

Active Spaghetti: Collective Organization in CyanobacteriaMixon K. Faluweki^{1,2}, Jan Cammann³, Marco G. Mazza^{3,4,*} and Lucas Goehring^{1,†}¹*School of Science and Technology, Nottingham Trent University, Nottingham NG11 8NS, United Kingdom*²*Malawi Institute of Technology, Malawi University of Science and Technology, S150 Road, Thyolo 310105, Malawi*³*Interdisciplinary Centre for Mathematical Modelling and Department of Mathematical Sciences, Loughborough University, Loughborough, Leicestershire LE11 3TU, United Kingdom*⁴*Max Planck Institute for Dynamics and Self-Organization (MPIDS), Am Faßberg 17, 37077 Göttingen, Germany*

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Filamentous cyanobacteria can show fascinating examples of nonequilibrium self-organization, which, however, are not well understood from a physical perspective. We investigate the motility and collective organization of colonies of these simple multicellular lifeforms. As their area density increases, linear chains of cells gliding on a substrate show a transition from an isotropic distribution to bundles of filaments arranged in a reticulate pattern. Based on our experimental observations of individual behavior and pairwise interactions, we introduce a nonreciprocal model accounting for the filaments' large aspect ratio, fluctuations in curvature, motility, and nematic interactions. This minimal model of active filaments recapitulates the observations, and rationalizes the appearance of a characteristic length scale in the system, based on the Péclet number of the cyanobacteria filaments.

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Collective organization is a defining feature of living matter. It has received vivid attention [1–8] for its applications in the life sciences [9,10], and as an example of how nonequilibrium forces can drive flows of matter and energy [11,12]. The first seminal studies of active matter treated the motion of pointlike particles [1,2,4]. Nonreciprocal interactions between even such simple objects, with a single orientation, allow access to states impossible in equilibrium systems [7], and rodlike motile particles extend the range of such emergent behavior [8]. Long, flexible filaments, whose orientation varies along their length, offer opportunities to study different classes of active matter [13–24]. With many possible interaction points per filament, correlations can spread over long distances, opening the door to novel behavior [21,25–30] whose complete understanding remains lacking.

An important example of active matter, cyanobacteria are among the Earth's most abundant and ancient organisms [31,32]. They evolved the original mechanisms of photosynthesis and perform nearly all nitrogen fixation in marine environments [33,34]. Filamentous cyanobacteria also straddle the boundary between single and multicellular organisms; they grow into long chains of cells through “filamentation,” perhaps the oldest form of multicellularity [35,36]. Many species live on surfaces, including

stromatolites [35,37], and move by gliding [38–40]. Colonies can develop complex structures of closely bundled filaments, such as reticulate patterns (Fig. 1), over hours or days [28,41,42]. Cell density is thought to be a trigger of such pattern formation [28,41], but this link has never been conclusively demonstrated. Found widely, including in Archean fossils [32], Antarctic lakes [43], and hot springs [44], these patterns can template more complex 3D morphogenesis [41,43]. They also provide rigidity [41] and enable collective mechanical responses, like rapid shape changes, to external cues [44,45].

Despite their importance to the development of complex life, and for, e.g., carbon-neutral biofuels [46], no general mechanism has been identified to rationalize the collective behavior of filamentous cyanobacteria. Here, we demonstrate that the emergent patterns of their colonies can be apprehended as the collective result of independently moving actors with simple interactions. Distinctive features of filamentous cyanobacteria, such as their large aspect ratio and the tendency of a filament to follow the trail laid down by its head, enable the accurate prediction of the critical density and emergent length scale associated with collective ordering.

We investigate *Oscillatoria lutea*, a typical strain of filamentous cyanobacteria, consisting of simple (non-branching, nonheterocystous) chains of cells. Cultivation and measurement methods are provided as Supplemental Material [47]. In our cultures, the filaments have well-defined widths $\sigma = 4.2 \pm 0.2 \mu\text{m}$ [52] and lengths $L = 1.5 \pm 0.5 \text{ mm}$. In all cases here, error ranges report standard deviations.

