Route to turbulence of bacterial suspensions under confinement

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with

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(UTokyo) → ~~Tokyo Tech~~ from Oct Institute of SCIENCE TOKYO
[experiment]

Sora Shiratani
(UTokyo)
[numerics]

Igor S. Aranson
(Penn State & UTokyo)
[theory]

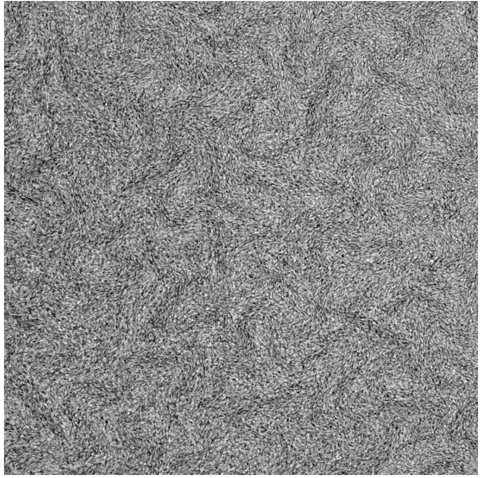
Nishiguchi et al., arXiv: 2407.05269

Funding
科研費 KAKENHI
INFO PHYS BIO
cmplx Flow
JST PRESTO (D.N.)
Active Matter c2c

x2 speed

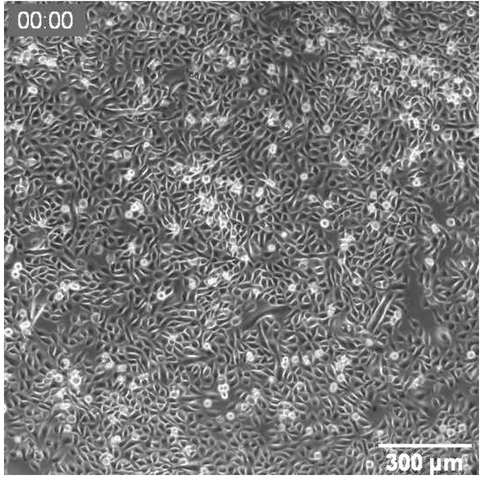
Collective motion is often chaotic

bacterial suspension



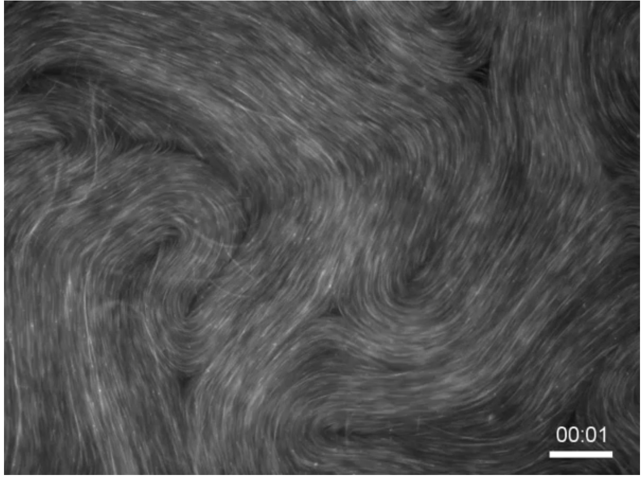
[Nishiguchi+, Nat Comm 2018]

epithelial cell sheet



[Blanch-Mercader+, PRL 2018]

reconstituted cytoskeletons



[Sanchez+, Nature 2012]

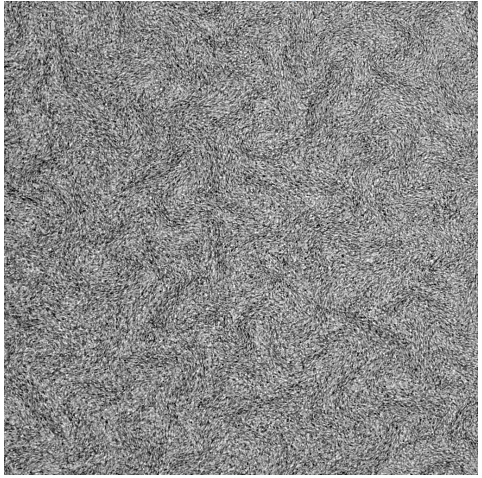
“active turbulence”

[review: Alert et al., Annu. Rev. Condens. Matter Phys. 13, 143 (2022)]

Vortices have a characteristic length scale.

