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Universality in two-dimensional cellular structures evolving by cell division and disappearance

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The dynamics of two-dimensional cellular networks is written in terms of coupled population equations, which describe how the population of s-sided cells is affected by cell division and disappearance. In these equations the effect of the rest of the foam on the disappearing or dividing cell is treated as a local mean field. Under not too restrictive conditions, the equilibrium distribution $P(s)$ of cells satisfies a linear difference equation of order two or higher. The population equations are asymptotically integrable. The asymptotic integrability implies a "universal" distribution $P(s) \sim Cs^{-\kappa}z^{s}$ for large values of s, which is also the Boltzmann distribution associated with the maximum entropy inference. Asymptotic integrability of the population equations is absent in a global mean-field approximation. The importance of short-range topological information to control the evolution of foams is thus confirmed.

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I. INTRODUCTION

Two-dimensional (2D) random cellular networks (2D foams) form the basic frame of many natural or engineered materials [1–4]. Soap froths [5], cork [6], magnetic bubbles in garnets [7], Benard-Marangoni convection patterns [8], nanostructured cellular networks [9], and biological epidermis [10–14] are a few examples. 2D foams are random partitions of the plane by cells, which are topological polygons. Disorder or absence of specific adjustment imposes minimal incidence numbers (three edges incident on a vertex). Foams evolve into a stationary state of statistical equilibrium, with an invariant distribution of cell shapes $P(s)$, where s, the number of sides of a cell, is the only topological random variable [1,15]. Statistical equilibrium is established through local, elementary topological transformations (ETTs), which can be an edge flip (T1 transformation) or the disappearance of a three-sided cell (T2 transformation).

Biological epithelia (skin of a cucumber and human epidermis) provide excellent examples of cellular structures where all the topological action is two-dimensional [10–13]. The epidermis of mammals can be regarded as a fluid of cells, filling the space between the dermis and the outer surface at random. Cells transit vertically upward through the Malpighi layer from the one-cell-deep basal layer, where they are born, to the corneum layer, where they die. The constant supply of cells needed for the renewal of the tissue is provided by division and detachment of basal cells. Each basal cell is attached to the basal membrane, through a polygonal facet. The imprints of basal cells fill the two-dimensional basal layer completely and, at first sight, randomly (Fig. 1). It constitutes a two-dimensional foam [16–18]. When a cell becomes detached from the basal membrane, its polygonal imprint disappears from the two-dimensional foam. The steady state of the basal layer (and, hence, the renewal of epidermis) has been studied through two-dimensional foams evolving by cell division and disappearance [16–19]. Cell division or its inverse, cell disappearance (coalescence of two cells by removal of their interface), are specific combinations of transformations T1 and T2.

Computer simulations of (biological) foams indicate that the asymptotic behavior of the probability distribution $P(s)$ for large values of s, is universal in the sense that it is independent of the type of foam, of the elementary topological transformations (which disorder the structure and maintain it in a steady, but disordered state), and of the initial structure. After transients have died off, foams have a distribution $P(s)$ that decays *exponentially* with s for large s. For example, for a froth generated by applying cell coalescence and division, $P(s)=0.37\exp[-0.9(s-6)]$ for $s \geqslant 6$, as Figs. 2 and 3 show [20]. The rare exception [21] supports the exponential rule.

One expects s-sided cells with $s>10$ to be rare. Thus, experiments do not provide an accurate distribution $P(s)$ for large s. On the other hand, simulations (numerical experiments) can produce numerous foams and good statistics of

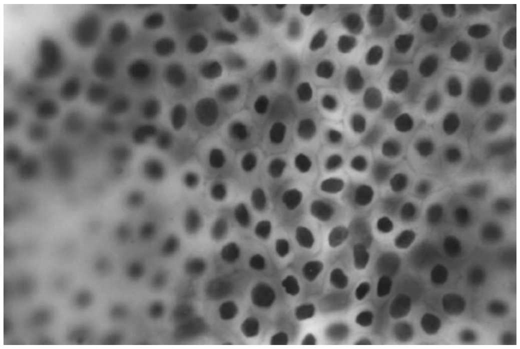

FIG. 1. Horizontal cut of the basal layer of a stained sample of human epidermis, viewed with an optical microscope (from [17] with permission). The polygonal shape of the attachment of basal cells appears clearly in the focal plane. The frequencies of s-sided cells are $P(4)=0.012$, $P(5)=0.208$, $P(6)=0.566$, $P(7)=0.194$, and $P(8)=0.020$ [17].

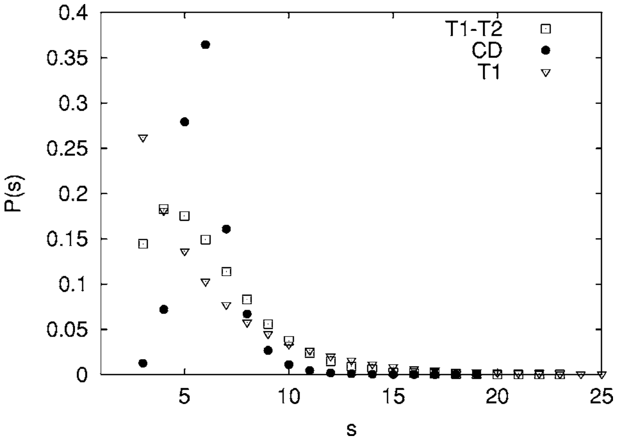

FIG. 2. Distribution of the number of edges per cell in the froths generated by T1 and T2 transformations (T1-T2), cell-division and coalescence transformations (CD), and T1 transformations (data from [20] with permission). For $s \geqslant 18$, the points are indistinguishable in this plot (but see Fig. 3).

s-sided cells and, more importantly, reveal the universal asymptotic behavior of $P(s)$. This power of simulations in statistical physics has been demonstrated before, e.g., the early simulations of Alder and Wainwright revealed an unexpected algebraic long-time tail in the velocity autocorrelation function of hard disks in two dimensions [22].

Here we aim to get some insight into the *universality* in 2D cellular structures. We study the stationary distribution $P(s)$ as the solution of coupled population equations, which account for the local, but correlated variations in the population of cells under ETT [16–19,21]. In a previous paper on foams evolving by cell disappearance [23], we have already shown that in a local mean-field approximation, which accounts for the *nearest-neighbor correlations* in statistical equilibrium, the population equations are *asymptotically integrable*. This means that the population equations, linear difference equations for $P(s)$ with polynomial coefficients, have their order reduced at large s. Here, we show asymptotic integrability of population equations describing foams (biological epithelia) evolving by cell division and disappearance. The asymptotic integrability (and, hence, the short-range topological information) implies that

$$P(s) \sim C s^{-\kappa} z^{s} \tag{1}$$

for large values of s. This asymptotic behavior is universal, although real numbers C, κ, and z are model dependent. We present examples where the dominant asymptotic behavior of $P(s)$ is exponential ($z<1$). In addition, we present several examples with power-law variation of $P(s)$ at large s ($z=1$). Notably, Delannay and Le Caër [21] have obtained, in a special case of fragmentation (cell division, but unrestricted), a distribution that decays *algebraically* as $P(s) \sim s^{-5.72}$ for $s \geqslant 45$.

Our paper is organized as follows. In Sec. II, we introduce the coupled population equations in the local mean-field approximation. In Sec. III, we show that for a wide class of models, integrodifference population equations can be transformed into linear difference equations. These linear difference equations are asymptotically integrable, as discussed in Sec. IV. Several classes of examples are analyzed in Secs. V–VII, to confirm the universality in 2D foams. A summary of our results and discussions are given in Sec. VIII. Conclusions are in Sec. IX.

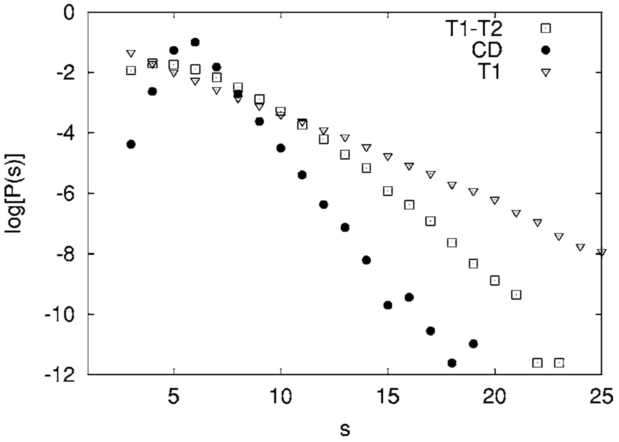

FIG. 3. $\log[P(s)]$ vs s for the foams mentioned in Fig. 2. In all three cases, the dominant asymptotic behavior of $P(s)$ is exponential.

II. COUPLED POPULATION EQUATIONS IN THE LOCAL MEAN-FIELD APPROXIMATION

The set of all possible arrangements of the topological polygons is explored through local topological transformations of the cellular structure: division (m, for mitosis) and disappearance (d) of cells. Topological transformations change the number of sides of the cells involved.

The numbers of sides of the cells directly involved in the division are related by

$$m + 4 = d_1 + d_2, \tag{2}$$

where m and d_i denote the numbers of sides of the mother and daughter cells, respectively. There are two other cells involved in the mitotic process, at both ends of the dividing membrane. They gain one side each (Fig. 4).

We denote by $\Gamma(s|k,m)$ the conditional probability that a k-sided dividing cell has an s-sided daughter ($3 \leqslant s \leqslant k+1$). Here m stands for mitosis. Since cell division obeys the topological rule (2), the kernel is symmetric

$$\Gamma(s|k,m) = \Gamma(k+4-s|k,m) \tag{3}$$

and follows two sum rules

$$\sum_{s} \Gamma(s|k,m) = 2,$$

$$\sum_{s} s\Gamma(s|k,m) = \frac{1}{2}\sum_{s} [s + (k+4-s)]\Gamma(s|k,m) = k+4. \tag{4}$$

The first sum rule states that a cell divides into two. The second is automatic; it follows from the first and from the symmetry of the kernel [16].

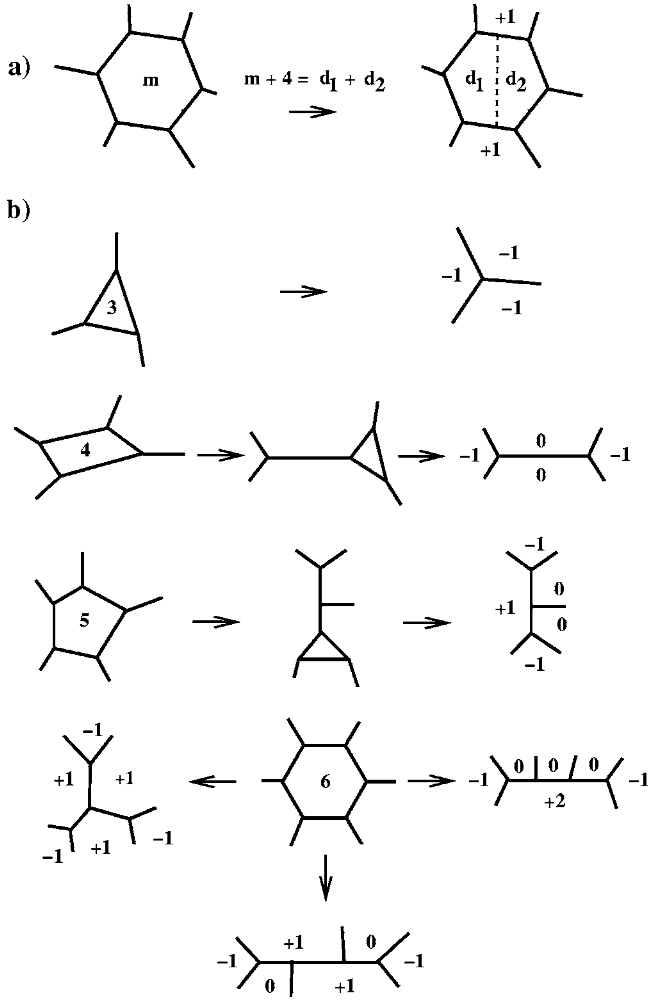

FIG. 4. (a) Cellular division. Note that during the process, one m-sided cell is lost, two cells are gained, and two neighbors gain one side. (b) Topological scars left after the disappearance of a four-, five-, and six-sided cell.