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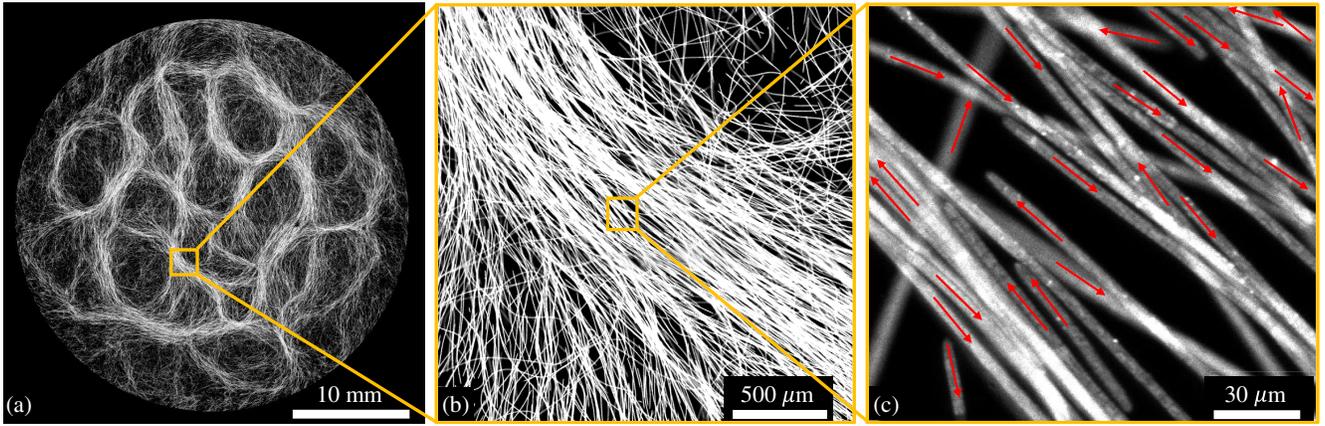


FIG. 1. A colony of *O. lutea* at density $\rho = 53 \text{ mm}^{-2}$ shows (a) a reticulate pattern, with (b) the local alignment of filaments within bundles, and (c) filament motion (arrows) that is predominantly parallel or antiparallel to neighbors.

In relative isolation, with area densities $\rho \simeq 1 \text{ mm}^{-2}$, filaments move at speeds $v_0 = 3.0 \pm 0.7 \text{ } \mu\text{m s}^{-1}$, as shown in Fig. 2(a). They glide along smoothly curving paths, which we characterized by tracking the orientation θ of the tangent to each filament’s midpoint through time (Supplemental Material, movie 1 [47]). The curvature $\kappa = d\theta/ds$ of the path $s(t)$ traced by any filament fluctuates slowly; the autocorrelation of κ is well described by an exponential relaxation with autocorrelation time $\tau = 470 \pm 290 \text{ s}$ (Fig. S1 [47]). Isolated filaments are biased towards clockwise motion, as in related species [38,39,52]. However, from densities as low as $\rho = 6$ and up to 49 mm^{-2} filaments adopt straighter shapes on average (Fig. S2 [47]). These distributions of curvatures peak around zero, with standard deviation $\delta\kappa = 340 \pm 40 \text{ m}^{-1}$.

To quantify the interactions between filaments, we observe cases where the head (leading end) of one filament approaches and intersects another filament. In most such pairwise interactions there is no direct effect, rather the filaments simply pass over or under each other without changing paths. However, about 4% of the time the incident filament is deflected, turning to travel alongside the other filament, which typically remains unperturbed. Aligning interactions only happen for small angles of incidence [Fig. 2(b)], and result in the two filaments moving parallel or antiparallel, depending on the angle of approach. After aligning, the filaments track each other for some distance, on average $430 \text{ } \mu\text{m}$, before one splits away. These interactions are fundamentally nonreciprocal [7], as the alignment response is path dependent [53].