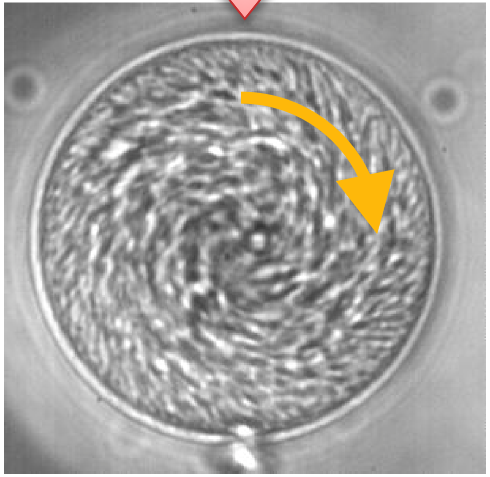
Active turbulence self-organizes by confinement

bacterial suspension



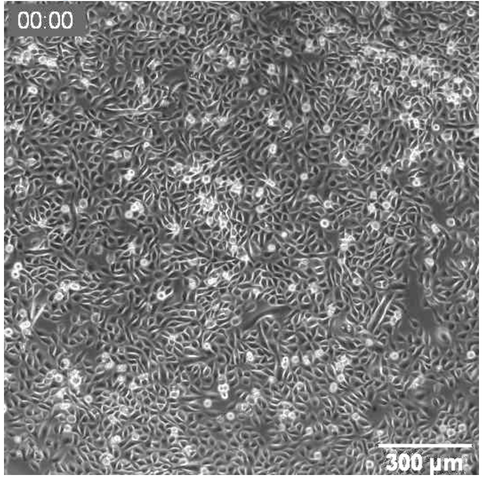
[Nishiguchi+, N Comm 2018]

confine



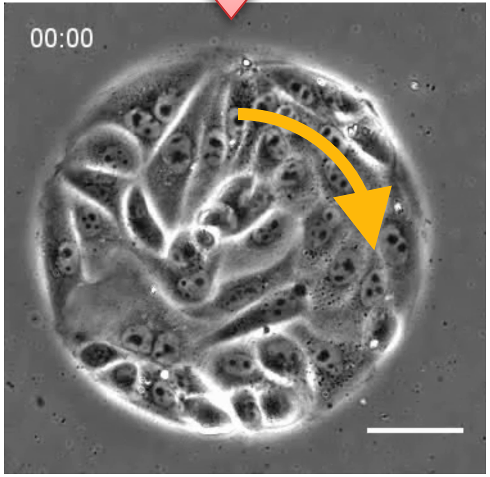
[Wioland+, PRL 2013]

epithelial cell sheet



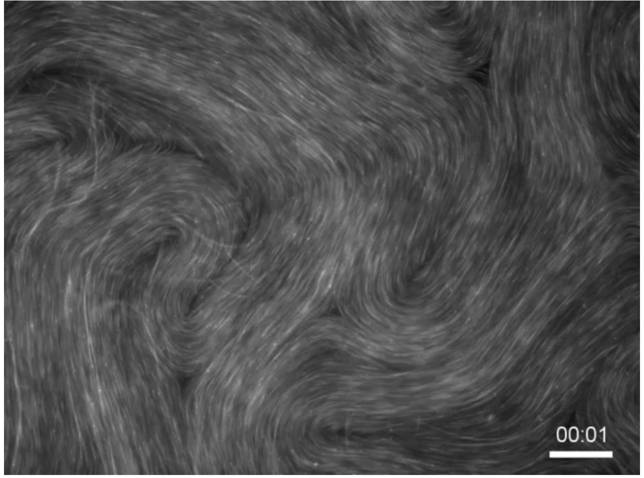
[Blanch-Merc er+, PRL 2018]

confine



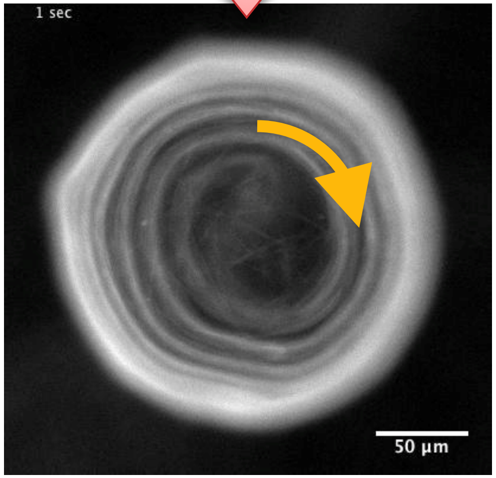
[Doxzen+, Integr. Biol. 2013]

reconstituted cytoskeletons



[Sanchez+, ture 2012]