Apart from cell division, there is another topological process that allows the tissue to reach statistical equilibrium: disappearance of cells. The disappearance of a k-sided cell leaves a characteristic trace on its neighbors. This topological scar is obtained by assuming that the k-sided cell disappears through a cascade of successive flips (T1) of its sides, starting usually, but not necessarily, with the smallest one and ending with the disappearance (T2) of the final triangular cell (Fig. 4).

If a three-sided cell disappears, its three neighbors lose one side each (T2 transformation). If a four-sided cell disappears, its four neighbors lose a total of $6-4=2$ sides. In general, when a k-sided cell disappears, its k neighbors lose $6-k$ sides in total, and a maximum of one side each [17]. The loss of one side is definitive. The gain of one side (through T1) may be temporary. However, at least two, non-edge-sharing neighbors must lose one side each (through the first flip and the final T2). When a three-, four-, or five-sided cell disappears, it leaves a unique topological scar on its neighbors: $(-1,-1,-1)$, $(-1,0,-1,0)$, and $(-1,0,0,-1,1)$, respectively. A disappearing six-sided cell has three topologically distinct ways of injecting zero sides into its neighbors, etc. (Fig. 4). In epithelia in statistical equilibrium, only three-, four- and five-sided cells can disappear [17]. The same conclusion follows from von Neumann's law in 2D soap froths: only three-, four-, and five-sided cells lose gas to their neighbors, on average [1]. Incidentally, the loss of one cell and a total of six sides (k from the disappearing cell and $6-k$ from its neighbors) satisfies Euler's relation for polyhedra.

The conditional probability $\Delta(i|k,d)$ that a k-sided disappearing cell gives i sides $(-1 \leqslant i \leqslant k-4)$ to one of its neighbors, follows two sum rules:

$$\sum_{i=-1}^{k-4} \Delta(i|k,d) = 1,$$

$$\sum_{i=-1}^{k-4} i\Delta(i|k,d) = 1 - \frac{6}{k}. \tag{5}$$

The first sum rule is normalization. The second sum rules states that a disappearing k-sided cell, gives $k-6$ sides to its neighbors.

The relations for Δ are obtained [17] by assuming that the k-sided cell disappears through a cascade of successive flips (T1) of its sides and ending with the disappearance (T2) of the final triangular cell (Fig. 4). For $k=3$, $\Delta(-1|3,d)=1$. The first flip has the following consequences: The original k-sided cell has now $k-1$ sides. One of its neighbors has forever lost a side. Two neighbors have temporarily gained a side. For $k \geqslant 4$, this yields the recursion relations in k and i

$$k\Delta(i|k,d) = (k-3)\Delta(i|k-1,d) + 2\Delta(i-1|k-1,d) + \delta_{i,-1}, \tag{6a}$$

where $\Delta(i|k,d)=0$ outside the range $-1 \leqslant i \leqslant k-4$. Indeed, after the first flip, the cell has $k-1$ sides. Which one of the k neighbors of the original disappearing cell is to gain the i sides? The two neighbors of the first flipped edge, having already gained one side, need only gain a further $i-1$ sides [second term on the right of Eq. (6a)]. The other $k-3$ neighbors must gain the full i sides (first term). The neighbor at the end of the first flipped side has definitively lost one side and enters the recursion relation for $i=-1$, with probability 1 (third term). For $i=-1$, one obtains [by writing $\Delta(-1|k,d)$ as a constant plus a term dependent on k] an explicit expression [17]

$$\Delta(-1|k,d) = \frac{1}{3} + \frac{4(k-3)!}{k!}. \tag{6b}$$

We assume that there is no correlation between successive topological events: When a cell divides or disappears, its neighbors are not topologically active. The evolution of $P(s)$ is therefore a Markov process.

The change $dN(s)$ in the number $N(s)$ of s-sided cells per (arbitrary) time interval dt is given by [16]

$$\frac{dN(s)}{dt} = \sum_k N(k)P(m|k)\left\{-\delta_{ks} + \Gamma(s|k,m) + \frac{2}{k}M_{s-1}(k) - \frac{2}{k}M_s(k)\right\} + \sum_k N(k)P(d|k) \times\left\{-\delta_{ks} + \sum_{i=-1}^{i=k-4} M_{s-i}(k)\Delta(i|k,d) - M_s(k)\right\}, \quad (7)$$

where $P(m|k)$ $[P(d|k)]$ is the conditional probability that an existing k-cell divides (disappears) weighted by the rate of division (disappearance) and $M_s(k)$ is the average number of s-cell neighbors of a k cell. In Eq. (7), the first bracket deals with cell division, the second with cell disappearance. The probability of finding a cell with s sides is $P(s)=N(s)/N$, where $N(s)$ is the number of s-sided cells and $N=\Sigma_s N(s)$ is the total number of cells. Then,

$$\frac{dP(s)}{dt} = \frac{1}{N}\left[\frac{dN(s)}{dt} - P(s)\frac{dN}{dt}\right] \quad (8)$$

and

$$\frac{1}{N}\frac{dN}{dt} = \sum_k P(k)[P(m|k) - P(d|k)]. \quad (9)$$

N is constant if cells divide (m) at the same rate as they disappear (d) (i.e., detach from the basal layer of the epidermis).

We look for a population of cells in statistical equilibrium. $P(s)$ is thus stationary, $dP(s)/dt=0$, and obeys the coupled population equations

$$\sum_k P(k)P(m|k)\left\{-\delta_{ks} + \Gamma(s|k,m) + \frac{2}{k}M_{s-1}(k) - \frac{2}{k}M_s(k) - P(s)\right\} + \sum_k P(k)P(d|k)\left\{-\delta_{ks} - M_s(k)[1-\Delta(0|k,d)] + \sum_{i=1}^{i=k-4} M_{s-i}(k)\Delta(i|k,d) + M_{s+1}(k)\Delta(-1|k,d) + P(s)\right\} = 0. \quad (10)$$

When a cell divides, the population of s-sided cells is affected if: (i) a s-sided cell divides; (ii) a dividing k cell has a s-sided daughter, for any k; (iii) the affected neighbor had $(s-1)$ sides before division; or (iv) a neighboring s-sided cell is affected by the division. The four terms in the first bracket of (10) corresponds to these four topological mechanisms. The fifth term expresses the production of one extra cell during mitosis (9).

When a cell disappears, the population of s-sided cells is affected if: (i) a s-sided cell disappears; (ii) a s-sided neighbor gains or loses sides; (iii) a disappearing k cell gives i sides to a $(s-i)$-sided neighbor; or (iv) a disappearing k cell takes one side from a $(s+1)$-sided neighbor. The terms in second bracket of (10) correspond to these four topological mechanisms. The fifth term accounts for the disappearance of one cell (9).

A geometrical solution must satisfy the constraints

$$\sum_s P(s) = 1, \quad (11)$$

$$\sum_s sP(s) = 6, \quad (12)$$

$$\sum_s M_s(k) = \sum_s A(k,s)P(s) = k. \quad (13)$$

The first constraint normalizes the distribution $P(s)$. The second states that $\langle s\rangle$ the mean number of sides of a cell is six. This comes from Euler's relation on the polygonal foam and minimal incidence numbers [1].

The third constraint states that a k-sided cell has k neighbors. $M_s(k)$, the average number of s-cell neighbors of a k cell, can be expressed as $M_s(k)=A(k,s)P(s)$. Since $N(s)A(k,s)N(k)$ is the total number of pairs of neighboring s and k cells, the correlator $A(k,s)$ can be regarded as the conditional probability that an existing s cell neighbors a k cell. By symmetry $A(s,k)=A(k,s)$. Furthermore, one can obtain the most probable correlator $A(k,s)$ by maximum entropy inference (making the third constraint redundant with the other two and thereby increasing the entropy). It is linear in k and s [24]

$$A(s,k) = \sigma(s-6)(k-6) + s + k - 6. \quad (14)$$

The parameter $\sigma \leqslant 1/6$ is usually <0 [15,25]. Thus, Eqs. (10) and (13) represent a local mean-field treatment of the cell population. Equation (14) gives the most probable form of the nearest-neighbor correlator.

III. TRANSFORMATION OF THE INTEGRODIFFERENCE POPULATION EQUATION TO A LINEAR DIFFERENCE EQUATION

The constrained system (10) is a complicated system of equations, in general. Numerical solutions of Eq. (10) or computer simulations of foams evolving by division or disappearance are reported in [16–21].

The population equations (10) are, or can be transformed into, a set of *linear difference equations*, in three cases: (i) cell disappearance only $[P(m|k)=0]$, restricted to three-, four-, and five-sided cells $[P(d|k)=0$ for $k\geqslant 6]$; (ii) only cell division takes place $[P(d|k)=0]$ with either a uniform division kernel $\Gamma(s|k,m)$, which is independent of the number of sides s of the daughter cell, or when the kernel is sum of δ functions $\delta(s-u)+\delta(s-k+u-4)$, where u is an integer [see Eq. (15a) below]; and (iii) cell division with a uniform kernel and disappearance of three-, four-, and five-sided cells. Since only cells with five sides or less can disappear, one side, at most, can be given to a neighbor and the sum in the second bracket of (10) reduces to one term $i=1$.

We consider the following division kernels [satisfying the sum rules given by Eq. (4)] for the conditional probability that a k-sided dividing cell has a s-sided daughter:

$$\Gamma_t^A(s|k,m)=\sum_{u=3}^{u=t} b_u[\delta(s-u)+\delta(s-k+u-4)] \tag{15a}$$

describes nonuniform division of a k-sided cell into a u-sided ($3\leqslant u\leqslant t$) and a $(k-u+4)$-sided daughter with probability b_u. The constraint $\Sigma_{u=3}^{u=t}b_u=1$ normalizes the distribution b_u;

$$\Gamma_{s_{\min}}^B(s|k,m)=\frac{2}{k-(2s_{\min}-5)}, \tag{15b}$$

for $s_{\min}\leqslant s\leqslant k+4-s_{\min}$. $s_{\min}$ is the minimum number of sides of the daughter cell. This kernel is uniform, i.e., independent of the number of sides of the daughter cells. For $s_{\min}=3$, this kernel is used in [21]. And,

$$\Gamma_{s_{\min}}^C(s|k,m)=\begin{cases}\dfrac{2}{k-(2s_{\min}-4)} \\ \text{for } s_{\min}+1\leqslant s\leqslant k+3-s_{\min} \\ \dfrac{1}{k-(2s_{\min}-4)} \\ \text{for } s=s_{\min},\quad k+4-s_{\min}\end{cases} \tag{15c}$$

describes nearly uniform division. It is independent of the number of sides of the daughter cells, except at the ends of the range, $s=s_{\min}$ and $s=k+4-s_{\min}$, penalized by a weight $1/2$ [16].

In the case of uniform kernel, the daughter cell has s sides, with $s_{\min}\leqslant s\leqslant k+4-s_{\min}$. Thus, the mother cell has k sides, with $k\geqslant 2s_{\min}-4$, which implies that $P(m|k)=0$ for $k<2s_{\min}-4$ ($k<3$ for $s_{\min}=3$). For cell disappearance, we have $P(d|k)=0$ for $k\geqslant 6$, which can be regarded as a corollary of von Neumann's law. Therefore, if $s_{\min}\geqslant 5$, the fate of a cell (division or disappearance—its differentiation and detachment from the basal layer of the epidermis [17]) is entirely determined by the number of its sides, that is, by its geometrical neighborhood: A cell divides if it has six sides or more. It disappears if it has five sides or less. This is, indeed, what happens in biological epithelia, as suggested analytically [17] and in simulations [19,26]. In the simplest model for the evolution and stability of biological tissues [26], only six-sided cells may rest instead of dividing.

By contrast, for $s_{\min}=4$, five-sided cells may divide or disappear. For $s_{\min}=3$, the fate of three-, four-, and five-sided cells is ambiguous. Moreover, one daughter may have more $(k+1)$ sides than its mother, which goes against the geometrical purpose of cell division, which is size reduction of the cell. The same discussion holds for the nearly uniform kernel, but with $P(m|k)=0$ for $k<2s_{\min}-2$.