The pairwise interactions promote the formation of bundles of aligned filaments, which can organize denser colonies into a higher-level architecture (Fig. 1). We confirmed the local nematic nature of this ordering by observing the motion of nearby filaments along one bundle, as in Fig. 1(c) and Supplemental Material, movie 2 [47]. All filaments in the bundle are well aligned, with approximately equal fractions [223 versus 282 filaments;

Fig. 2(c)] traveling in either direction. Between the bundles is a dilute “gas” of more randomly oriented filaments, similar in appearance to disordered colonies at lower densities.

Some of these behaviors, such as nematic alignment and the tendency to form dynamic bundles and networks, are reminiscent of those of microtubules at an interface [10,27,54]. However, there are also conspicuous differences. Critically, the average filament length is comparable to other characteristic lengths of this system, such as the filament’s radius of curvature, or the emergent pattern lengthscale. Hence, there is no *a priori* clear separation of scales, and we will show that the elongated nature of the cyanobacteria filaments affects the nature of their collective self-organization.

A benefit of this perspective is that it leads directly to a relatively simple model that can be informed in all its parameter choices by experimental observations. We treat the cyanobacteria as motile one-dimensional chains of pointlike beads [Fig. 2(d)], as befits their large aspect ratio, $L/\sigma > 100$. For simplicity, all chains have length $L = 1.5 \text{ mm}$, and representative disorder is introduced via their motion. Their speeds are constant in time, but drawn from a normal distribution with average $v_0 = 3 \text{ } \mu\text{m s}^{-1}$ and standard deviation $0.7 \text{ } \mu\text{m s}^{-1}$, matching experimental values [Fig. 2(a)]. The position $\mathbf{r}_{i,\alpha}$ of bead α of chain i follows the track laid out by its head, so that $\mathbf{r}_{i,\alpha}(t) = \mathbf{r}_{i,\alpha-1}(t - \Delta t)$. At each time step, of duration Δt , the end bead is removed from the tail of each chain, and a new bead is added at its head, displaced by distance $v_i \Delta t$ at angle θ_i (Fig. S4). Similar models have been applied to isolated filaments [23] and filaments on lattices [55]. Although this system has some similarities to active polymers [14,16–18,56], those lack a unique curvature autocorrelation time, as each polymer segment fluctuates independently; in contrast, the fluctuations and curvature of our chains are solely determined by their heads.

Motivated by models of active nematic particles used to simulate microtubules [27,57], *C. elegans* [58] and

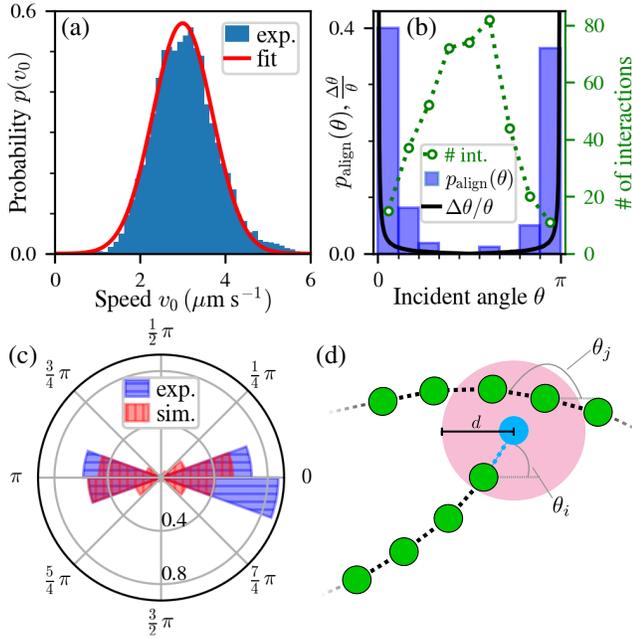


FIG. 2. Filament behavior. (a) The distribution of experimentally observed gliding speeds (blue) is well fit by a Gaussian (red, used for simulations). (b) Histogram showing how the alignment probability (left axis, blue bars) and interaction frequency (right axis, green circles) depend on incidence angle θ . The data are experimental; see Supplemental Material [47], Sec. II—Interacting filaments, for more details. In the model, an incident chain is deflected on average by the relative angle $\Delta\theta/\theta$ (black line). (c) In bundles, the directions of motion have a nematic distribution: a polar histogram compares experimental (blue) and simulated (red) cases. (d) Schematic of modeled interaction: when a chain’s head is within distance d of another chain, it experiences an aligning effect.