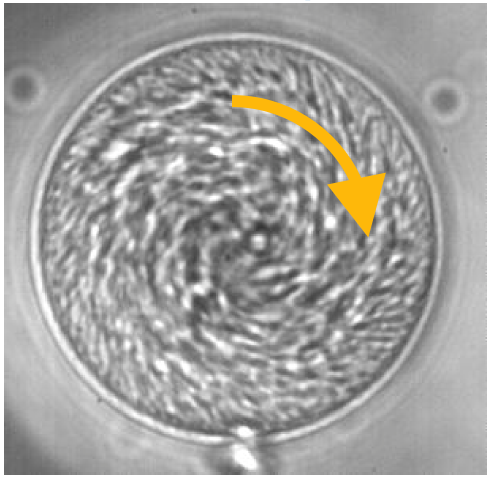
confine



[Opathalage+, PNAS 2019]

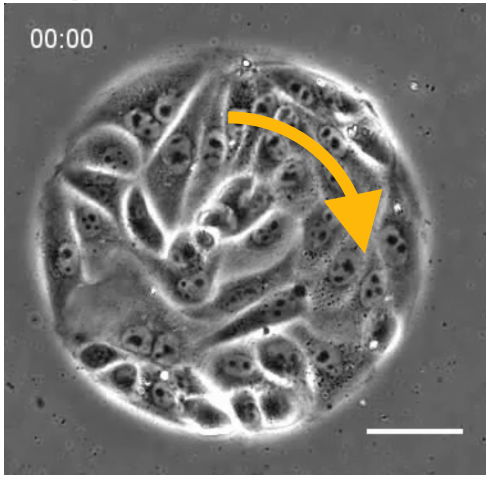
How does the vortex get destabilized?

bacterial suspension



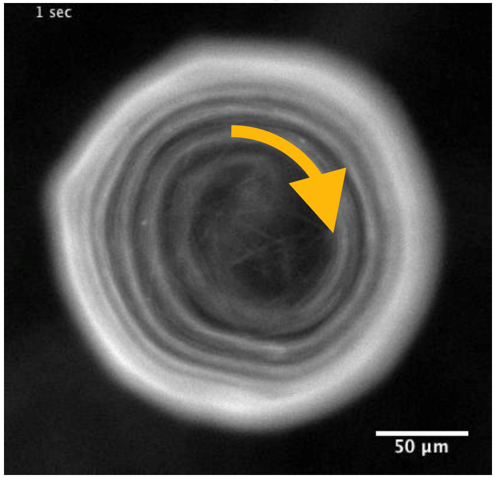
[Wioland+, PRL 2013]

epithelial cell sheet



[Doxzen+, Integr. Biol. 2013]

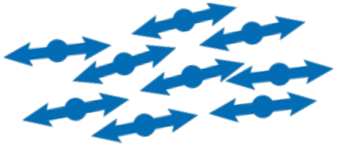
reconstituted cytoskeletons



[Opathalage+, PNAS 2019]

polar

nematic



What's the "route to turbulence" & underlying mechanism for this case?

Today's question

unbinding of ±1/2 defects destabilizes vortices, leading to active turbulence

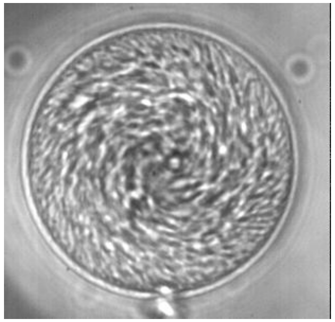
[Opathalage+, PNAS 116, 4788 (2019)]

Let’s change the degree of confinement!