Let us introduce the following notations:

$$\phi(s)=\sum_k P(k)P(m|k)\Gamma(s|k,m),$$

$$a_1'(s)=-\sum_k P(k)\frac{2}{k}P(m|k)A(s,k)-\sum_k P(k)P(m|k)-P(m|s),$$

$$a_0'(s)=\sum_k P(k)\frac{2}{k}P(m|k)A(s,k),$$

$$a_2(s)=\sum_k P(k)P(d|k)A(s,k)\Delta(-1|k,d),$$

$$a_1(s)=-\sum_k P(k)P(d|k)A(s,k)[1-\Delta(0|k,d)] + \sum_k P(k)P(d|k)-P(d|s),$$

$$a_0(s)=\sum_k P(k)P(d|k)A(s,k)\Delta(1|k,d). \tag{16}$$

Then, the population equation (10) can be written as

$$[\phi(s+1)+a_1'(s+1)P(s+1)+a_0'(s)P(s)] + [a_2(s+2)P(s+2)+a_1(s+1)P(s+1)+a_0(s)P(s)]=0. \tag{17}$$

In Eq. (17), the first bracket deals with cell division and the second with cell disappearance. Apart from the first term $\phi(s+1)$, (17) is already a difference equation.

For the kernel Γ_t^A,

$$\phi(s)=\sum_{u=3}^{u=t} b_u P(m|s-4+u)P(s-4+u),$$

for $s\geqslant t+1$, i.e., in the asymptotic limit. [There are source terms proportional to $\delta(s-u)$ for $u\leqslant t$]. The population equation for this kernel is the linear difference equation

$$\sum_{u=6}^{u=t}[b_uP(m|s-3+u)]P(s-3+u)+[a_2(s+2)+b_5 \times P(m|s+2)]P(s+2)+[a_1(s+1)+a_1'(s+1) + b_4P(m|s+1)]P(s+1)+[a_0(s)+a_0'(s)+b_3P(m|s)]P(s) =0, \tag{18}$$

for $s\geqslant t+1$.

For uniform and nearly uniform kernels, the population equation (10) is an integrodifference equation but can be transformed to a linear difference equation. Let us define the difference operator D by

$$Df(s)=f(s)-f(s-1). \tag{19}$$

For the uniform kernel,

$$D\phi(s)=\left[\frac{-2P(m|s-5+s_{\min})}{s-s_{\min}}\right]P(s-5+s_{\min})$$

and the population equation (17) can be transformed into a linear difference equation by applying operator D

$$a''_{s_{\min}-3}(s+s_{\min}-3)P(s+s_{\min}-3)+a_3''(s+3)P(s+3) + a_2''(s+2)P(s+2)+a_1''(s+1)P(s+1)+a_0''(s)P(s)=0, \tag{20}$$

where

$$a''_{s_{\min}-3}(s)=-2P(m|s)\theta(s_{\min}-6),$$

$$a_3''(s) = a_2(s)(s - s_{\min} - 1) - 2P(m|s)\delta_{s_{\min},6},$$

$$a_2''(s) = [a_1'(s) + a_1(s) - a_2(s)](s - s_{\min}) - 2P(m|s)\delta_{s_{\min},5},$$

$$a_1''(s) = [-a_1'(s) + a_0'(s) - a_1(s) + a_0(s)](s - s_{\min} + 1) - 2P(m|s)\delta_{s_{\min},4},$$

$$a_0''(s) = [-a_0'(s) - a_0(s)](s - s_{\min} + 2) - 2P(m|s)\delta_{s_{\min},3}, \tag{21}$$

and $\theta(s)$ is the step function: $\theta(s)=1$ if $s>0$ and $\theta(s)=0$ if $s \leqslant 0$.

For the nearly uniform kernel, the same method is used to transform the integrodifference equation into a linear difference equation

$$a_{s_{\min}-2}''(s + s_{\min} - 2)P(s + s_{\min} - 2) + a_{s_{\min}-3}''(s + s_{\min} - 3)P(s + s_{\min} - 3) + a_3''(s+3)P(s+3) + a_2''(s+2)P(s+2) + a_1''(s+1)P(s+1) + a_0''(s)P(s) = 0, \tag{22}$$

for $s > s_{\min}+2$, where

$$a_{s_{\min}-2}''(s) = -(s - 2s_{\min} + 3)P(m|s)\theta(s_{\min} - 5),$$

$$a_{s_{\min}-3}''(s) = -(s - 2s_{\min} + 5)P(m|s)\theta(s_{\min} - 6),$$

$$a_3''(s) = a_2(s)(s - s_{\min} - 2)(s - s_{\min} - 1) - (s-7)P(m|s)(\delta_{s_{\min},6} + \delta_{s_{\min},5}),$$

$$a_2''(s) = [a_1'(s) + a_1(s) - a_2(s)](s - s_{\min} - 1)(s - s_{\min}) - (s-5)P(m|s)(\delta_{s_{\min},5} + \delta_{s_{\min},4}),$$

$$a_1''(s) = [-a_1'(s) + a_0'(s) - a_1(s) + a_0(s)](s - s_{\min})(s - s_{\min} + 1) - (s-3)P(m|s)(\delta_{s_{\min},4} + \delta_{s_{\min},3}),$$

$$a_0''(s) = [-a_0'(s) - a_0(s)](s - s_{\min} + 1)(s - s_{\min} + 2) - (s-1)P(m|s)\delta_{s_{\min},3}. \tag{23}$$

IV. ASYMPTOTIC INTEGRABILITY

The population equation for $P(s)$, under the not too restrictive conditions mentioned in Sec. III, is a linear difference equation

$$a_u(s+u)P(s+u) + a_{u-1}(s+u-1)P(s+u-1) + \cdots + a_0(s)P(s) = 0. \tag{24}$$

Here, the $a_i(s)$ $(i=0,\ldots,u)$ are general coefficients. They are related to the coefficients $a_i(s)$, $a_i'(s)$, $a_i''(s)$ $(i=0,\ 1,\ 2)$ introduced in Sec. III for specific cases. The coefficients $a_u(s)$, $a_{u-1}(s)$, etc., depend on s but are all polynomials of same degree n,

$$a_u(s) = A_{u,n}s^n + A_{u,n-1}s^{n-1} + \cdots + A_{u,0}. \tag{25}$$

For the kernel Γ_t^A, $n=1$. For the uniform kernel, $n=2$. For the nearly uniform kernel, $n=3$.

As emphasized before, it is through the s dependence of $M_s(k)$ that the *local environment* of the cell is represented. By contrast, a global mean-field approximation (see [27] for the cell disappearance case) assumes that a transforming cell gives away its edges to *any* cell of the foam instead of to its nearest neighbors. The coefficients of Eq. (24) are then constant (polynomials of degree zero in s). The general solution is then a combination of u independent eigensolutions $P^u(s)$, $P^{u-1}(s)$, $\ldots, P^1(s)$, all decaying exponentially for large s. But in all natural foams, $P(s)$ has a single, universal exponential decay, characteristic of one eigensolution only. Which solution is the physical one is a much debated problem [27–33], but an academic one, since it arises only in the global mean-field approximation.

In the local mean-field approximation, the coefficients $a_u(s)$, $a_{u-1}(s)$, etc., are polynomials in s. The constraints (11)–(13) make the population equation (24) *asymptotically integrable* (integrable for large s).

The linear difference equation (24) is *integrable* if it can be written as

$$D[b_{u-1}(s+u-1)P(s+u-1) + \cdots + b_1(s+1)P(s+1) + b_0(s)P(s)] = 0, \tag{26}$$

where the difference operator D is defined by Eq. (19). Thus, integrability of linear difference equation (24) is equivalent to

$$a_u(s+u) = b_{u-1}(s+u),$$

$$a_{u-1}(s+u-1) = b_{u-2}(s+u-1) - b_{u-1}(s+u-1),$$

$$\cdots$$

$$a_1(s+1) = b_0(s+1) - b_1(s+1),$$

$$a_0(s) = -b_0(s). \tag{27}$$

It follows that

$$a_u(s) + a_{u-1}(s) + a_{u-2}(s) + \cdots + a_0(s) = 0. \tag{28}$$

Inversely, if the above condition holds, we can define

$$b_{u-1}(s+u) = a_u(s+u),$$

$$b_{u-2}(s+u-1) = a_{u-1}(s+u-1) + a_u(s+u-1),$$

$$\cdots$$

$$b_0(s) = a_1(s) + \cdots + a_u(s), \tag{29}$$

to show that Eq. (24) integrates to Eq. (26).

Now consider the case where all the coefficients of (24) are polynomials (25) of the same degree n and

$$q(s) = a_u(s) + a_{u-1}(s) + a_{u-2}(s) + \cdots + a_0(s) \tag{30}$$

is a polynomial of lower degree n_q. Then population equation (24) can be written as

$$D[b_{u-1}(s+u-1)P(s+u-1) + \cdots + b_0(s)P(s)] + q(s)P(s) = 0. \tag{31}$$

For large s, it reduces to a lower-order equation

$$b_{u-1}(s+u-1)P(s+u-1) + \cdots + b_0(s)P(s) = 0, \tag{32}$$

since $n_q < n$. The right-hand side of Eq. (32) is zero because the solution $P(s)$ must satisfy constraints (11) and (12).

To find the asymptotic behavior of the u solutions of difference equation (24) with polynomial coefficients (25), we set $P(s) \sim Cs^{-\kappa}z^s$ for large s in the equation and equate to zero the coefficients of the highest powers in s [34]. The leading term yields a linear algebraic equation for z

$$G(z) = z^u A_{u,n} + z^{u-1}A_{u-1,n} + \cdots + z^1 A_{1,n} + A_{0,n} = 0. \tag{33}$$

The next term yields κ, which is given explicitly for a single root of (33)

$$\kappa = n + \frac{S_{0,n-1}}{S_{1,n}}, \tag{34}$$

where

$$S_{j,n} = \sum_{p=0}^{u} p^j z^p A_{p,n} \tag{35}$$

for $j=0,1,\ldots$ A double root exists if $G(z)=S_{0,n}=0$ and $dG(z)/dz=S_{1,n}/z=0$. In our models, a double root $z=1$ appears, but simultaneously, $S_{0,n-1}=0$, or equivalently, $n-n_q \geqslant 2$ (Secs. V and VII). Then κ satisfies

$$H(\kappa) = \kappa^2 S_{2,n} + \kappa[(1-2n)S_{2,n} - 2S_{1,n-1}] + n(n-1)S_{2,n} + 2(n-1)S_{1,n-1} + 2S_{0,n-2} = 0. \tag{36}$$

Asymptotic integrability $n_q < n$ implies that $A_{u,n}+A_{u-1,n}+\ldots+A_{p,n}+\ldots+A_{0,n}=0$, so that $z=1$ is also a root of Eq. (33). Thus, at least one of the u solutions of Eq. (24) decays algebraically, in contrast with the global mean-field results that all solutions decay exponentially. Asymptotic integrability selects the physical solution and filters out the irrelevant ones, as we shall see in Secs. V–VII.

For completeness, consider the case where $v+1$ coefficients of the linear difference equation (24) $a_0(s)$, $a_1(s)$, $\ldots, a_{v-1}(s)$, $a_v(s)$ are polynomials of the same degree, but $a_{v+1}(s)$, $a_{v+2}(s)$, $\ldots, a_u(s)$ are polynomials of a lower degree. One can use the method of dominant balance [34] to obtain the asymptotic behavior of the distribution $P(s)$. At large s, the terms $a_{v+1}(s)$, $a_{v+2}(s)$, $\ldots, a_u(s)$ are negligible, and we recover a vth-order linear difference equation. The asymptotic integrability and behavior of the physical solutions of this vth-order equation, namely, the values of z and κ in Eq. (1), can be found by the methods developed above. The remaining $u-v$ solutions of the linear equation can be obtained by looking for other possible dominant balances. Of course, any oscillating (negative) or non-normalizable solutions for $P(s)$ must be discarded. This immediately reduces the number of possible balances. For example, any population equation with positive coefficients need not be considered, since it has no non-negative solutions for $P(s)$. Examples of the method will be given in Secs. V–VII.

Polynomials $q(s)=a_u(s)+a_{u-1}(s)+a_{u-2}(s)+\ldots+a_0(s)$ for the various population equations of Sec. III are given in Appendix A. One sees readily that $n_q < n$.

Solutions behaving as $P(s) \sim Cs^{-\kappa}z^s$ for large s are physical (i.e., normalizable and non-negative) if only $0 < z \leqslant 1$. To satisfy constraints (11) and (12), we must have $\kappa > 2$ if $z=1$. Moreover, the finiteness of

$$\mu_2 = \sum_{s=3} P(s)(s-6)^2, \tag{37}$$

a measure of randomness [1], implies $\kappa > 3$ if $z=1$.