Pseudanabaena sp. [59], we now introduce a model of interacting active chains, appropriate to the behavior of filamentous cyanobacteria. Here, the orientation θ_i and angular velocity ω_i of the head of each chain i evolves by a modified Ornstein-Uhlenbeck process

$$\frac{d\omega_i}{dt} = -\frac{1}{\tau}[\omega_i - J\mathcal{F}(\theta_i)] + \sqrt{2D_\omega}\xi_i(t), \quad (1)$$

$$\frac{d\theta_i}{dt} = \omega_i - J\mathcal{F}(\theta_i), \quad (2)$$

where τ is the curvature autocorrelation time, J is an interaction strength, D_ω is a diffusion coefficient, and $\xi_i(t)$ introduces Gaussian white noise with zero mean and unit variance. D_ω is not directly accessible experimentally, but is linked to other parameters. Without any filament-filament interactions, Eq. (1) produces a normal distribution of angular velocities with zero mean and variance $\langle\omega^2\rangle = D_\omega\tau$. For chains with speed v_0 this translates into a curvature distribution with standard deviation $\delta\kappa = \sqrt{\langle\omega^2\rangle}/v_0$. Hence, $D_\omega = (v_0\delta\kappa)^2/\tau$. Finally, the

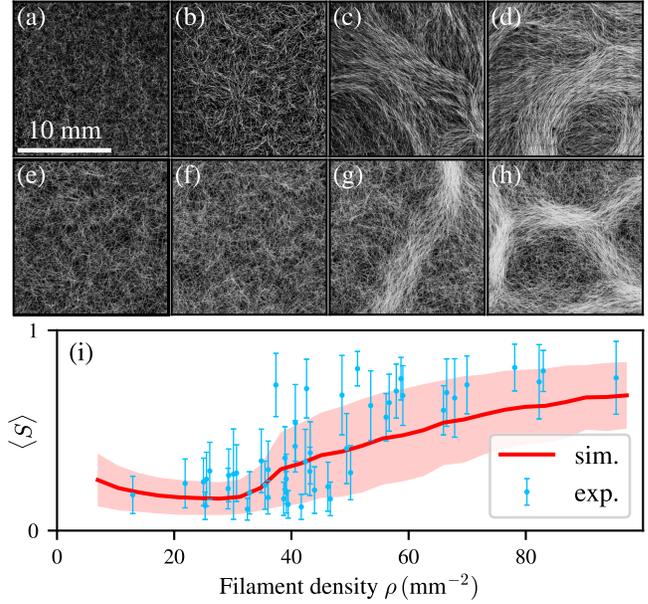


FIG. 3. Collective behavior and order-disorder transition. Panels (a)–(d) show micrographs of colonies at densities $\rho = 25, 31, 42,$ and 59 mm^{-2} , respectively. Panels (e)–(h) show snapshots of simulations at comparable densities of $\rho = 24, 31, 41,$ and 59 mm^{-2} . To avoid boundary effects, the simulated domains had sides $4.5\times$ larger than shown; panels are cropped to match the micrograph size. (i) Order parameter $\langle S \rangle$, averaged over 1 mm^2 blocks covering the experimental (blue) or simulated (red) domain; see Supplemental Material, Fig. S3 [47] for more details. Error bars and shading give the standard deviation of $\langle S \rangle$ over the blocks. At low ρ the filaments are randomly aligned, but locally nematic bundles and a reticulated structure emerge above $\rho \sim 40 \text{ mm}^{-2}$.

interactions are modeled by $\mathcal{F}(\theta_i) = (1/N_{ij}) \times \sum_{j \sim i} (\partial/\partial\theta_i) U(\theta_i, \theta_j)$, using a nematic Lebwohl–Lasher potential, $U = -\cos[2(\theta_i - \theta_j)]$, averaged over the N_{ij} chains within an interaction range d of the head of chain i , where θ_j is the orientation of the nearest bead on chain j (see Fig. 2(d)).

