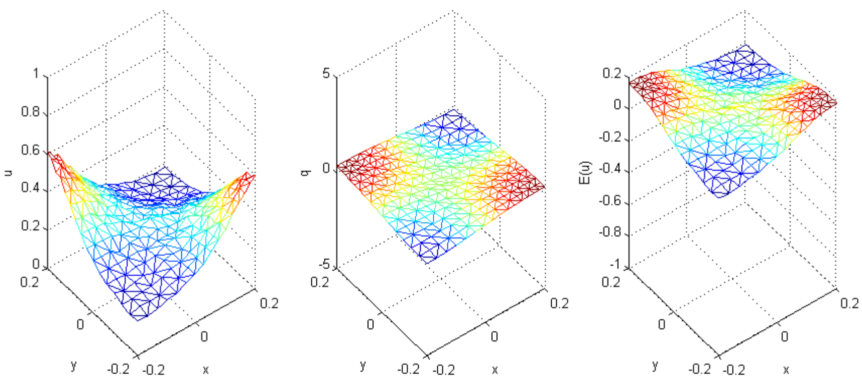

Figure 1: A solution of the 2D population equations after 350 time steps at $t = 0.35$, with $\epsilon = 0.005$ and $\delta = 0.01$.

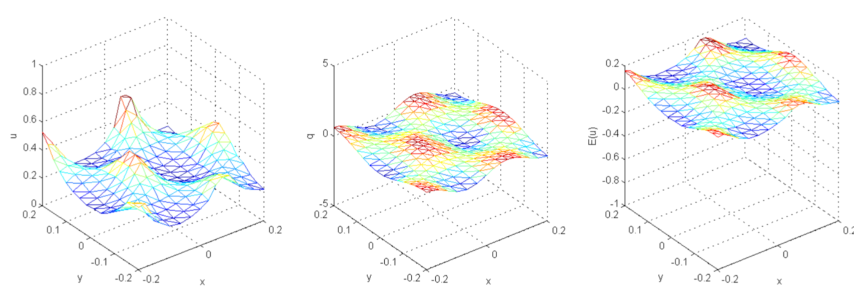

Figure 2: A solution of the 2D population equations after 10 time steps at $t = 0.01$, with $\epsilon = 0.001$ and $\delta = 0.01$.

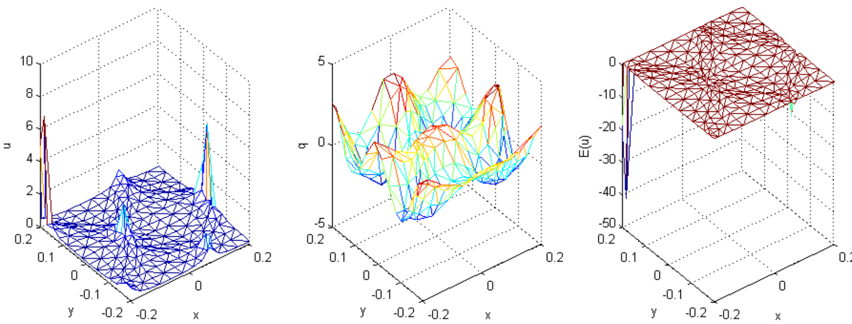

Figure 3: An approximately balanced solution of the 2D population equations, with $\epsilon = 0.001$ and $\delta = 0.01$, plotting (from left to right) u, q and $E(u)$. Whilst there is overcrowding in the centres of the clusters, giving a dramatically negative $E(u)$, the rate of the resulting population decline is balanced by the attraction of the cluster to individuals nearby. These two effects mean that the shape of the solution does not evolve further, with only minor local effects observed.

6 Conclusions

We have examined the effect of an aggregating term based on a survival strategy in a population balance equation for a single species and built a moving mesh finite element method for its approximate solution in two dimensions, exhibiting clustering behaviour for sample parameters. In particular we observed that the reproductive potential is very low in the centre of the clusters, due to overcrowding which tends to disperse individuals away from the centre of the cluster, whereas the population densities at the edges of the cluster are low enough to draw individuals in. Eventually the two effects balance out and an approximately balanced solution is observed.

It would be interesting to compare the behaviour of the model against an empirical data set. The model easily lends itself to adaptions in the sizes and shapes of the domain, alterations to the logistic terms and of course changes to parameters, without the need for further theory, which means there are a wide range of potential biological and ecological systems on which the models could be tested to validate the model behaviour. Further research will focus on collaboration to understand the particular modelling requirements of real-world systems which can be described in a similar manner to this model. The aim should be to understand the requirements from both a mathematical and value perspective. Subsequent development will be in the direction of the research requirements of those ecological systems which would most benefit from a study which has access to this modelling capability.

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