V. EXAMPLE: THE CASE OF CELL DIVISION ONLY

The steady state of a cellular structure evolving by cell division depends on two sets of parameters, $\Gamma(s|k,m)$ and $P(m|k)$. We consider uniform and nearly uniform kernels. With cell division as the only elementary topological transformation, $s_{\min} \leqslant 5$ for the distribution $P(s)$ to obey constraint (12). With $s_{\min}=3$ and $s_{\min}=4$, this concerns 2D foams generated by fragmentation [21]. Note that $P(d|k)=0$ here, and the fate of cells is unambiguous (see Sec. III).

Two algorithms of cell selection have been considered [21]. The first algorithm S_1 selects a cell at random among all cells. The second algorithm S_2 first selects an edge at random among all edges, then chooses between the two cells separated by that edge. The k-sided selected cell is then fragmented into two cells by an additional edge bridging two different sides chosen at random among its k sides. As discussed in Sec. III, $P(m|k)$ must be consistent with $\Gamma(s|k,m)$. For algorithm S_1, the conditional probability is $P(m|k)=1$, and for algorithm S_2, $P(m|k)=k/6$. Moreover, $P(m|k)=0$ if $k < 2s_{\min}-4$ or $k < 2s_{\min}-2$ for kernels $\Gamma^B_{s_{\min}}$ and $\Gamma^C_{s_{\min}}$, respectively.

The population equations corresponding to various kernels and cell selections (topological transformations TT) are given in Eqs. (18), (20), and (22), and summarized in Table I. Since $A(s,k)$ is linear in s and k, $a'_1(s)$ and $a'_0(s)$ are polynomials in s of degree $n=1$ in the local mean-field approximation (maximum entropy)

$$a'_1(s) = A'_{1,1}s + A'_{1,0},$$

$$a'_0(s) = A'_{0,1}s + A'_{0,0}. \tag{38}$$

The particular values of the coefficients $A'_{1,1}$, $A'_{1,0}$, etc., depend on the choice of the division kernel and of the algorithm of cell selection. These values and the corresponding structural parameters $0 < \eta_{-1} < 1/6$, $0 < \eta_0 \leqslant 1$ and $0 < \eta_1$ are given in Appendix B.

With kernel Γ^A_t and algorithm S_1, the population equation *is* first order if $t \leqslant 4$. Its solution decays asymptotically as $s^{-1-(2-b_3-b_4)/\beta}$, where

TABLE I. Population equations for foams evolving by cell division. $a'_1(s)=A'_{1,1}s+A'_{1,0}$ and $a'_0(s)=A'_{0,1}s+A'_{0,0}$. Coefficients $A'_{1,1}$, $A'_{1,0}$, etc., are given explicitly in Appendix B.

TT	Population equation for $P(s)$
Γ^A_t, S_1	$\sum_{u=6}^{u=t} b_u P(s-3+u) + b_5 P(s+2) + [a'_1(s+1)+b_4]P(s+1) + [a'_0(s)+b_3]P(s) = 0$
$\Gamma^B_{s_{\min}}$, S_1	Eq. (20) with $a''_2(s)=a'_1(s)(s-s_{\min})-2\delta_{s_{\min},5}$ $a''_1(s)=[-a'_1(s)+a'_0(s)](s-s_{\min}+1)-2\delta_{s_{\min},4}$ $a''_0(s)=-a'_0(s)(s-s_{\min}+2)-2\delta_{s_{\min},3}$
$\Gamma^C_{s_{\min}}$, S_1	Eq. (22) with $a''_3(s)=-(s-7)\delta_{s_{\min},5}$ $a''_2(s)=a'_1(s)(s-s_{\min}-1)(s-s_{\min})-(s-5)(\delta_{s_{\min},5}+\delta_{s_{\min},4})$ $a''_1(s)=[-a'_1(s)+a'_0(s)](s-s_{\min})(s-s_{\min}+1)-(s-3)\times(\delta_{s_{\min},4}+\delta_{s_{\min},3})$ $a''_0(s)=-a'_0(s)(s-s_{\min}+1)(s-s_{\min}+2)-(s-1)\delta_{s_{\min},3}$
Γ^A_t, S_2	$\sum_{u=6}^{u=t} b_u(s-3+u)P(s-3+u) + b_5(s+2)P(s+2) + [s(b_4-3)+(b_4-9)]P(s+1) + (b_3+2)sP(s) = 0$
$\Gamma^B_{s_{\min}}$, S_2	Eq. (20) with $a''_2(s)=6a'_1(s)(s-s_{\min})-2s\delta_{s_{\min},5}$ $a''_1(s)=6[-a'_1(s)+a'_0(s)](s-s_{\min}+1)-2s\delta_{s_{\min},4}$ $a''_0(s)=-6a'_0(s)(s-s_{\min}+2)-2s\delta_{s_{\min},3}$
$\Gamma^C_{s_{\min}}$, S_2	Eq. (22) with $a''_3(s)=-s(s-7)\delta_{s_{\min},5}$ $a''_2(s)=6a'_1(s)(s-s_{\min}-1)(s-s_{\min})-s(s-5)(\delta_{s_{\min},5}+\delta_{s_{\min},4})$ $a''_1(s)=[-6a'_1(s)+6a'_0(s)](s-s_{\min})(s-s_{\min}+1)-s(s-3)(\delta_{s_{\min},4}+\delta_{s_{\min},3})$ $a''_0(s)=-6a'_0(s)(s-s_{\min}+1)(s-s_{\min}+2)-s(s-1)\delta_{s_{\min},3}$

$$\beta = 2\sigma + (2-12\sigma)\sum_{s=3} \frac{P(s)}{s} \tag{39}$$

is a positive structural parameter. For $t \geqslant 5$, the coefficients of the new terms $u \geqslant 5$ in the population equation are constant, whereas the coefficients for $u=3,4$ are linear in s and dominate the asymptotic behavior of the distribution $P(s)$. That there are no other physical (real, non-negative, and normalizable with $\langle s\rangle=6$) solutions can be deduced from the following argument: Note first that only one of the coefficients of the population equation $[a'_1(s+1)+b_4]$ is negative at large s; the others are positive. Balancing two terms with positive coefficients would yield an unacceptable negative solution. Thus, the dominant balance method is reduced to $b_t P(s+t-3) = \beta s P(s+1)$, with a non-normalizable solution that grows like $(s!)^{1/(t-4)}(\beta/b_t)^{s/(t-4)}$.

With kernel $\Gamma^B_{s_{\min}}$ and algorithm S_1, the population equation is second order since $s_{\min} \leqslant 5$. It is asymptotically integrable, since $n_q=0<n=2$. The population equation has solutions of the type $P(s) \sim Cs^{-\kappa}z^s$ for large s. Equation (33) is then $A'_{1,1}(z-1)^2=0$, with a double root $z=1$. The corresponding κ is a solution of Eq. (36), namely,

$$H_1(\kappa) = \kappa^2(-A'_{1,1}) + \kappa(A'_{1,1} - \eta_0 - 1) + 2 = 0, \tag{40}$$

where $H_1(0)=2$, $H_1(1)=1-\eta_0 \geqslant 0$, and $H_1(2)=-2(\eta_0+A'_{1,1}) < -(4/3)\eta_0$ (see Appendix B). Thus, Eq. (40) has one root between 1 and 2, which is unphysical. The other root, κ_1, is positive and physical if $A'_{1,1}<0$.

With kernel $\Gamma^C_{s_{\min}}$ and algorithm S_1, the population equation is second (third) order, if $s_{\min}<5$ ($s_{\min}=5$). The population equation is asymptotically integrable since $n_q=1<n=3$. Using Eq. (33) to find the asymptotic behavior, we recover the same equations for z as for the uniform kernel. Again, $z=1$ is a double root, and κ satisfies the equation

$$H_2(\kappa) = \kappa^2(-A'_{1,1}) + \kappa(A'_{1,1} - \eta_0 - 1) + \delta_{s_{\min},5} + 2\delta_{s_{\min},4} + 2\delta_{s_{\min},3} = 0, \tag{41}$$

with new values for $A'_{1,1}$ and η_0 (see Appendix B). The same conclusions can be drawn (*mutatis mutandis*): There is only one distribution decaying algebraically with κ_2, the physical root of Eq. (41).

With kernel Γ^A_t and algorithm S_2, the population equation *is* first order if $t \leqslant 4$. Its solution decays asymptotically as $s^{-1+6/(b_4-3)}$. For $t > 4$, the population equation (multiplied by six) is asymptotically integrable since $q(s) = -6$ and $n = 1 > n_q = 0$. Solutions of the population equation decay as $P(s) \sim Cs^{-\kappa}z^s$. Equation (33) is

$$G_1(z) = z^{t-3}b_t + z^{t-4}b_{t-1} + \cdots + z^2 b_5 + z(b_4 - 3) + b_3 + 2 = 0. \tag{42}$$

The sum rule $\Sigma b_u = 1$ guarantees that $z_3 = 1$ is an acceptable root of the above algebraic equation (42). Then κ_3, corresponding to the root $z_3 = 1$, can be found from Eq. (34)

$$\kappa_3 = \frac{-6}{b_4 - 3 + [2b_5 + 3b_6 + \cdots + (t-3)b_t]} + 1. \tag{43}$$

The algebraic equation (42) can be analyzed further with Descartes' theorem, which states that the number of positive real roots of a real algebraic equation is either equal to N_0, the number of sign changes in the sequence of coefficients, or is less than N_0 by a positive even integer [35]. Equation (42) has $b_t > 0$, $b_{t-1} > 0, \ldots$, $b_5 > 0$, $b_4 - 3 < 0$, $b_3 + 2 > 0$, that is $N_0 = 2$ and at most two positive roots. One is $z = 1$. To investigate the magnitude of the second positive root [the only positive root of polynomial $G_1(z)/(z-1)$], we use Jury's theorem on a polynomial equation given by Eq. (33) with $A_{u,n} > 0$. The theorem states that $(-1)^u G(-1) > 0$ is a necessary condition for the equation to have no root outside the unit circle $|z| = 1$ (see, e.g, [35,36] for the necessary and sufficient conditions). Since $(-1)^{t-4}G_1(z)/(z-1)|_{z=-1} = -(b_{t-1} + b_{t-3} + \cdots + b_3 + 2) < 0$, the second positive root of $G_1(z)$ is greater than one and unphysical.

With kernel $\Gamma^B_{s_{\min}}$ and algorithm S_2, the population equation is second order since $s_{\min} < 6$. It is asymptotically integrable because Eq. (A3) implies $q(s) = \eta_1 + 6\eta_0 - s$ and $n = 2 > n_q = 1$. Here the first solution decays exponentially with

$$z_4 = -\frac{A'_{0,1}}{A'_{1,1}},$$

$$\kappa_4 = 2 + \frac{S_{0,1}}{S_{1,2}}, \tag{44}$$

where

$$S_{0,1} = [A'_{0,1}(6s_{\min} - 12) - 6A'_{0,0} - 2\delta_{s_{\min},3}] + z_4[(6A'_{0,1} - 6A'_{1,1}) \times (1 - s_{\min}) + (6A'_{0,0} - 6A'_{1,0}) - 2\delta_{s_{\min},4}] + z_4^2[-6s_{\min}A'_{1,1} + 6A'_{1,0} - 2\delta_{s_{\min},5}],$$

$$S_{1,2} = z_4(6A'_{0,1} - 6A'_{1,1}) + z_4^2(12A'_{1,1}). \tag{45}$$

The second solution decays asymptotically with $z = 1$ and $\kappa = 3$.

With kernel $\Gamma^C_{s_{\min}}$ and algorithm S_2, the population equation is asymptotically integrable if $s_{\min} \leqslant 5$, since $n = 3 > n_q = 1$. Here the first solution decays asymptotically with

$$z_5 = -\frac{A'_{0,1}}{A'_{1,1}},$$

$$\kappa_5 = 3 + \frac{S_{0,2}}{S_{1,3}}, \tag{46}$$

where

$$S_{0,2} = [A'_{0,1}(12s_{\min} - 18) - 6A'_{0,0} - \delta_{s_{\min},3}] + z_5[(6A'_{0,1} - 6A'_{1,1}) \times (1 - 2s_{\min}) + (6A'_{0,0} - 6A'_{1,0}) - \delta_{s_{\min},4} - \delta_{s_{\min},3}] + z_5^2[A'_{1,1}(-12s_{\min} - 6) + 6A'_{1,0} - \delta_{s_{\min},5} - \delta_{s_{\min},4}],$$

$$S_{1,3} = z_5(6A'_{0,1} - 6A'_{1,1}) + z_5^2(12A'_{1,1}). \tag{47}$$

Note that z_4 and z_5 are not equal, since the values of $A'_{0,1}$ and $A'_{1,1}$ for uniform and nearly uniform kernels are not the same. But the second solution of the population equation decays again asymptotically with $z = 1$ and $\kappa = 3$. Our results are summarized in Table II.