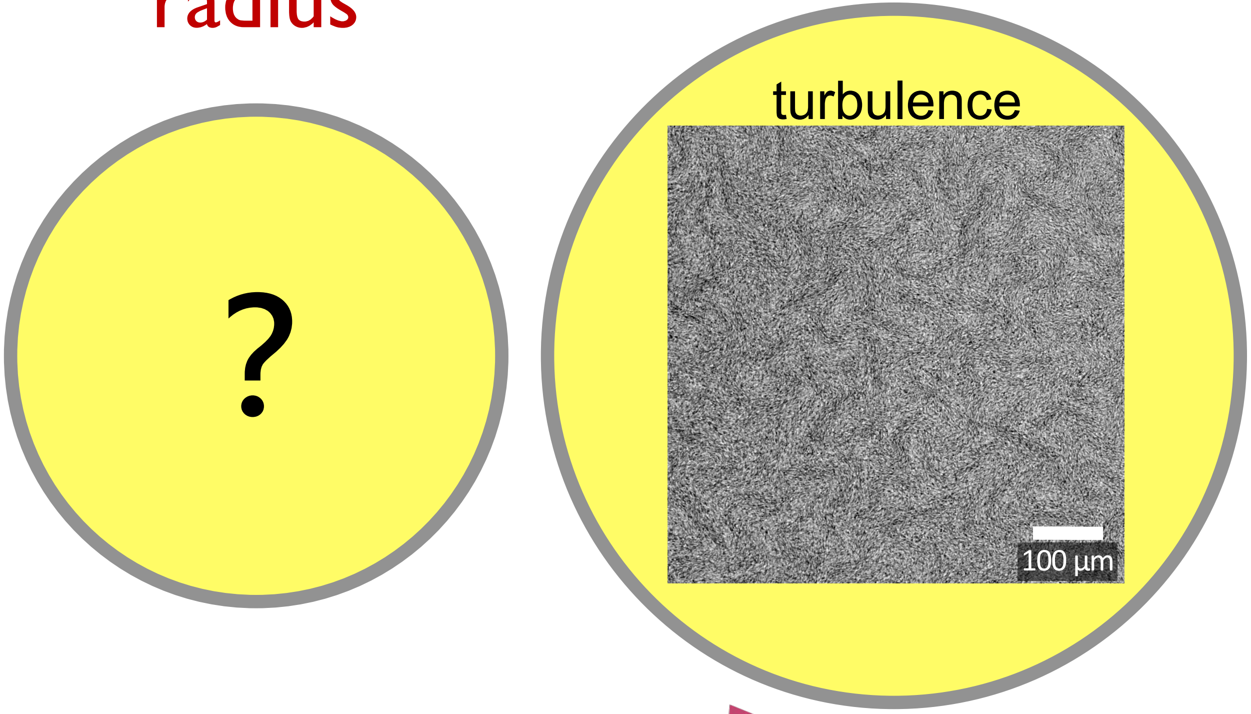
Consider varying radius of confining wells

radius

stable vortex



[Wioland+, PRL 2013]

