Active crystals are highly ordered structures that emerge from the self-organization of motile objects, and have been widely studied in synthetic and bacterial active matter. Whether persistent crystalline order can emerge in groups of autonomously developing multicellular organisms is currently unknown. Here we show that swimming starfish embryos spontaneously assemble into chiral crystals that span thousands of spinning organisms and persist for tens of hours. Combining experiments, theory and simulations, we demonstrate that the formation, dynamics and dissolution of these living crystals are controlled by the hydrodynamic properties and the natural development of embryos. Remarkably, living chiral crystals exhibit self-sustained chiral oscillations as well as various unconventional deformation response behaviours recently predicted for odd elastic materials. Our results provide direct experimental evidence for how non-reciprocal interactions between autonomous multicellular components may facilitate non-equilibrium phases of chiral active matter.
AP axis, fluid moves radially inwards towards the embryo, reaches a maximum speed of 0.1–0.2 mm s⁻¹ lateral to the embryo surface (Fig. 2b), and eventually moves towards the bottom of the well (Fig. 1e). The radial in-flow generated by isolated embryos can be described as a Stokeslet flow (Fig. 2b, blue curve), a solution of the Stokes equation that describes the generic fluid flow around an external force (Supplementary Section 3.2.2). This force is related to the negative buoyancy of embryos. Indeed, the buoyant weight force $F_g = 1.7 \pm 0.4$ nN estimated from sedimentation speeds of immobilized embryos (Supplementary Section 1.4) is close to the Stokeslet strength $F_s = 2.6 \pm 0.3$ nN obtained from fitting radial in-plane flow fields (Fig. 1b and Supplementary Section 2.1.6).

The self-generated Stokeslet flow stabilizes the upright AP-axis orientation of embryos below the fluid surface (Supplementary Section 2.1.6). In addition, it induces an effective long-ranged hydrodynamic attraction between embryos, facilitating the assembly of clusters. Similar effects have been observed previously for bacterial and algal microswimmers near rigid surfaces. Once two embryos are close together, their intrinsic spinning motions lead to an additional exchange of hydrodynamic forces and torques (Fig. 2d). Similar to pairs of Volvox colonies near a rigid surface, nearby starfish embryos orbit each other, and their spinning frequency decreases compared with that of a freely spinning embryo. The excess cilia-generated torque from slower-rotating embryos manifests itself in systematic azimuthal flow contributions (Fig. 2c). To confirm our understanding of these hydrodynamic interactions, we complemented the Stokeslet flow of each embryo with additional contributions that reflect the effects of hydrodynamic interactions (Supplementary Section 3.2.2 and Supplementary Fig. 5). Flow fields

**Fig. 1** Developing starfish embryos self-organize into living chiral crystals. a, Time sequence of still images showing crystal assembly and dissolution (Supplementary Video 1). $t = 0$ h corresponds to the onset of clustering. Scale bar, 1 mm. b, Embryo morphology (left) and flow fields (right) change with developmental time. Shape scale bar, 100 μm. Flow-field scale bar, 200 μm. See Supplementary Information for uncropped morphology images. c, Embryos assembled in a crystal perform a global collective rotation (Supplementary Video 2). Scale bar, 2 mm. d, Spinning embryos (yellow arrows) in the crystal form a hexagonal lattice, containing fivefold (purple) and sevenfold (orange) defects. Scale bar, 0.5 mm. e, Schematic of embryo dynamics and fluid flows from side view (left) and top view (right). Crystals of spinning embryos form near the air–water interface. Self-generated hydrodynamic flows lead to an effective attraction between surface-bound embryos. Blue arrows depict fluid flows, dark red arrows indicate rotations of groups of embryos.
**Fig. 2** Single-embryo properties facilitate formation, rotations and dissolution of clusters. a. Top view of a single embryo. The arrows indicate the spinning direction and the dotted lines visualize the streamlines. 

b. Measured radial in-flow velocities (grey dots) are well described by Stokeslet flow below a free surface (blue line) (Supplementary Section 2.1.6). 

c. In-plane flows $v_{xy}$ surrounding bound pairs (experiment; Supplementary Video 3 and Supplementary Section 3.2.1) fitted by a solution of the Stokes equation (theory; Supplementary Section 3.2.2) taking into account hydrodynamic interactions (d). $e_x$ and $e_y$ denote radial and azimuthal basis vectors, respectively. d. Hydrodynamic interactions cause nearby embryos to orbit each other and reduce individual spinning frequencies. Yellow arrows indicate embryo rotations. Brown and red arrows depict effective forces and torques due to hydrodynamic interactions. 