VI. EXAMPLE: THE CASE OF CELL DISAPPEARANCE ONLY

In the case of cell disappearance, it has been assumed that only three-, four-, and five-sided cells disappear. Thus, $P(d|k) = 1$ for $k \leqslant 5$ and $P(d|k) = 0$ for $k \geqslant 6$. The sum rules [(5), (6a), and (6b)] yield $\Delta(-1|3,d) = 1$, $\Delta(-1|4,d) = 1/2$, $\Delta(0|4,d) = 1/2$, $\Delta(-1|5,d) = 2/5$, $\Delta(0|5,d) = 2/5$, and $\Delta(1|5,d) = 1/5$. Thus for $s \geqslant 5$, Eq. (17) reads

$$a_2(s+2)P(s+2) + a_1(s+1)P(s+1) + a_0(s)P(s) = 0, \tag{48}$$

where

$$a_2(s) = \gamma_3 A(s,3) + \frac{\gamma_4}{2}A(s,4) + \frac{2\gamma_5}{5}A(s,5),$$

$$a_1(s) = -\gamma_3 A(s,3) - \frac{\gamma_4}{2}A(s,4) - \frac{3\gamma_5}{5}A(s,5) + \gamma_3 + \gamma_4 + \gamma_5,$$

$$a_0(s) = \frac{\gamma_5}{5}A(s,5), \tag{49}$$

and

$$\gamma_k = P(k)P(d|k). \tag{50}$$

[We used the simpler notation $a(s) = a_2(s)$, $b(s) = a_1(s)$, and $c(s) = a_0(s)$ for $u = 2$ in our previous paper [23]]. Since $A(s,k)$ is linear in s and k in the local mean-field approximation (maximum entropy), the coefficients of the linear difference

TABLE II. Asymptotic integrability of the population equations and the distribution $P(s) \sim Cs^{-\kappa}z^{s}$ for various foams evolving by cell division. u: order of the difference equation, n: the largest degree of the coefficients, n_q: degree of $q(s)$. The values for z and κ are given in the text.

TT		u	$q(s)$	n	n_q	Integrability	z	κ
Γ_t^A, S_1	$t \leqslant 4$	1		1	-	First order	1	$1+\frac{2-b_3-b_4}{\beta}$
Γ_t^A, S_1	$t \geqslant 5$	$t-3$		1	-	Asymp. integr.	1	$1+\frac{2-b_3-b_4}{\beta}$
$\Gamma_{s_{\text{min}}}^B$, S_1	$s_{\text{min}} < 6$	2	$\eta_0 - 1$	2	0	Asymp. integr.	$z_1 = 1$	κ_1
$\Gamma_{s_{\text{min}}}^C$, S_1	$s_{\text{min}} < 5$	2	$-2a_0'(s)+2\eta_0(s-s_{\text{min}})$ $+(-2s_{\text{min}}+8\delta_{s_{\text{min}},4}+4\delta_{s_{\text{min}},3})s$	3	1	Asymp. integr.	$z_2 = 1$	κ_2
$\Gamma_{s_{\text{min}}}^C$, S_1	$s_{\text{min}} = 5$	3		3	-	Asymp. integr.	$z_2 = 1$	κ_2
Γ_t^A, S_2	$t \leqslant 4$	1		1	-	First order	1	$1-\frac{6}{b_4-3}$
Γ_t^A, S_2	$t \geqslant 5$	$t-3$	-6	1	0	Asymp. integr.	$z_3 = 1$	κ_3
$\Gamma_{s_{\text{min}}}^B$, S_2	$s_{\text{min}} < 6$	2	$\eta_1 + 6\eta_0 - s$	2	1	Asymp. integr.	z_4	κ_4
							1	3
$\Gamma_{s_{\text{min}}}^C$, S_2	$s_{\text{min}} < 5$	2	$(-2s_{\text{min}}+8\delta_{s_{\text{min}},4}+4\delta_{s_{\text{min}},3})s$ $-12a_0'(s)+(s-s_{\text{min}})(12\eta_0+2\eta_1)$	3	1	Asymp. integr.	z_5	κ_5
							1	3
$\Gamma_{s_{\text{min}}}^C$, S_2	$s_{\text{min}} = 5$	3		3	-	Asymp. integr.	z_5	κ_5
							1	3

equation (48) are polynomials in s of degree $n=1$

$$a_2(s) = A_{2,1}s + A_{2,0},$$

$$a_1(s) = A_{1,1}s + A_{1,0},$$

$$a_0(s) = A_{0,1}s + A_{0,0}. \tag{51}$$

The values of coefficients $A_{2,1}$, $A_{2,0}$, etc., are listed in Appendix B.

Equation (48) is asymptotically integrable because $q(s) = \gamma_3 + \gamma_4 + \gamma_5$ and $n_q = 0 < n = 1$. For cellular structures evolving by disappearance, the parameters $\tilde{z}$ and $\tilde{\kappa}$, characterizing the asymptotic behavior of $P(s) \sim Cs^{-\tilde{\kappa}}\tilde{z}^{s}$, have a tilde. The first solution of Eq. (48) decays exponentially with

$$\tilde{z}_1 = \frac{A_{0,1}}{A_{2,1}} < 1,$$

$$\tilde{\kappa}_1 = 1 + \frac{\frac{A_{0,1}A_{2,0}}{A_{2,1}} + A_{1,0} + \frac{A_{2,1}A_{0,0}}{A_{0,1}}}{A_{0,1} - A_{2,1}}, \tag{52}$$

and the second solution decays, algebraically, with

$$\tilde{z}_2 = 1,$$

$$\tilde{\kappa}_2 = 1 - \frac{A_{0,0} + A_{1,0} + A_{2,0}}{A_{0,1} - A_{2,1}}. \tag{53}$$

Our results are summarized in Table III.

VII. EXAMPLE: THE CASE OF CELL DIVISION AND DISAPPEARANCE

The steady state of a cellular structure evolving by division and disappearance depends on three parameters,

TABLE III. Asymptotic integrability of the population equations and the distribution $P(s) \sim Cs^{-\tilde{\kappa}}\tilde{z}^{s}$ for foams evolving by cell disappearance. u: order of the difference equation, n: the largest degree of the coefficients, n_q: degree of $q(s)$. The values for $\tilde{z}$ and $\tilde{\kappa}$ are given in the text.

TT		u	$q(s)$	n	n_q	Integrability	$\tilde{z}$	$\tilde{\kappa}$
$\Delta(i\vert k,d)$	$P(d\vert k)=1$ for $k \leqslant 5$	2	$\gamma_3+\gamma_4+\gamma_5$	1	0	Asymp. integr.	$\tilde{z}_1$	$\tilde{\kappa}_1$
	$P(d\vert k)=0$ for $k \geqslant 6$						$\tilde{z}_2 = 1$	$\tilde{\kappa}_2$

TABLE IV. Population equations for foams evolving by cell division and disappearance. $a_1'(s)=A_{1,1}'s+A_{1,0}'$, $a_0'(s)=A_{0,1}'s+A_{0,0}'$, $a_2(s)=A_{2,1}s+A_{2,0}$, $a_1(s)=A_{1,1}s+A_{1,0}$, and $a_0(s)=A_{0,1}s+A_{0,0}$. Coefficients $A_{1,1}'$, $A_{1,0}'$, etc., are given explicitly in Appendix B.

TT	Population equation for $P(s)$
Γ^A, S_1	$\sum_{u=6}^{u=t} b_u P(s-3+u)+a_2(s+2)P(s+2)+[a_1(s+1)+a_1'(s+1)]P(s+1)+[a_0(s)+a_0'(s)]P(s)=0$
Γ^B, S_1	Eq. (20) with $a''_{s_{\min}-3}(s)=-2\theta(s_{\min}-6)$ $a_3''(s)=a_2(s)(s-s_{\min}-1)-2\delta_{s_{\min},6}$ $a_2''(s)=[a_1'(s)+a_1(s)-a_2(s)](s-s_{\min})-2\delta_{s_{\min},5}$ $a_1''(s)=[-a_1'(s)+a_0'(s)-a_1(s)+a_0(s)](s-s_{\min}+1)$ $a_0''(s)=[-a_0'(s)-a_0(s)](s-s_{\min}+2)$
Γ^C, S_1	Eq. (22) with $a''_{s_{\min}-2}(s)=-(s-2s_{\min}+3)\theta(s_{\min}-5)$ $a''_{s_{\min}-3}(s)=-(s-2s_{\min}+5)\theta(s_{\min}-6)$ $a_3''(s)=a_2(s)(s-s_{\min}-2)(s-s_{\min}-1)-(s-7)(\delta_{s_{\min},6}+\delta_{s_{\min},5})$ $a_2''(s)=[a_1'(s)+a_1(s)-a_2(s)](s-s_{\min}-1)(s-s_{\min})-(s-5)\delta_{s_{\min},5}$ $a_1''(s)=[-a_1'(s)+a_0'(s)-a_1(s)+a_0(s)](s-s_{\min})(s-s_{\min}+1)$ $a_0''(s)=[-a_0'(s)-a_0(s)](s-s_{\min}+1)(s-s_{\min}+2)$
Γ^A, S_2	$\sum_{u=6}^{u=t} b_u(s-3+u)P(s-3+u)+6a_2(s+2)P(s+2)+[6a_1(s+1)+6a_1'(s+1)]P(s+1)+[6a_0(s)+6a_0'(s)]P(s)=0$
Γ^B, S_2	Eq. (20) with $a''_{s_{\min}-3}(s)=-2s\theta(s_{\min}-6)$ $a_3''(s)=6a_2(s)(s-s_{\min}-1)-2s\delta_{s_{\min},6}$ $a_2''(s)=6[a_1'(s)+a_1(s)-a_2(s)](s-s_{\min})-2s\delta_{s_{\min},5}$ $a_1''(s)=6[-a_1'(s)+a_0'(s)-a_1(s)+a_0(s)](s-s_{\min}+1)$ $a_0''(s)=6[-a_0'(s)-a_0(s)](s-s_{\min}+2)$
Γ^C, S_2	Eq. (22) with $a''_{s_{\min}-2}(s)=-s(s-2s_{\min}+3)\theta(s_{\min}-5)$ $a''_{s_{\min}-3}(s)=-s(s-2s_{\min}+5)\theta(s_{\min}-6)$ $a_3''(s)=6a_2(s)(s-s_{\min}-2)(s-s_{\min}-1)-s(s-7)\times(\delta_{s_{\min},6}+\delta_{s_{\min},5})$ $a_2''(s)=6[a_1'(s)+a_1(s)-a_2(s)](s-s_{\min}-1)(s-s_{\min})-s(s-5)\delta_{s_{\min},5}$ $a_1''(s)=6[-a_1'(s)+a_0'(s)-a_1(s)+a_0(s)](s-s_{\min})(s-s_{\min}+1)$ $a_0''(s)=6[-a_0'(s)-a_0(s)](s-s_{\min}+1)(s-s_{\min}+2)$

$P(m|k)$, $\Gamma(s|k,m)$, and $P(d|k)$. It is assumed that $P(d|k)=0$ for $s\geqslant 6$, in agreement with von Neumann's law and with simulations on the renewal of the epidermis [17]. As before, we consider two algorithms S_1 and S_2 for selection of dividing cells. But here, we take kernel Γ_t^A with $b_3=b_4=b_5=0$, kernels $\Gamma_{s_{\min}}^B$ and $\Gamma_{s_{\min}}^C$ with $s_{\min}\geqslant 5$, and the corresponding $P(m|k)$, to avoid ambiguity in the fate of three-, four-, and five-sided cells (see Sec. III). The population equations corresponding to various division kernels and selection algorithms [topological transformations (TT)] can be found from the general equations (18), (20), and (22), and are summarized in Table IV. Asymptotic integrability of these population equations can be checked using the criterion discussed in Sec. IV. For cellular structures evolving by division *and* disappearance, the parameters $\bar{z}$ and $\bar{\kappa}$ characterizing the asymptotic behavior of $P(s)$ have a bar.