The model parameters were matched to experimental values of relatively isolated cyanobacteria, and fine-tuned based on the collective behavior at higher densities. Unless otherwise stated, we set $\tau = 480 \text{ s}$, $\delta\kappa = 200 \text{ m}^{-1}$ (giving $D_\omega = 7.5 \times 10^{-10} \text{ s}^{-3}$) and $d = 5 \text{ }\mu\text{m}$, close to the observed values of 470 s , 340 m^{-1} and the filament diameter of $4.2 \text{ }\mu\text{m}$, respectively. The interaction strength, $J = 0.006 \text{ s}^{-1}$, was chosen by considering filaments meeting at an angle θ . On average, the effects of interactions are comparable if the incident filament is either deflected by a relative angle $\Delta\theta/\theta$, or by the whole angle θ with probability $p_{\text{align}}(\theta)$. As shown in Fig. 2(b), in this sense J gives a similar average response to the observed interactions.

Experimentally, colonies of cyanobacteria filaments are disordered at low density, but show emergent patterns at

higher densities, Figs. 3(a)–3(d). The simulated chains order in a similar way, Figs. 3(e)–3(h), with reticulated structures appearing at higher ρ . Once formed, these structures remain relatively static, and the emergence of the ordered state in the model is demonstrated in the Supplemental Material, movie 3 [47]. We quantify local order in the steady-state by the 2D nematic order parameter [60–63]. For this, each experimental or simulated system is divided up into blocks of size $l = 1$ mm. At this scale the filament density is relatively homogeneous, but the blocks are large enough to have good statistics. The local order parameter $S = \langle \cos(2\hat{\theta}) \rangle$ is measured for filament orientations $\hat{\theta}$ taken with respect to the local nematic director (see Supplemental Material [47]). We then calculate $\langle S \rangle$ as a block average, which can quantify the emergence of local order, even in a globally heterogeneous system [62,64].

Both experiments and simulations show low nematic order at low densities. At higher ρ , the appearance of collective structures is captured by a sharp increase in $\langle S \rangle$, as shown in Fig. 3(i). Experimentally, the transition from a disordered state, with $\langle S \rangle \simeq 0.2$, to an ordered state of $\langle S \rangle \simeq 0.7$ is seen at a critical density of $\rho = 40\text{--}50 \text{ mm}^{-2}$. Simulations show a similar response, and demonstrate that

density inhomogeneities are correlated with the nematic ordering (Fig. S6 [47]). In no case is there any clear laning of filaments [see Figs. 1(c), 2(c)], in contrast to stiff active rods [8,65]. Varying the model parameters somewhat does not change the qualitative nature of the ordering transition, but does affect the critical value of ρ . This quantifies prior speculation of a density-driven ordering transition [28,41], and enables predictions.

For a gas of weakly interacting filaments, can we predict when interactions will become important enough to lead to collective behavior? For simplicity, consider filaments of density ρ and speed v_0 . Filaments interact when they first cross, at some local tangent angle θ anywhere along a length L . Averaging over all configurations, filaments thus present a mean cross-sectional length $\bar{L} = \langle L \sin \theta \rangle = 2L/\pi$ to each other. As one filament advances, it then encounters others on average at frequency $f = \bar{L}\rho v_0 = 2L\rho v_0/\pi$. Experimentally, only a small fraction a of interactions cause alignment, so the rate of filament ordering scales as af . Aligned filaments can also split up, which we assume happens randomly at rate b . Under these representative assumptions, interactions should become important when the rates of filament alignment and breakup