e. Stokeslet-mediated attraction (a,b) and hydrodynamic near-field interactions of spinning particles (d) in an experimentally constrained minimal model (Supplementary Section 2.2) reproduce crystal formation as seen in experiments (Supplementary Video 4). f. Single-embryo spinning frequencies in small (<4 embryos) and large (about 100 embryos) clusters. The error bars denote standard deviations of measurements (experiment) and simulations (model) (Supplementary Section 2.2.3). g. Cluster-size dependent reduction of individual embryo’s spinning activity (Supplementary Section 2.2.2) leads to good agreement with measured whole-cluster rotation frequencies. 

h. Ellipticity of embryo shapes (right: top-view outlines in red; Supplementary Section 3.5) increases during development, leading to increasingly noisy steric interactions among spinning embryos in clusters. The grey band depicts standard deviation. i. Embryos at cluster boundaries exhibit progressively increasing AP-axis tilt angles (right: projection outlines in yellow; Supplementary Section 3.5). The dashed line indicates the critical angle at which bound states of late embryos become unstable. j. Stationary orientations and stability of microswimmers with hydrodynamic properties akin to developing embryos (Supplementary Sections 2.1.1–2.1.5). A decreasing critical angle (grey line) and the increase in effective noise (b,h,i) increase the rate of embryos leaving cluster boundary and fluid surface, ultimately driving clusters dissolution. Scale bars, 200 μm (a,e), 100 μm (d), 1 mm (e) and 500 μm (h).

fitted via this approach show good quantitative agreement with experimental measurements (Fig. 2c and Supplementary Fig. 6).

On the basis of these insights, we experimentally constrained a minimal model in which upright spinning embryos are represented by rigid disks interacting through hydrodynamic Stokeslet-mediated pairwise attraction, and through pairwise transverse force and torque exchanges (Supplementary Section 2.2). Using the Stokeslet strength determined from fits as in Fig. 2b, and a parameterization of transverse interactions based on rotation frequency measurements of bound pairs and triplets (Supplementary Section 2.2.2), this minimal model predicts the self-organized formation of rotating clusters similar to those seen in the experiments (Fig. 2e and Supplementary Video 4). Assuming a cluster-size dependent reduction of the individual embryo’s spinning activity to match whole-cluster rotation rates (Supplementary Section 2.2.2), the model quantitatively captures the experimentally observed reduction of individual embryo rotation frequencies in both small and large clusters (Fig. 2f), as well as their collective translation into global cluster rotation rates (Fig. 2g).

To investigate how developmental changes of embryos contribute to the dissolution of a cluster, we followed the time-dependent morphology and hydrodynamics of embryos. Body-shape anisotropies perpendicular to the AP axis increase almost fivefold over the course of experiments (Fig. 2h). Such anisotropies cause neighbouring embryos...
to ‘bump’ into each other when closely packed and spinning within a cluster, introducing an effective source of noise in the LCC lattice. The increased interaction noise is particularly visible at cluster boundaries, where embryos become increasingly tilted as their morphological development progresses (Fig. 2i), increasing their tendency to leave or to be scattered off a cluster. Using additional flow-field measurements of single embryos at different time points (Supplementary Section 3.3), we parameterized an orientational stability diagram that reveals a bistable nature of bound-state orientations (Fig. 2j and Supplementary Video 5). Measurements of ψ6 indicate increased variation in the distance between nearest neighbours. The error bars indicate the 95% confidence interval from a Gaussian fit. Inset: example pair distribution function, g(r), and Gaussian fit to the first peak (Supplementary Section 3.7). The increase of the dynamic Lindemann parameter with developmental time signals a progressive destabilization of the crystal lattice. The error bars indicate the standard deviation of 20 consecutive time points (Supplementary Section 3.8).

**Temporal evolution of crystalline order**

A striking feature of the LCCs is that they nucleate, grow and dissolve naturally as embryos progressively develop (Fig. 1a and Supplementary Video 1). To quantify the evolution of crystalline order, we calculated the local order parameter ψi(r) = |ri|e0i, where i is the imaginary number and r denotes embryo positions in the co-rotating frame of the cluster (Supplementary Sections 3.1 and 3.6). Measurements of ψi(r) determine the local phase ϕi representing the crystal orientation, as well as the magnitude of hexagonal order |ψi|6. Initially, small clusters merge together along different crystal axes, resulting in grain boundaries and broad distributions of |ψ|, and ϕi (Fig. 3a–d(i) and Supplementary Video 5). Within 5 h of crystal formation, LCCs undergo rapid internal restructuring, during which subdomains align. This results in large, nearly defect-free crystals with a high degree of hexagonal order ⟨|ψi|6⟩ = 0.9 and a narrow distribution of local bond orientation (Fig. 3a–d(ii),(iii)). This highly ordered state persists for several hours.