First, we consider kernel Γ_t^A and algorithm S_1 for selection of dividing cells, with the constraints $b_3=b_4=b_5=0$, and $P(m|3)=P(m|4)=P(m|5)=0$. Three of the coefficients of the population equation are polynomials of degree one, but the remainder are polynomials of degree zero (constant). The method of dominant balance is thus useful here. Neglecting constant polynomials at large s, we obtain a second-order linear difference equation, which is asymptotically integrable. This second-order difference equation has two solutions decaying with

$$\bar{z}_1 = \frac{A_{0,1}+A'_{0,1}}{A_{2,1}},$$

$$\bar{\kappa}_1 = 1 + \frac{(A_{0,0}+A'_{0,0}) + \bar{z}_1(A_{1,0}+A'_{1,0}) + \bar{z}_1^2 A_{2,0}}{\bar{z}_1(A_{1,1}+A'_{1,1}) + 2\bar{z}_1^2 A_{2,1}}, \qquad (54)$$

and

$$\bar{z}_2 = 1,$$

$$\bar{\kappa}_2 = 1 + \frac{\gamma_3+\gamma_4+\gamma_5-\eta_0-1}{A_{2,1}-A_{0,1}-A'_{0,1}}. \qquad (55)$$

The first solution (54) must be discarded if $\bar{z}_1$ is negative or >1, corresponding to an oscillatory or non-normalizable distribution $P(s)$. Use of the dominant balance method to find the other real positive solutions leads to the equation $b_t P(s-3+t)+[a_1(s+1)+a'_1(s+1)]P(s+1)=0$, with an unacceptable solution growing like $(s!)^{1/(t-4)}(-A'_{1,1}/b_t - A_{1,1}/b_t)^{s/(t-4)}$.

With kernel $\Gamma^B_{s_{\min}}$ and algorithm S_1, the population equation is a third-order linear difference equation if $5 \leqslant s_{\min} < 7$. This linear difference equation is asymptotically integrable since $n_q=0<n=2$. Solutions of this population equation decay as $P(s) \sim C s^{-\bar{\kappa}} \bar{z}^s$, where $\bar{z}$ is a root of Eq. (33), which is here $A_{2,1}(\bar{z}-\bar{z}_3)(\bar{z}-1)^2=0$, with

$$\bar{z}_3 = \frac{A_{0,1}+A'_{0,1}}{A_{2,1}}. \qquad (56)$$

This root coresponds to a physical solution only if it is positive and $\leqslant 1$. $\bar{z}_3$ is a single root, thus by Eq. (34), we have

$$\bar{\kappa}_3 = 2 + \frac{E_0(s_0-s_{\min}+2) + \bar{z}_3 E_1(s_1-s_{\min}+1) + \bar{z}_3^2 E_2(s_2-s_{\min}) + \bar{z}_3^3(-E_0-E_1-E_2)(s_3-s_{\min}-1)}{\bar{z}_3 E_1 + 2\bar{z}_3^2 E_2 + 3\bar{z}_3^3(-E_0-E_1-E_2)}. \qquad (57)$$

The values of parameters E_0, E_1, E_2, s_0, s_1, s_2, and s_3 are listed in Appendix B. $\bar{z}=1$ is a double root; thus according to Eq. (36), the corresponding $\bar{\kappa}$'s satisfy

$$H_3(\bar{\kappa}) = \bar{\kappa}^2(A'_{0,1}+A_{0,1}-A_{2,1}) + \bar{\kappa}(-\eta_0-1+\gamma_3+\gamma_4+\gamma_5 - A'_{0,1}-A_{0,1}+A_{2,1}) + 2\delta_{s_{\min},5} + 2\delta_{s_{\min},6} = 0. \qquad (58)$$

Note that if $0<\bar{z}_3<1$ or $A_{0,1}+A'_{0,1}<A_{2,1}$, the product of the roots of the algebraic equation (58), $2/(A'_{0,1}+A_{0,1}-A_{2,1})$, is negative. Thus only $\bar{\kappa}_4$, the positive solution of Eq. (58), must be considered. If $\bar{z}_3>1$, both $\bar{\kappa}_4$ and $\bar{\kappa}_5$ could be positive. We expect one of the roots to be unacceptable [i.e., corresponding distribution $P(s)$, contradicting constraints given by Eq. (12)], although we have not been able to show this explicitly. For $s_{\min} \geqslant 7$, one of the coefficients of the population equation is a polynomial of degree zero. The dominant balance method leads to the previous population equation, but here we must exclude the non-normalizable solution with $\bar{z}=1$, $\bar{\kappa}=0$, which Eq. (58) allows.

With kernel $\Gamma^C_{s_{\min}}$ and algorithm S_1, the population equation is a third-order linear difference equation if $s_{\min}=5$. This linear difference equation is asymptotically integrable since $n_q=1<n=3$. Solutions of this population equation decay as $P(s) \sim C s^{-\bar{\kappa}} \bar{z}^s$, where Eq. (33) implies $A_{2,1}(\bar{z}-\bar{z}_6)(\bar{z}-1)^2=0$, with

$$\bar{z}_6 = \frac{A_{0,1}+A'_{0,1}}{A_{2,1}}. \qquad (59)$$

This root is physically unacceptable if it becomes negative or >1. $\bar{z}_6$ is a single root; thus by Eq. (34), we have

$$\bar{\kappa}_6 = 3 + \frac{E_0(s_0-2s_{\min}+3) + \bar{z}_6 E_1(s_1-2s_{\min}+1) + \bar{z}_6^2 E_2(s_2-2s_{\min}-1) + \bar{z}_6^3(-E_0-E_1-E_2)(s_3-2s_{\min}-3)}{\bar{z}_6 E_1 + 2\bar{z}_6^2 E_2 + 3\bar{z}_6^3(-E_0-E_1-E_2)}. \qquad (60)$$

$\bar{z}=1$ is a double root; thus according to Eq. (36), the corresponding $\bar{\kappa}$'s satisfy

$$H_4(\bar{\kappa}) = \bar{\kappa}^2(A'_{0,1} + A_{0,1} - A_{2,1}) + \bar{\kappa}(-\eta_0 - 1 + \gamma_3 + \gamma_4 + \gamma_5 - A'_{0,1} - A_{0,1} + A_{2,1}) + 2\delta_{s_{\min},5} + \delta_{s_{\min},6} = 0. \qquad (61)$$

Note that if $0 < \bar{z}_6 < 1$ or $A_{0,1} + A'_{0,1} < A_{2,1}$, the product of roots of the algebraic equation (61), $2/(A'_{0,1} + A_{0,1} - A_{2,1})$, is negative. Thus only $\bar{\kappa}_7$, the positive solution of Eq. (61) must be considered. If $\bar{z}_6 > 1$, both $\bar{\kappa}_7$ and $\bar{\kappa}_8$ could be positive. As with the previous case, we expect one of the roots to be unacceptable, although we have not been able to show this explicitly. For $s_{\min} \geqslant 6$, one or two of the coefficients of the population equation are a zero-degree polynomial. The dominant balance method leads to the previous population equation, but here we must exclude the non-normalizable solution with $\bar{z} = 1$, $\bar{\kappa} = 0$, which is allowed from Eq. (61).

Now we consider kernel Γ_t^A and algorithm S_2 for selection of dividing cells, with the constraints $b_3 = b_4 = b_5 = 0$, and $P(m|3) = P(m|4) = P(m|5) = 0$. The population equation is asymptotically integrable since $n = 1 > n_q = 0$. Solutions of the population equation decay as $P(s) \sim Cs^{-\bar{\kappa}}\bar{z}^s$. Equation (33) implies $G_2(\bar{z}) = 0$, where

$$G_2(\bar{z}) = \bar{z}^{t-3}b_t + \bar{z}^{t-4}b_{t-1} + \cdots \cdot + \bar{z}^3 b_6 + \bar{z}^2(6A_{2,1}) + \bar{z}(6A_{1,1} + 6A'_{1,1}) + 6A_{0,1} + 6A'_{0,1}. \qquad (62)$$

The sum rule $\Sigma b_u = 1$ guarantees that $\bar{z}_9 = 1$ is an acceptable root of the algebraic equation (62). Then $\bar{\kappa}_9$, corresponding to acceptable root $\bar{z}_9 = 1$, can be found from Eq. (34)

$$\bar{\kappa}_9 = 1 + \frac{6(\gamma_3 + \gamma_4 + \gamma_5 - \eta_0) - \eta_1}{6A_{1,1} + 6A'_{1,1} + 12A_{2,1} + [3b_6 + \cdots + (t-3)b_t]}. \qquad (63)$$

The algebraic equation (62) can be analyzed further with Descartes' theorem. $b_t > 0$, $b_{t-1} > 0, \ldots,$ $b_6 > 0$, $6A_{2,1} > 0$, $6A_{1,1} + 6A'_{1,1} < 0$, and $6A_{0,1} + 6A'_{0,1} > 0$, so the number of sign changes is two. Hence, Eq. (63) has two positive roots, $\bar{z}_9 = 1$ and $\bar{z}_{10}$. $\bar{z}_{10}$ is the only positive root of $G_2(\bar{z})/(\bar{z} - 1) = 0$ or $\bar{z}G_3(\bar{z}) + 6A_{2,1}\bar{z} - (6A_{0,1} + 6A'_{0,1}) = 0$, where

$$G_3(\bar{z}) = b_t(\bar{z}^{t-5} + \bar{z}^{t-6} + \cdots + 1) + \cdots + b_6(\bar{z} + 1). \qquad (64)$$

$\bar{z}_{10}$ thus satisfies $\bar{z}_{10} = (6A_{0,1} + 6A'_{0,1})/[6A_{2,1} + G_3(\bar{z}_{10})] < (6A_{0,1} + 6A'_{0,1})/(6A_{2,1}) < 1$. Then $\bar{\kappa}_{10}$, corresponding to the acceptable root $0 < \bar{z}_{10} < 1$, can be found from

$$\bar{\kappa}_{10} = 1 + \frac{6A_{0,0} + 6A'_{0,0} + \bar{z}_{10}(6A_{1,0} + 6A'_{1,0}) + \bar{z}_{10}^2(6A_{2,0})}{\bar{z}_{10}(6A_{1,1} + 6A'_{1,1}) + 2\bar{z}_{10}^2(6A_{2,1}) + [3\bar{z}_{10}^3 b_6 + 4\bar{z}_{10}^4 b_7 + \cdots + (t-3)\bar{z}_{10}^{t-3} b_t]}. \qquad (65)$$

With kernel $\Gamma^B_{s_{\min}}$ and algorithm S_2, the population equation is a third order linear difference equation if $5 \leqslant s_{\min} \leqslant 6$. This linear difference equation is asymptotically integrable since $n_q = 1 < n = 2$. Solutions of this population equation decay as $P(s) \sim Cs^{-\bar{\kappa}}\bar{z}^s$. Equation (33) yields $(\bar{z} - 1)G_4(\bar{z}) = 0$, where

$$G_4(\bar{z}) = \bar{z}^2(-E_0 - E_1 - E_2) + \bar{z}(-E_0 - E_1) - E_0. \qquad (66)$$

$\bar{\kappa}_{11}$ corresponding to the single root $\bar{z}_{11} = 1$ is

$$\bar{\kappa}_{11} = 1 + 2\delta_{s_{\min},5} + 2\delta_{s_{\min},6}. \qquad (67)$$

The second-degree polynomial $G_4(\bar{z})$ has at least one root between zero and one, since $G_4(0)G_4(1) < 0$. However, its second root does not lie between zero and one, since $G_4(1) < 0$. We denote the acceptable root of Eq. (66) by $\bar{z}_{12}$. $\bar{\kappa}_{12}$ corresponding to the single root $0 < \bar{z}_{12} < 1$ is then

$$\bar{\kappa}_{12} = 2 + \frac{S_{0,1}}{S_{1,2}}, \qquad (68)$$

where

$$S_{0,1} = E_0(6s_0 - 6s_{\min} + 12) + \bar{z}_{12}E_1(6s_1 - 6s_{\min} + 6) + \bar{z}_{12}^2[6E_2(s_2 - s_{\min}) - 2\delta_{s_{\min},5}] + \bar{z}_{12}^3[-6(E_0 + E_1 + E_2) \times (s_3 - s_{\min} - 1) - 2\delta_{s_{\min},6}],$$

$$S_{1,2} = 6\bar{z}_{12}E_1 + 12\bar{z}_{12}^2E_2 + 18\bar{z}_{12}^3(-E_0 - E_1 - E_2). \qquad (69)$$

For $s_{\min} \geqslant 6$, one of the coefficients of the population equation is a first-degree polynomial. The dominant balance method then leads to the previous asymptotic behavior. Note that for $s_{\min} > 6$, we must eliminate the solution decaying with $\bar{z} = 1$ and $\bar{\kappa} = 1$, which Eq. (67) allows.