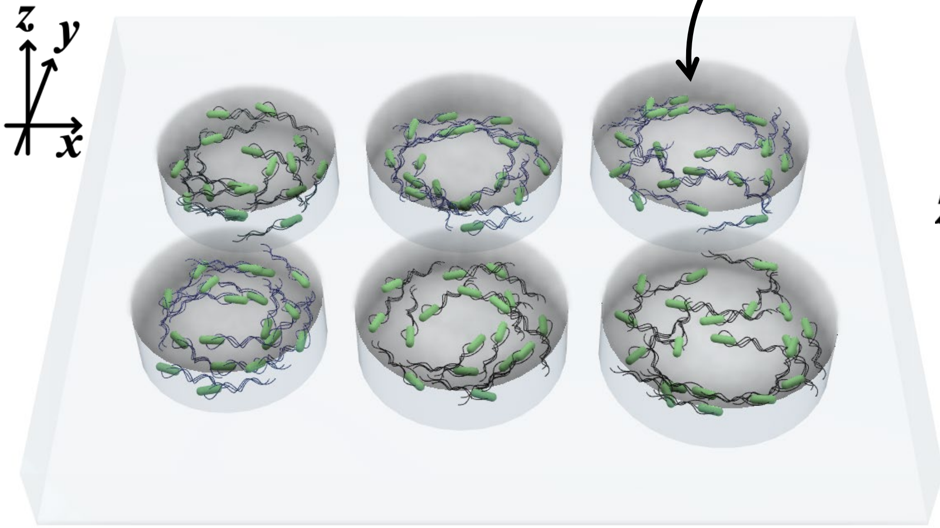


Route to active turbulence

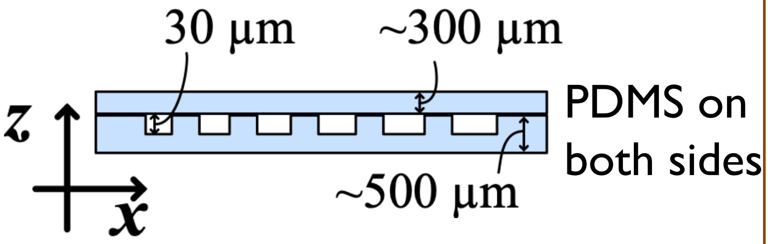
Experiment

Daiki Nishiguchi

Our setup



dense suspensions of *Bacillus subtilis*



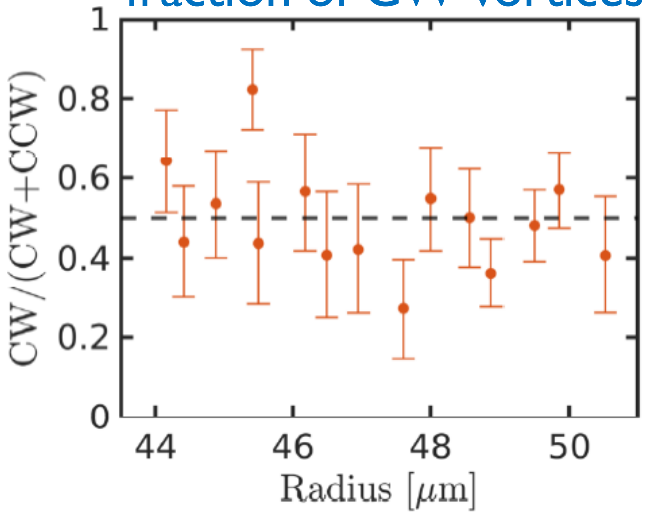
PDMS on both sides

well radius: 42.0-51.0 μm,
0.5 μm step

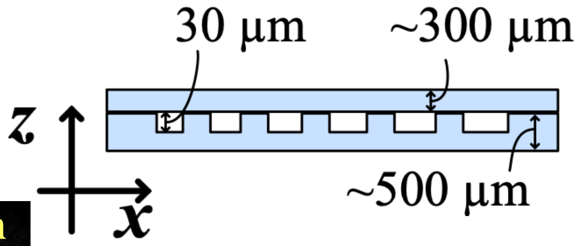
Key points