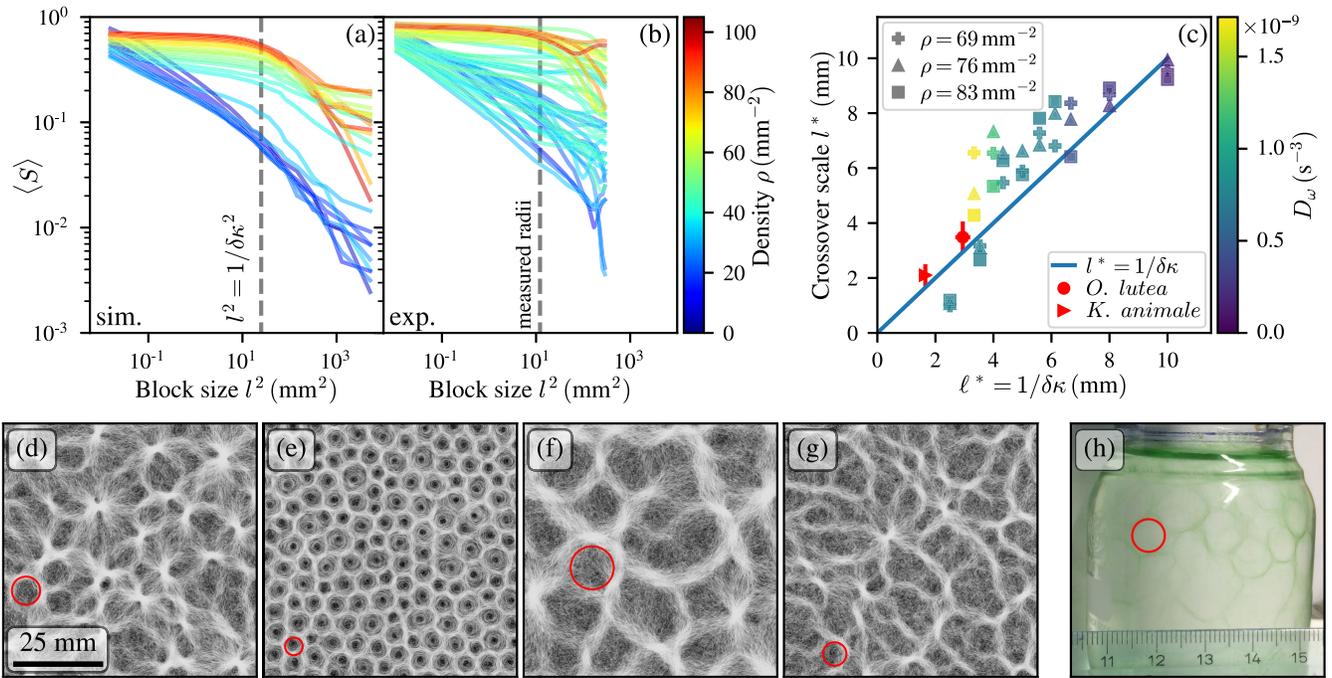


FIG. 4. Emergence of large-scale patterning. Finite-size scaling of the block-average order parameter $\langle S \rangle$ was investigated in (a) simulations and (b) experiments, by varying the block size l for the same data shown in Fig. 3. The power-law decay at low density indicates a disordered, isotropic state. The emergence of structures at high density is marked by a plateau lasting until l reaches the size of the emerging structures, which we term the crossover length scale l^* , after which a more rapid decay is observed. (c) For different model parameters l^* can be compared to the characteristic scale at which activity and fluctuations balance, ℓ^* . Snapshots show the resulting patterns for some simulations with (d): $\rho = 83 \text{ mm}^{-2}$, $D_\omega = 1.2 \times 10^{-9} \text{ s}^{-3}$, $\tau = 480 \text{ s}$. (e): $\rho = 76 \text{ mm}^{-2}$, $D_\omega = 7.5 \times 10^{-10} \text{ s}^{-3}$, $\tau = 1920 \text{ s}$. (f): $\rho = 83 \text{ mm}^{-2}$, $D_\omega = 7.5 \times 10^{-10} \text{ s}^{-3}$, $\tau = 320 \text{ s}$. (g): $\rho = 69 \text{ mm}^{-2}$, $D_\omega = 1.7 \times 10^{-9} \text{ s}^{-3}$, $\tau = 480 \text{ s}$, and (h) for filaments growing naturally under typical incubation conditions. The characteristic scales of the patterns are shown by red circles of radius ℓ^* . The scale bar in (d) also applies to (e)–(g).

balance, $af \simeq b$, and this cross-over condition defines a characteristic density $\rho_c = \pi b / (2aLv_0)$. Using experimental values, $a = 0.04$ and $b = 0.007 \text{ s}^{-1}$ (see Supplemental Material [47]), predicts $\rho_c \sim O(50) \text{ mm}^{-2}$. A disordered gas of filaments would be expected for densities $\rho \ll \rho_c$, with ordered states starting to appear at densities $\rho \approx \rho_c$. This prediction agrees well with the density of the order-disorder transition shown in Fig. 3.