With kernel $\Gamma^C_{s_{\min}}$ and algorithm S_2, the population equation is a third-order linear difference equation if $s_{\min} = 5$. This linear difference equation is asymptotically integrable since $n_q = 1 < n = 3$. Solutions of this population equation decay as $P(s) \sim Cs^{-\bar{\kappa}}\bar{z}^s$. Equation (33) implies $(\bar{z} - 1)G_4(\bar{z}) = 0$. $\bar{\kappa}_{13}$, corresponding to the single root $\bar{z}_{13} = 1$, is

$$\bar{\kappa}_{13} = 1 + 2\delta_{s_{\min},5} + \delta_{s_{\min},6}. \qquad (70)$$

The second-degree polynomial $G_4(\bar{z})$ has at least one root between zero and one, since $G_4(0)G_4(1) < 0$. However, its second root is not between zero and one, since $G_4(1) < 0$. We denote the acceptable root of Eq. (66) by $\bar{z}_{14}$. $\bar{\kappa}_{14}$, corresponding to the single root $0 < \bar{z}_{14} < 1$, is then

$$\bar{\kappa}_{14} = 3 + \frac{S_{0,2}}{S_{1,3}}, \qquad (71)$$

where

TABLE V. Asymptotic integrability of the population equations and the distribution $P(s) \sim Cs^{-\bar{\kappa}}\bar{z}^{s}$ for various foams evolving by cell division and disappearance. u: order of the difference equation, n: the largest degree of the coefficients, n_q: degree of $q(s)$. The values for $\bar{z}$ and $\bar{\kappa}$ are given in the text.

TT		u	$q(s)$	n	n_q	Integrability	$\bar{z}$	$\bar{\kappa}$
Γ_t^A, S_1	$b_3=b_4=0,\ b_5=0$	$t-3$		1	-	Asymp. integr.	$\bar{z}_1$	$\bar{\kappa}_1$
							$\bar{z}_2=1$	$\bar{\kappa}_2$
$\Gamma_{s_{\min}}^B$, S_1	$5 \leqslant s_{\min} < 7$	3	$\eta_0-1-\gamma_3-\gamma_4-\gamma_5$	2	0	Asymp. integr.	$\bar{z}_3$	$\bar{\kappa}_3$
							$\bar{z}_4=1$	$\bar{\kappa}_4$
							$\bar{z}_5=1$	$\bar{\kappa}_5$
$\Gamma_{s_{\min}}^B$, S_1	$s_{\min} \geqslant 7$	$s_{\min}-3$		2	-	Asymp. integr.	$\bar{z}_3$	$\bar{\kappa}_3$
							$\bar{z}_4=1$	$\bar{\kappa}_4$
$\Gamma_{s_{\min}}^C$, S_1	$s_{\min}=5$	3	$2+2(\eta_0-\gamma_3-\gamma_4-\gamma_5)(s-5)+2a_2(s)-2a_0(s)-2a_0'(s)$	3	1	Asymp. integr.	$\bar{z}_6$	$\bar{\kappa}_6$
							$\bar{z}_7=1$	$\bar{\kappa}_7$
							$\bar{z}_8=1$	$\bar{\kappa}_8$
$\Gamma_{s_{\min}}^C$, S_1	$s_{\min} > 5$	$s_{\min}-2$		3	-	Asymp. integr.	$\bar{z}_6$	$\bar{\kappa}_6$
							$\bar{z}_7=1$	$\bar{\kappa}_7$
Γ_t^A, S_2	$b_3=b_4=0,\ b_5=0$	$t-3$	$-\eta_1-6\eta_0+6(\gamma_3+\gamma_4+\gamma_5)$	1	0	Asymp. integr.	$\bar{z}_9=1$	$\bar{\kappa}_9$
							$\bar{z}_{10}$	$\bar{\kappa}_{10}$
$\Gamma_{s_{\min}}^B$, S_2	$5 \leqslant s_{\min} \leqslant 6$	3	$\eta_1+6\eta_0-6(\gamma_3+\gamma_4+\gamma_5)-s$	2	1	Asymp. integr.	$\bar{z}_{11}=1$	$\bar{\kappa}_{11}$
							$\bar{z}_{12}$	$\bar{\kappa}_{12}$
$\Gamma_{s_{\min}}^B$, S_2	$s_{\min} \geqslant 7$	$s_{\min}-3$		2	-	Asymp. integr.	$\bar{z}_{12}$	$\bar{\kappa}_{12}$
$\Gamma_{s_{\min}}^C$, S_2	$s_{\min}=5$	3	$(2s-10)(\eta_1+6\eta_0-6\gamma_3-6\gamma_4-6\gamma_5)+2s+12a_2(s)-12a_0(s)$ $-12a_0'(s)$	3	1	Asymp. integr.	$\bar{z}_{13}=1$	$\bar{\kappa}_{13}$
							$\bar{z}_{14}$	$\bar{\kappa}_{14}$
$\Gamma_{s_{\min}}^C$, S_2	$s_{\min} \geqslant 6$	$s_{\min}-2$		3	-	Asymp. integr.	$\bar{z}_{14}$	$\bar{\kappa}_{14}$

$$S_{0,2} = E_0(6s_0 - 12s_{\min} + 18) + \bar{z}_{14}E_1(6s_1 - 12s_{\min} + 6) + \bar{z}_{14}^2[6E_2(s_2 - 1 - 2s_{\min}) - \delta_{s_{\min},5}] + \bar{z}_{14}^3[-6(E_0 + E_1 + E_2)(s_3 - 2s_{\min} - 3) - \delta_{s_{\min},6} - \delta_{s_{\min},5}],$$

$$S_{1,3} = 6\bar{z}_{14}E_1 + 12\bar{z}_{14}^2E_2 + 18\bar{z}_{14}^3(-E_0 - E_1 - E_2). \qquad (72)$$

For $s_{\min} \geqslant 6$, two of the coefficients of the population equation are polynomials of degree two. The dominant balance method then leads to the previous asymptotic behavior. Note that for $s_{\min} > 6$, we must eliminate the solution decaying with $\bar{z}=1$ and $\bar{\kappa}=1$, which Eq. (70) allows.

Our results are summarized in Table V.

VIII. DISCUSSION

For a cellular structure evolving by cell fragmentation under the uniform kernel $\Gamma_{s_{\min}}^B$ with $s_{\min}=3$ and cell selection algorithm S_1, $q(s)=\eta_0-1=0$; thus, the population equation *integrates* to a first-order equation $a_2''(s)P(s+1)-a_0''(s)P(s)=0$ or

$$\frac{P(s)}{P(s-1)} = \frac{\beta s^2 + s(2-9\beta) + 14\beta - 2}{(s-3)(\beta s - 6\beta + 4)}.$$

Asymptotic behavior of $P(s)$ is then characterized by $z_1=1$ and $\kappa_1=2/\beta$, as Eq. (40) implies. Our results are in complete agreement with Ref. [21]. This model has been investigated further with numerical simulations, and a power-law variation $P(s) \sim s^{-5.72}$ for large s is found [21]. Simulations estimate $\beta=0.356$; thus, the theoretical value $\kappa_1=2/\beta=5.61$ and the numerical value $\kappa_1=5.72$ agree.

Delannay and Le Caër discussed such a power-law variation of $P(s)$ for large s [21], but this is not a rare situation. We have presented many other examples in Tables II and V, where the population equation has *one* physically acceptable solution, whose tail decays algebraically.

More frequently, numerical simulations indicate an exponential variation of $P(s)$ for large s. Tables II, III, and V often show that population equations have *two* physically acceptable solutions, one exponentially decaying solution $P^1(s)$ and one algebraically decaying solution $P^2(s)$ implied by the asymptotic integrability (Sec. IV). The general solution is then $P(s)=F_1P^1(s)+F_2P^2(s)$, where F_1 and F_2 are constants, but F_2 is negligible. These foams are described by the exponentially decaying solution $P^1(s)$. This is because the physical process of statistical equilibrium under ETT, constrained by $\langle s\rangle=6$, has nearly exhausted all the nonvanishing $P^1(s)$ by $s_{as} \approx 6+\sqrt{\mu_2}$. Note $\mu_2=\Sigma P(s)(s-6)^2$ is a measure of width of distribution around the mean value 6. The algebraic solution $P^2(s)$ is a negligible smooth background. We can estimate F_2, noting that the constraint $\Sigma P(s)=1$ implies $\Sigma F_2P^2(s) \ll 1$. So $F_2\Sigma_{s=3}^{\infty}s^{-\kappa} \ll 1$ or $F_2[\zeta(k)-1-2^{-\kappa}] \ll 1$ where ζ is Riemann's ζ function.

As an example, consider a cellular structure evolving by cell fragmentation under the uniform kernel $\Gamma^{B}_{s_{\min}}$ with $s_{\min}=3$ and cell selection algorithm S_2. Equation (44) then implies that the first solution decays exponentially as $(2/3)^s$, whereas the second solution decays algebraically as s^{-3}. Numerical simulations of this model show that $P(s)$ decreases as $(2/3)^s$ for $10 \leqslant s \leqslant 120$ and as s^{-3} for $s \geqslant 130\,[P(125) \approx 10^{-21}]$, and moreover, $\mu_2=8.168$ [21]. Therefore, $10^{-21} = F_2(125)^{-3}$, $F_2=10^{-14}$, quite negligible. Our estimate $s_{as} \approx 9$ and the simulation value of 10 are in good agreement.

The above arguments based on asymptotic integrability explain the exponential tail of $P(s)$ for foams evolving by cell disappearance only [23]. In the global mean-field approximation of Stavans *et al.* [27], the coefficients $a_2(s)$, $a_1(s)$, and $a_0(s)$ of Eq. (48) are zero-degree polynomials, adding up to a nonvanishing constant: Equation (48) is not asymptotically integrable, and one must use *ad hoc* criteria to select the exponentially decaying physical solution. Flyvbjerg's [28] is also a global mean-field approximation; the edges of the disappearing cell are redistributed to any cell of the foam, but in proportion to the number of sides of the latter. The coefficients of Eq. (48) are polynomials of degree 1, adding up to a constant, and the population equation is asymptotically integrable. But Flyvbjerg did not ascribe the universality of the distribution $P(s)$ to the asymptotic integrability of the equation, as argued here. Flyvbjerg's global mean-field approximation is mathematically identical to the "topological gas" [$\sigma=1/6$, no correlation between neighbors, $A(k,s)=sk/6$], which is only a limit, inaccessible experimentally or through simulations [15,21,37].

In Sec. VII, we discussed models for cellular structures evolving by division and disappearance. Our results in Table V confirm the asymptotic integrability of the population equations, and the universal nature of asymptotic decay of $P(s)$. The population equation has either only one physically acceptable solution whose tail decays algebraically or two physically acceptable solutions, one exponentially decaying and one algebraically decaying. The second and fourth cases in Table V show two algebraically decaying solutions, but as stated in Sec. VII, there are indications (but no rigorous proof) that $\bar{\kappa}_5$ and $\bar{\kappa}_8$ are not physically acceptable. This awaits confirmation by simulations.

Some features of our results deserve attention. (i) The algebraic decay of $P(s)$ is not specific to models with cell-selection algorithm S_1. (ii) It is possible to have population equations that *are* first-order, instead of asymptotically integrable to a first-order equation; for example, foams evolving by cell division under the kernel Γ^{A}_{t} with $t \leqslant 4$, and cell-selection algorithm S_1 or S_2. (iii) With a specific choice of parameters, an asymptotically integrable equation can become integrable; for example, foams evolving by cell division under the kernel $\Gamma^{B}_{s_{\min}}$ and cell-selection algorithm S_1, with $q(s)=\eta_0-1=0$. (iv) Our results show that the asymptotic behavior of $P(s)$ is slightly sensitive to a modification in the division kernel. For example, variations of the set $\{b_i\}$ in Γ^{A}_{t}, variation of $s_{\min}$ in $\Gamma^{B}_{s_{\min}}$ or $\Gamma^{C}_{s_{\min}}$, and switch from the uniform kernel to the nearly uniform kernel, modify the values of z and κ. Thus, in addition to $P(6)$ and $\mu_3 = \Sigma_{s=3} P(s)(s-6)^3$ proposed in [19], the asymptotic behavior of $P(s)$ is symptomatic of the dynamics of the cellular system. (v) If $\Sigma P(k)P(d|k) < \Sigma P(k)P(m|k)$, the division process dominates and the number of cells in the system increases. The number of cells decreases if the disappearance process dominates. In the basal layer of the epidermis, it is vital, not only that a stationary distribution is maintained, but also that the total number of cells remains within upper and lower bounds. This requires a balance between the rates of cell division and cell disappearance, $\Sigma P(k)P(m|k) = \Sigma P(k)P(d|k)$ as Eq. (9) implies. The examples of Table V can be balanced accordingly by an appropriate choice of parameters. The number of cells fluctuates, but is kept within bounds [19,26].