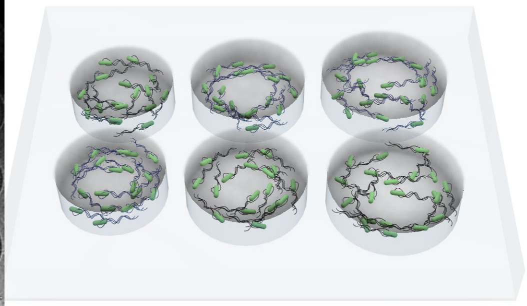
- Entirely covered by PDMS (high O_2 permeability)
  → Long observation (several minutes)
- Same solid surface on both sides
  → No chirality

fraction of CW vortices



Experiment





well radius: 42.0-51.0 µm,
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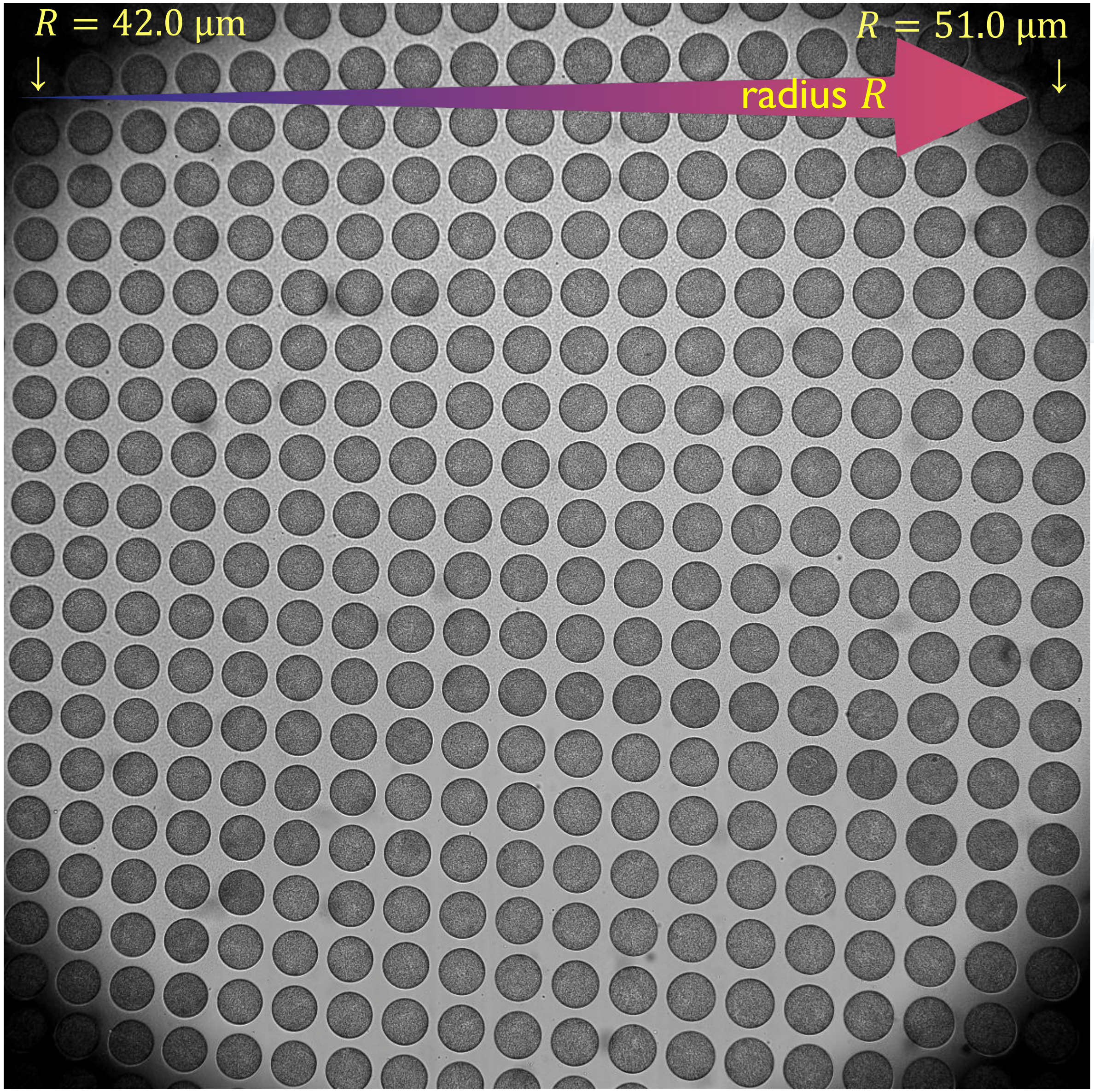