We can rationalize the emergent length scale of the reticulate pattern as a signature of the balance struck between activity and fluctuations. By nondimensionalizing Eqs. (1) and (2), the ratio between the angular rate of change and diffusion defines a Péclet number, $Pe = v_0 / (\ell \sqrt{D_\omega \tau})$, where ℓ is some reference length. In the steady state, the nonequilibrium probability fluxes associated with active motion and curvature fluctuations will strike a balance, determining a specific length scale ℓ^* , corresponding to $Pe = 1$, as the smallest scale over which patterns can emerge. Using $D_\omega = v_0^2 \delta \kappa^2 / \tau$ we predict $\ell^* = v_0 (D_\omega \tau)^{-1/2} = 1 / \delta \kappa \approx 5 \text{ mm}$.

To substantiate this prediction, we perform a scaling analysis [61,62] of how the block-averaged order parameter $\langle S \rangle$ depends on the block size l . Figures 4(a) and 4(b) show the results for simulations and experiments. At low densities we see the power-law decay expected for a disordered system [62]. With increasing ρ , the experimental data are noisier, but potentially show structure developing more continuously than in the simulations. For $\rho > 40 \text{ mm}^{-2}$, $\langle S(l) \rangle$ develops two distinct regimes: a plateau at low l , reflecting the local order within bundles, and a faster decay at large l . From the position of the crossover between these responses we extract a length scale l^* [Fig. 4(c), methods in Supplemental Material [47]]. The drop in $\langle S \rangle$ above l^* is attributed to bundles with different orientations appearing within the same block.

In simulations, we explore the dependence of l^* on the model parameters, by varying τ , D_ω , and ρ . Some steady-state snapshots are shown in Figs. 4(d)–4(g). While the fine details of the patterns vary, l^* is always consistent with the radius of the emergent structures, with no significant dependence on ρ . As shown in Fig. 4(c), this feature size generally matches the characteristic length $\ell^* = 1 / \delta \kappa$ predicted via Pe . In *O. lutea*, the radius of the structures of dense colonies is $l^* = 3.5 \pm 0.6 \text{ mm}$, see Fig. 4(h), consistent with $\ell^* = 1 / \delta \kappa = 2.9 \text{ mm}$. Repeating measurements on the related species *Kamptonema animale* (see Supplemental Material [47]; $l^* = 2.1 \pm 0.4 \text{ mm}$, $\ell^* = 1.7 \pm 0.1 \text{ mm}$) further confirms this correspondence of length scales.

Summarizing, we studied colonies of filamentous cyanobacteria and their collective organization. The filament length is comparable to other scales in this problem (e.g., curvature) and can couple with them; one cannot assume

separation of scales. A nonequilibrium theoretical model accounting for fluctuations, large aspect ratios, motility, and nematic alignment reproduces the structure of reticulate patterns seen in the lab [41] and nature [42–44]. Our results thus point to a new class of active matter characterized by the following features: (i) Elongated filaments with position-dependent orientation and multiple interaction sites along each filament. (ii) Gliding motility induced by polar forces [24], unlike extensile or contractile microtubule-kinesin systems [54]; and (iii) path-tracking dynamics of the body following its head, subject to fluctuations and active motion, which are ultimately responsible for the reticulate pattern and length scale selection. Cyanobacteria are an important class of microbial life, and among the earliest form of multicellular organisms. We note that the parameters governing their self-organization identified here are evolutionarily selectable traits, influencing collective responses [44,45], mechanical properties [41], and 3D morphologies [41,43], and can inform the study of the fossil record [32,42].

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