Our asymptotic analysis of population equation as a linear difference equation cannot be applied to one important case, the symmetric division kernel where the mother cell divides in half as much as possible. With a suitable choice of $s_{\min}$ in kernels $\Gamma^{B}_{s_{\min}}$ or $\Gamma^{C}_{s_{\min}}$, the symmetric division kernel can be approximated. For example with $s_{\min}=5$ and kernel $\Gamma^{B}_{s_{\min}}$, three-, four-, and five-sided cells do not divide, six-sided cells divide into the pair of daughters (5,5), seven-sided cells into the pair (5,6), eight-sided cells into the pairs (5,7), (6,6), nine-sided cells into the pairs (5,8), (6,7), etc. However, (nearly) uniform kernels are not expected to produce all the details of the distribution $P(s)$. Rivier *et al.* [16] reproduced experimental data on the cucumber [12] with a complicated kernel favoring symmetric division, and found that the kernel $\Gamma^{C}_{s_{\min}}$ with $s_{\min}=4$ did not reproduce the observed narrow distribution, peaked at $s=6$. This required solving the integrodifference population equation (17) directly [17], or numerical simulations [19,26]. To gain a deeper understanding of epithelial tissues, we aim to extend our analytic approach to the symmetric division kernel.

IX. CONCLUSIONS

Local, topological correlations between cells determine the stationary state of foams. In a local mean-field approximation, which accounts for nearest-neighbor correlations in statistical equilibrium, the population equations (linear difference equations of order $u \geqslant 2$) are asymptotically integrable. The population equations have *one* unique solution, which decays as $P(s) \sim Cs^{-\kappa}z^s$ for large values of s. The characteristics equation for z (33), an algebraic equation of degree u has only one physical root (<1). There is always one root ($=1$) associated with asymptotic integrability. The other $(u-2)$ roots are all unphysical.

The general solution of the linear difference equation of order u is $\Sigma_{i=1}^{u} F_i P^i(s)$, where the F_i and $P^i(s)$ are real coefficients and eigensolutions, respectively. To have a unique, physical, and exponentially decaying solution $P^1(s)$, the other $(u-1)$ solutions are either (i) incompatible with the physical constraints of a non-negative normalized distribution of cells, six-sided on average (and thus $F_{i\geqslant 2}=0$), or (ii) they constitute a negligible, algebraically decaying background noise ($F_{i\geqslant 2} \ll 1$), associated with asymptotic integrability. In some cases, the population equation has only one physically acceptable solution, whose tail decays algebraically as $P^1(s) \sim s^{-\kappa}(z=1)$. The other solutions are then incompatible with the physical constraints.

The asymptotic integrability of the equation, which imposes a unique and universal solution, is absent in the global mean-field approximation. Thus, local environment and statistical equilibrium mold the stationary distribution of cell shapes, as had been surmised in the epidermis of mammals [17,18], and confirmed in simulations [20,26].

The universal distribution $P(s) \sim Cs^{-\kappa}z^s$ for large values of s, imposed by the asymptotic integrability, is indeed the Boltzmann distribution resulting from maximum entropy inference [1,15]. The entropy is $S=-\Sigma P(s)\ln[P(s)/Q(s)]$, where $Q(s)$ is the *a priori* probability of having a s-sided cell. One maximizes the entropy restricted by the independent constraints [(11) and (12)] to get $P(s)=Q(s)\exp(-\beta s)$. $Q(s)$ includes the normalization factor and β is a Lagrange multiplier enforcing the constraint. Direct comparison shows that $z=\exp(-\beta)$ and $Q(s)$ behave as $s^{-\kappa}$ for large values of s. Foams at the “infinite temperature” ($\beta=0$) are then described by an algebraically decaying distribution.

The foams discussed here are purely topological and combinatorial, without any control of the energy carried by interfaces. In order to impose a given average energy and control disorder, the variance μ_2 of the distribution $P(s)$ should be added to the constraints (12). As a consequence, $P(s)$ would acquire a Gaussian tail for very large s, with an additional equation of state, Lemaître’ law, relating μ_2 to $1-P(6)$ [38,39].

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APPENDIX A: POLYNOMIALS $q(s)$ FOR THE VARIOUS POPULATION EQUATIONS OF SEC. III.

For the kernel Γ_t^A, the population equation is given by Eq. (18). The polynomial $q(s)$ (30) is the sum of the coefficients

$$\sum_{u=6}^{u=t} b_u P(m|s) + [a_2(s) + b_5 P(m|s)] + [a_1(s) + a_1'(s) + b_4 P(m|s)] + [a_0(s) + a_0'(s) + b_3 P(m|s)] = -\nu - P(d|s), \tag{A1}$$

where

$$\nu = \sum_k P(k)P(m|k) - \sum_k P(k)P(d|k). \tag{A2}$$

For the kernel $\Gamma_{s_{\min}}^B$, the population equation is given by Eqs. (20) and (21). The polynomial $q(s)$ (30) is the sum of the coefficients

$$a''_{s_{\min}-3}(s) + a''_3(s) + a''_2(s) + a''_1(s) + a''_0(s) = \nu - P(m|s) + P(d|s). \tag{A3}$$

Likewise, for the kernel $\Gamma_{s_{\min}}^C$, the population equation is given by Eqs. (22) and (23). The polynomial $q(s)$ (30) is the sum of the coefficients

$$\begin{aligned} &a''_{s_{\min}-2}(s) + a''_{s_{\min}-3}(s) + a''_3(s) + a''_2(s) + a''_1(s) + a''_0(s) \\ &= 2a_2(s) - 2a_0(s) - 2a_0'(s) + 2(s-s_{\min})[\nu + P(d|s)] \\ &\quad + [s(2-\delta_{s_{\min},6} - 2\delta_{s_{\min},5} - 2\delta_{s_{\min},4} - 2\delta_{s_{\min},3}) \\ &\quad - (s-2s_{\min}+3)\theta(s_{\min}-5) + 8\delta_{s_{\min},4} + 4\delta_{s_{\min},3} \\ &\quad - (s-2s_{\min}+5)\theta(s_{\min}-6) - 2s_{\min} + 7\delta_{s_{\min},6} \\ &\quad + 12\delta_{s_{\min},5}]P(m|s). \end{aligned} \tag{A4}$$

APPENDIX B: COEFFICIENTS OF THE POLYNOMIALS $a_1'(s)$, $a_0'(s)$, $a_2(s)$, $a_1(s)$ AND $a_0(s)$

For the division algorithm S_1 and the uniform kernel $\Gamma_{s_{\min}}^B$, the coefficients introduced in Eq. (38) are

$$\begin{aligned} A'_{1,1} &= -\tfrac{1}{3}[\eta_0 - (1-6\sigma)(\eta_0 - 6\eta_{-1})], \\ A'_{1,0} &= -2(1-6\sigma)(\eta_0 - 6\eta_{-1}) - \eta_0 - \theta(s-2s_{\min}+5), \\ A'_{0,1} &= \tfrac{1}{3}[\eta_0 - (1-6\sigma)(\eta_0 - 6\eta_{-1})], \\ A'_{0,0} &= 2(1-6\sigma)(\eta_0 - 6\eta_{-1}), \end{aligned} \tag{B1}$$

where

$$\begin{aligned} \eta_{-1} &= \sum_{2s_{\min}-4} \frac{P(k)}{k} < \frac{1}{6}, \\ \eta_0 &= \sum_{2s_{\min}-4} P(k) \leqslant 1, \\ \eta_1 &= \sum_{2s_{\min}-4} P(k)(k-6) \geqslant 0 \end{aligned} \tag{B2}$$

are non-negative structural parameters. Moreover, $\eta_0 - 6\eta_{-1} > 0$, and $6\eta_0 + \eta_1 \leqslant 6$. Equalities hold for $s_{\min} \leqslant 4$. Recall that $(1-6\sigma) \geqslant 0$. It follows that $A'_{1,1} > -(1/3)\eta_0$.

For algorithm S_2 and the uniform kernel $\Gamma_{s_{\min}}^B$, the coefficients are

$$\begin{aligned} A'_{1,1} &= -\tfrac{1}{18}[(6\eta_0 + \eta_1) - (1-6\sigma)\eta_1] - \tfrac{1}{6}\theta(s-2s_{\min}+5), \\ A'_{1,0} &= -\tfrac{1}{3}(1-6\sigma)\eta_1 - \tfrac{1}{6}(6\eta_0 + \eta_1), \\ A'_{0,1} &= \tfrac{1}{18}[(6\eta_0 + \eta_1) - (1-6\sigma)\eta_1], \\ A'_{0,0} &= \tfrac{1}{3}(1-6\sigma)\eta_1. \end{aligned} \tag{B3}$$

Asymptotically in s, the step function in (B1) and (B3) is equal to 1. Thus, $A'_{1,1} > -1/2$.

It is useful to express all the coefficients in terms of $6A'_{0,1}=(1/3)[(6\eta_0+\eta_1)-(1-6\sigma)\eta_1]$. Thus,

$$-6A'_{1,1}=6A'_{0,1}+1,$$

$$A'_{1,0}=6A'_{0,1}-\tfrac{1}{2}(6\eta_0+\eta_1),$$

$$A'_{0,0}=6A'_{0,1}-\tfrac{1}{3}(6\eta_0+\eta_1). \tag{B4}$$

For $s_{\min}\leqslant 4$, $\eta_0=1$, $\eta_1=0$, $-6A'_{1,1}=3$, $A'_{1,0}=-1$, $6A'_{0,1}=2$, and $A'_{0,0}=0$.

For the nearly uniform kernel $\Gamma^{C}_{s_{\min}}$, all the relations above are valid if one modifies the lower limit of the summations in Eq. (B2) to $2s_{\min}-2$, and the argument of the step function in Eqs. (B1) and (B3) to $s-2s_{\min}+3$. The inequalities in (B2) are strict.

For cell disappearance, the population equation is given in Eq. (48), with the coefficients in Eq. (51). They are

$$A_{2,1}=\gamma_3(1-3\sigma)+\frac{\gamma_4}{2}(1-2\sigma)+\frac{2\gamma_5}{5}(1-\sigma),$$

$$A_{2,0}=-(1-6\sigma)\left(3\gamma_3+\gamma_4+\frac{2\gamma_5}{5}\right),$$

$$A_{1,1}=-\left[\gamma_3(1-3\sigma)+\frac{\gamma_4}{2}(1-2\sigma)+\frac{3\gamma_5}{5}(1-\sigma)\right],$$

$$A_{1,0}=(1-6\sigma)\left(3\gamma_3+\gamma_4+\frac{3\gamma_5}{5}\right)+\gamma_3+\gamma_4+\gamma_5,$$

$$A_{0,1}=\frac{\gamma_5}{5}(1-\sigma),$$

$$A_{0,0}=-(1-6\sigma)\frac{\gamma_5}{5}. \tag{B5}$$

The polynomials appearing in Tables I and IV can be grouped in a simpler notation

$$-a'_0(s)-a_0(s)=E_0(s+s_0),$$

$$-a'_1(s)+a'_0(s)-a_1(s)+a_0(s)=E_1(s+s_1),$$

$$a'_1(s)+a_1(s)-a_2(s)=E_2(s+s_2),$$

$$a_2(s)=(-E_0-E_1-E_2)(s+s_3), \tag{B6}$$

where

$$E_0=-A'_{0,1}-A_{0,1},$$

$$s_0=\frac{-A'_{0,0}-A_{0,0}}{-A'_{0,1}-A_{0,1}},$$

$$E_1=-A'_{1,1}+A'_{0,1}-A_{1,1}+A_{0,1},$$

$$s_1=\frac{-A'_{1,0}+A'_{0,0}-A_{1,0}+A_{0,0}}{-A'_{1,1}+A'_{0,1}-A_{1,1}+A_{0,1}},$$

$$E_2=A'_{1,1}+A_{1,1}-A_{2,1},$$

$$s_2=\frac{A'_{1,0}+A_{1,0}-A_{2,0}}{A'_{1,1}+A_{1,1}-A_{2,1}},$$

$$s_3=\frac{A_{2,0}}{A_{2,1}}. \tag{B7}$$

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