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LETTER TO THE EDITOR

Bioconvective percolation on an incomplete Voronoi grid

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Abstract. Bioconvection is a fluid instability common to many biological organisms including swimming bacteria, alga and protozoa. The statistics of bioconvective pattern formation is tested against percolation models for space-filling. A percolation threshold is found ($p = 0.63$) and compared to theoretical point distributions for random tesselations. Simulations reveal that a percolation backbone defines a complete path across the observation window but remains incomplete as an equal partitioning grid (Voronoi diagram). The generic development of incomplete Voronoi grids and their yet unknown statistical properties captures some interest as an alternative to traditional point-based lattices.

Bioconvection is a biological example of complex pattern formation [1–7]. As shown in figure 1, the pattern can correspond to an array of dots, stripes or polygons. The fluid instability called bioconvection has been studied for at least 100 years [1] and has attracted more recent interest [2–7] as a fascinating and rich field for considering the mechanisms of how order can appear from seemingly disordered driving forces. In particular for some species of swimming bacteria, alga and protozoa, the onset of a bioconvective fluid instability can be summarized schematically as (i) the mobile cell orients itself in a preferred swimming direction; (ii) at high concentrations, the cells accumulate as a heavy surface layer of suspended organisms; and (iii) when surface crowding reaches a maximum, downstreaming or fingering of dense pockets of cells and fluid begins to settle. As a result, a disordered medium produces the lines of concentration which characterize bioconvection. Many interesting phenomena [2–7] have recently been added to this simplified picture, but the importance of active cells swimming in a slightly less dense medium remains the instability's hallmark.

To analyse pattern formation, Zaninetti [8] has recently proposed an incomplete Voronoi diagram. The Voronoi method [9] generically chooses the most democratic partitioning of space based on centroids or seed nuclei. In the case of bioconvection, the seed points can be equated to randomly placed fluid packets containing slightly more organisms than their surrounding areas. These dense neighbourhoods nucleate the pattern. A characteristic of Zaninetti's algorithm is that, in contrast to traditional polygons produced by Voronoi diagrams, his method selectively removes some edges and thus forms a grid pattern much akin to a percolation lattice. Observations of bioconvection, likewise, have revealed this morphology [10] and the present work considers whether the bioconvective fluid instability can be compared to percolation and incomplete Voronoi lattices.

To produce bioconvection, *Polytomella parva* (swimming speed, 100 $\mu m\ s^{-1}$; diameter 10 μm; density, 1.05 g cm^{-3}) were examined in shallow dishes [11]. The algal suspensions

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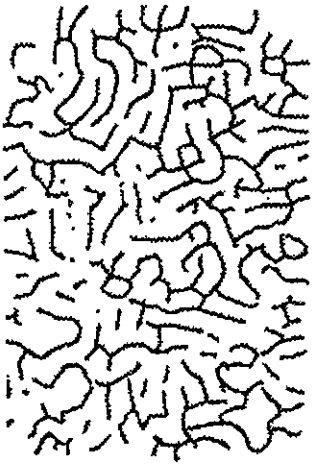

Figure 1. Typical bioconvective lattice with incomplete polygons or Voronoi filling. Light regions correspond to 'down' flow; dark regions correspond to 'up' flow. Differences in organism count between up and down regions can reach between 2 to 100 fold. Digitized photograph of the incomplete Voronoi diagram of bioconvection patterns in shallow, dense suspensions of the mobile biological cell, *Polytomella parva*. Organism count 1 million cells/ml in suspension of 4 mm uniform depth. The white areas correspond to regions of lower cell count. Average distance between stripe patterns is 0.2 mm.

were grown to a final concentration of 10^6 ml^{-1} in an aqueous yeast medium. Substantial work has appeared characterizing these bioconvection patterns [12, 13]. Lighting was provided uniformly from the top using collimated, cool incandescent lamps (intensity $l = 12$ lux, constant temperature $T = 25\,^{\circ}$C, suspension depth $d = 4$ mm and dish diameter $D = 50$ mm).

The bioconvection pattern of incomplete Voronoi diagrams is shown in figure 2. The lattice is polygonal in character, but with some edges removed. The parameter of interest is the percolation threshold [8]. This value ranges between 0 and 1 and corresponds to the probability of a connected skeleton reaching from one side to the opposite side of the working box. In physical terms, this threshold can be calculated as the fractional number of sides selected. For two-dimensional simulations [8] (figure 2), this fraction turns out to be approximately 0.6. This critical value of percolation separates the finite clusters of sites from an infinite cluster. In other typical systems, phase behaviour can be defined for transitions between conductor–superconductors or magnet–paramagnets.

To compare these experimental lattices to incomplete Voronoi diagrams, we conducted a number of simulations. The simulation began with an initial distribution of points taken as (x, y) coordinates. Theoretical distributions of centroids were tested for random, exponential, normal and uniform distributions. The centroid of each experimental pattern was also found and the (x, y) coordinates were used to generate a comparable Voronoi diagram. When overlayed with the experimental lattice, a measure of the lattice incompleteness is found as the missing number of sides or percolation threshold. The bioconvective lattice (figure 1) meets the definition of a percolation threshold: the connected backbone reaches from top to bottom within the observation window. The experimental value equals $p = 0.63$. For comparison, a complete Voronoi diagram is derived in figure 2 assuming centroids from an unconnected bioconvective lattice.