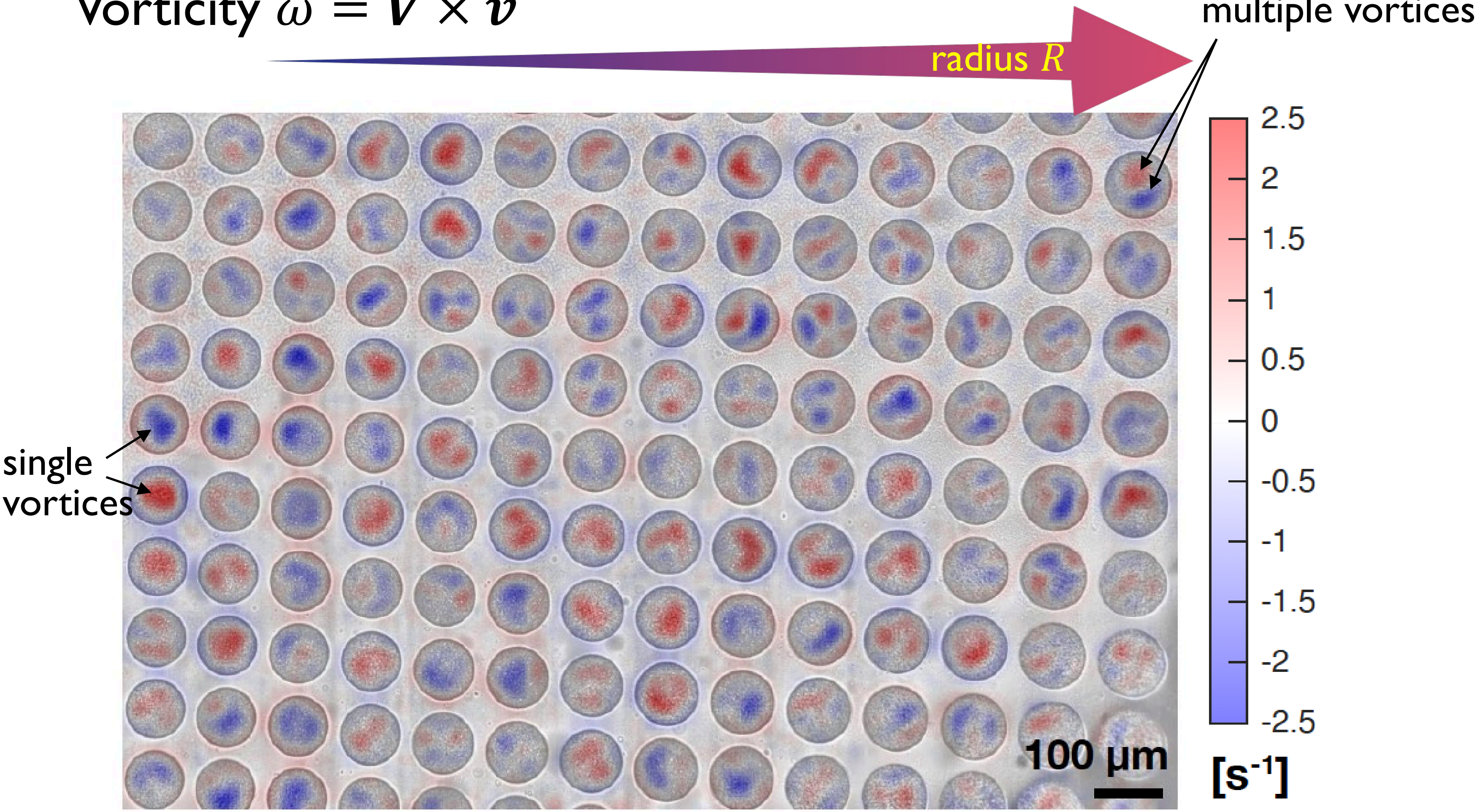
Key points

Simultaneous observation of numerous wells
➜ allowed us to capture transitions!

200 µm

Vortices get destabilized as radius increases

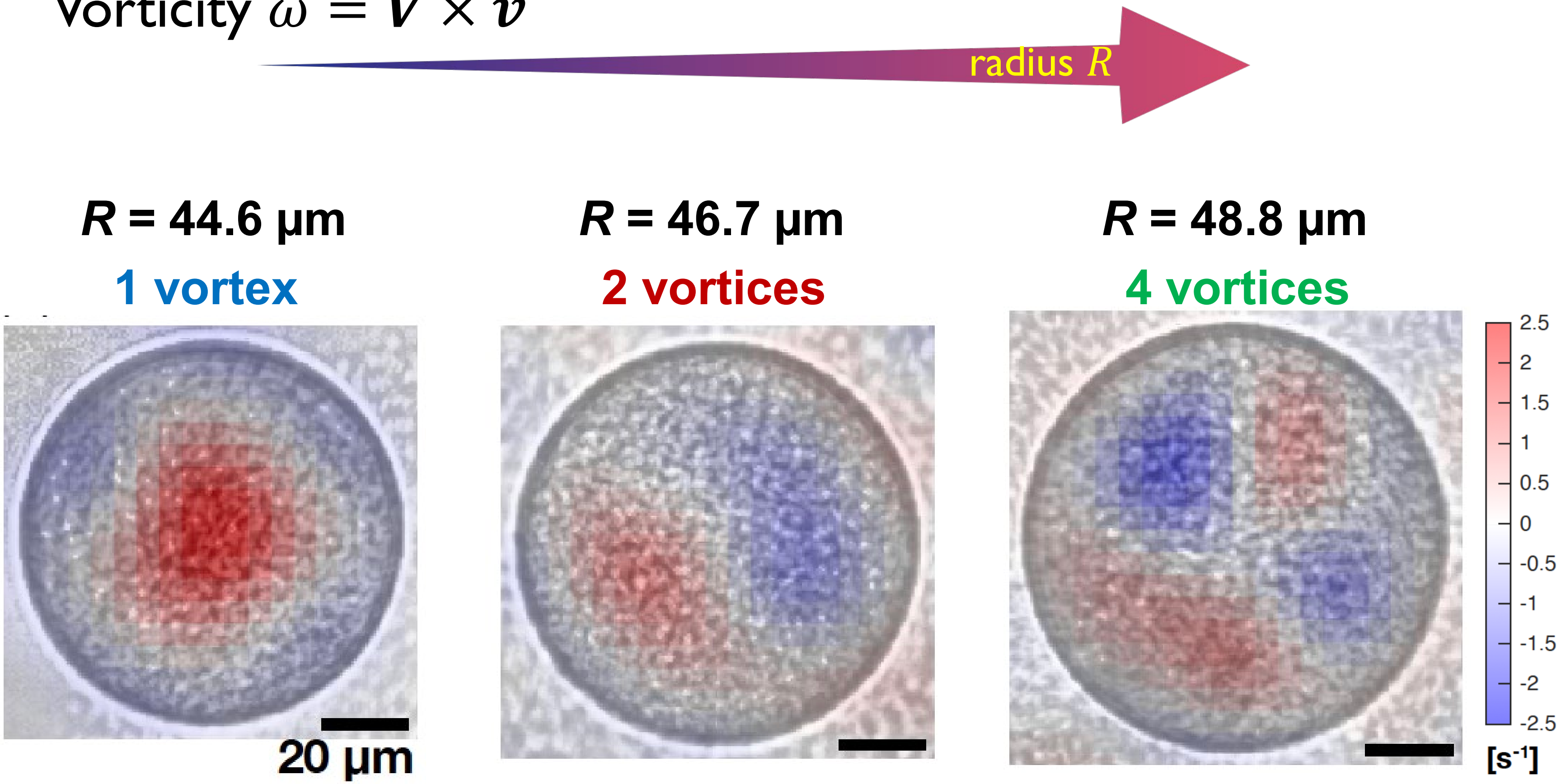
Vorticity $\omega = \boldsymbol{\nabla} \times \boldsymbol{v}$



Single vortex in small wells, multiple vortices in larger wells.