As development progresses, changes in morphology and surrounding flow fields (Figs. 1b and 2h) lead to a decreased crystalline order. Specifically, the probability density of |ψi|, spreads to smaller values (Fig. 3b,e, t > 20 h), quantitatively indicating a loss of orientational order. A similar spread is observed in the average phase angle ϕi, indicating the loss of a well defined, global crystal orientation (Fig. 3c, t > 20 h). After about 30 h, disorder dominates and the crystal dissolves over a period of 10 h (Fig. 3a–d(iv),(v)).
Furthermore, we identified a progressive loss of translational order before dissolution as quantified by the radial pair distribution function \( g(r) \) (inset in Fig. 3f and Supplementary Section 3.7). Specifically, the first peak width of \( g(r) \)—representing the variability of nearest-neighbour distances—was found to increase with development (Fig. 3f). Consequently, deviations from an ideal hexagonal lattice become more frequent and translational order is reduced as embryos develop.

To examine whether the evolution of orientational and translational order is also reflected in dynamic crystal properties, we determined the dynamic Lindemann parameter (Supplementary Section 3.8), which characterizes the strength of fluctuations in the crystal lattice. In the crystalline phase (5–25 h), the dynamic Lindemann parameter increases with time (Fig. 3g) and indicates a progressive destabilization of the crystal lattice, consistent with the observed loss of orientational (Fig. 3e) and translational order (Fig. 3f), and with the increased interaction noise due to changes in the embryo morphology (Fig. 2h, i). Large fluctuations of the dynamic Lindemann parameter at early and late times are due to the small crystal sizes and the highly dynamic nature of growing and dissolving clusters.

Taken together, the systematic decay of orientational, translational and dynamic order with developmental time shows how morphological changes at the single-embryo level (Figs. 1b and 2h) can autonomously drive LCCs through a dissolution transition reminiscent of solid–gas phase transitions.

**Odd elasticity and emergent chiral waves**

Starfish embryos are inherently chiral and spin about their AP axis in a left-handed manner (Figs. 1d and 2a). This chiral spinning motion leads to distance-dependent, transverse lubrication interactions between pairs of...
Strain waves in materials with finite odd elastic moduli can give rise to work and dissipation cycles\textsuperscript{7}. To quantify the lower bounds of the associated entropy production rates, we estimated the statistical irreversibility of strain cycles using recently developed frameworks of stochastic thermodynamics\textsuperscript{41,42}. By calculating the local phase-space currents in strain space (Supplementary Section 3.12), we constructed spatial maps of the local entropy production rates arising in the relevant strain component spaces (Fig. 4f, h and Supplementary Video 10). These maps reveal spatio-temporal variations of the entropy production rates, with higher rates appearing mostly in the vicinity of vacancy defects and boundary regions. Spatially integrated entropy production rates exhibit in both spaces temporal maxima during the period of most active wave propagation (Supplementary Fig. 15).

Discussion

Our combined experimental and theoretical results demonstrate how morphological changes in developing multicellular organisms can lead to the self-assembly and dissolution of living crystals with broken chiral symmetry. By observing starfish embryos over two days post gastrulation, we have identified hydrodynamic and morphological single-embryo properties that facilitate these self-organized processes. Over the course of several hours, thousands of embryos can come together to form a macroscopic non-equilibrium material that carries signatures of odd elasticity. Driven by the embryos’ inherent activity, these living crystal structures support self-sustained chiral waves that exemplify upward energy transport from the individual microscopic constituents to the macroscale. More broadly, such living chiral crystals can serve as a paradigmatic active-matter system to elucidate the principles of collective self-organization, non-equilibrium thermodynamics and exotic material properties that emerge from non-reciprocal interactions.

Online content

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Data availability
All data that support the plots within this paper and other findings of this study are available from the corresponding author upon reasonable request.

Code availability
The computational methods that support the plots within this paper are described in the Supplementary Information and the underlying code is available from the corresponding author upon reasonable request.

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Author contributions
N.F., J.D., T.H.T. and A.M. conceived the project. T.H.T. and A.M. are joint first authors. J.L. and Y.C. are joint second authors. T.H.T. designed and performed experiments and analysed data. A.M. developed the theory, performed simulations and analysed data. J.L. performed experiments and analysed data. Y.C. analysed data. H.H. performed experiments. P.J.F. performed experiments and analysed data. S.G. analysed data. N.F. and J.D. designed experiments and theory and supervised research. All authors discussed the results and co-wrote the paper.

Competing interests
The authors declare no competing interests.

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