In conclusion, we have shown that bioconvection is an experimental manifestation of

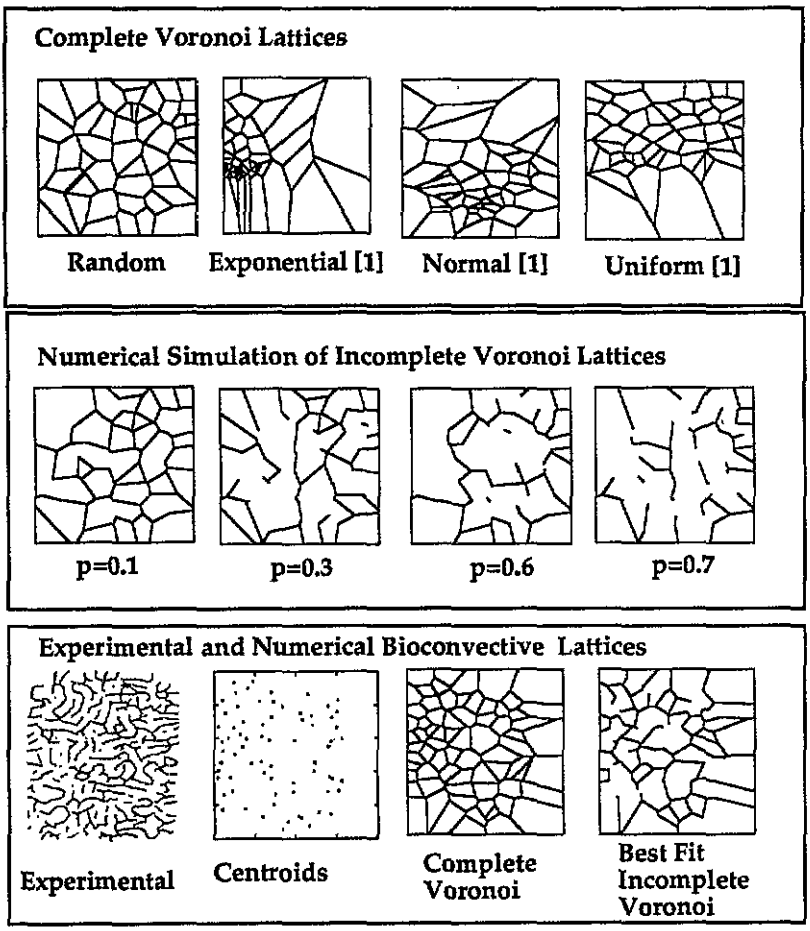

Figure 2. Numerical simulations of incomplete Voronoi diagrams for bioconvection. Theoretical distributions of centroids for random, exponential, normal and uniform distributions. The centroid of each experimental pattern (gravity centre for backbone or connected percolation lattice) is found and the x, y coordinates are used to generate a perfect Voronoi diagram. When overlayed with the experimental lattice, a measure of the lattice incompleteness is found as the missing number of sides. Comparison is made with a random distribution of centroid points (95% confidence level). The well known Gaussian model suggests that spatial fluctuations are random with a bell-shaped signature distributed around the mean. An exponential distribution, on the other hand, is equivalent to Brownian noise, with a kind of thermal randomness which distinguishes (flattens) its spatial fluctuations particularly at the small scale end (large (x, y)) of the spectrum. The difference between uniform and normal distributions is that normal (x, y) values are selected randomly from a normal distribution with standard deviation of [1] and mean [0]; alternatively, the uniform distribution include values selected randomly between 0 and 1 with mean [0.5]. It is noteworthy to consider the failure of an exponential distribution, since this effectively excludes a thermal (Brownian) cause for spatial fluctuations. The bias of high (y) values is seen in the uniform distribution; low (y) values in the normal distribution.

incomplete Voronoi lattices. Experimental nuclei are found for polygonal patterns and compared to theoretical distributions. The percolation threshold is calculated over 20 representative windows as 0.63. Numerical simulations of incomplete Voronoi diagrams

offer a quantitative realization of these biological lattices for random, exponential, normal and uniform seed distributions. The completeness of the various random Voronoi simulations is shown for four different percolation thresholds between 0.1 and 0.7. In addition to extending the range of traditional Voronoi lattices to include incomplete or percolation results, this representation differs from usual statistical lattices. Most notably rather than specifying the backbone as connected points, the points themselves serve as centroids to define the surrounding neighbourhood. Thus, percolation threshold can be understood as removal of polygonal sides rather than connection of random points on a backbone. The unique quality of Voronoi tesselations [9] (e.g. as the most democratic partitioning of space) can thus translate into the powerful methods developed for statistically treating percolation problems (such as renormalization, scaling and universality). Although applied to biological lattices here, the Voronoi technique is general and can characterize a number of related problems in statistical physics. Recent work [14] has developed Voronoi tesselations for galactic modelling and stellar distributions.

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