Vortices get destabilized as radius increases

Vorticity $\omega = \boldsymbol{\nabla} \times \boldsymbol{v}$



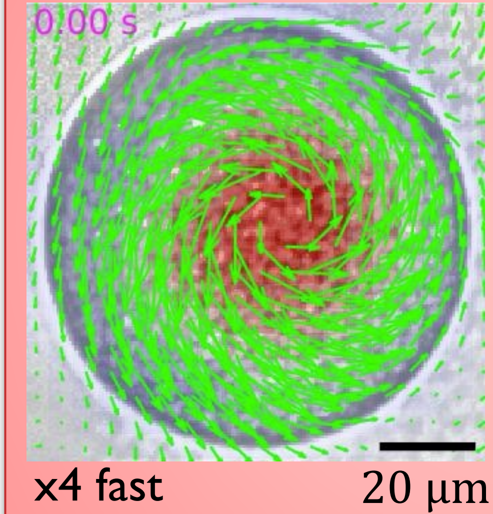
Single vortex in small wells, multiple vortices in larger wells.

Vortices get destabilized as radius increases

Vorticity $\omega = \boldsymbol{\nabla} \times \boldsymbol{v}$

R = 44.6 µm

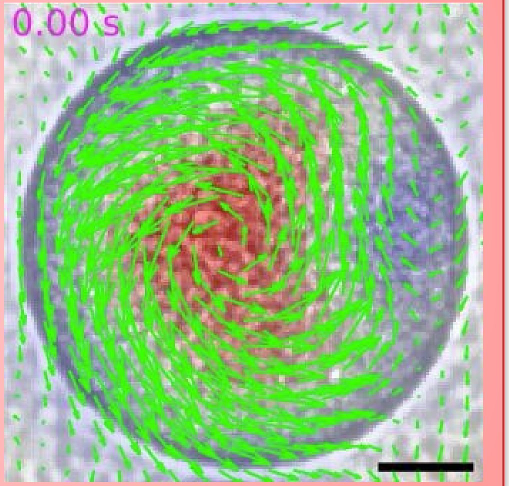
1 vortex



stable for long time

R = 46.7 µm

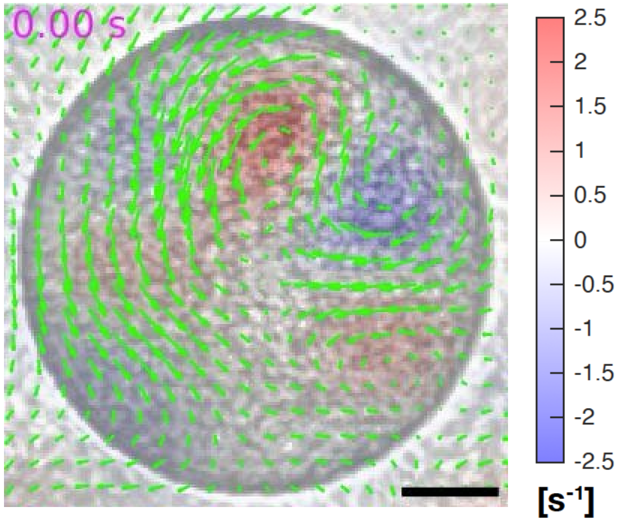
2 vortices



reversals

R = 48.8 µm

4 vortices



pulsations

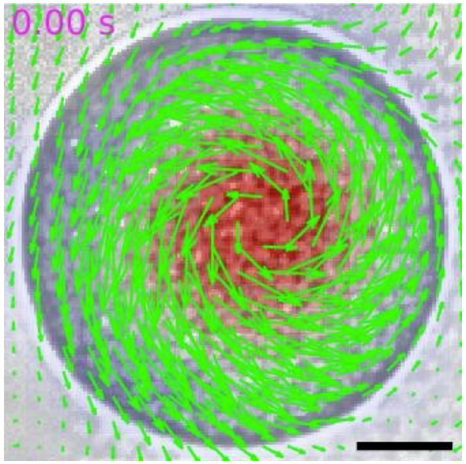
Let's focus on this transition!

Detecting the vortex reversals

Sign of vortex: “spin”

$$S_i(t) := \frac{\hat{\mathbf{z}} \cdot \sum_{\mathbf{r}\in\text{well}} (\mathbf{r}-\mathbf{r}_{\text{center}}) \times \mathbf{v}(\mathbf{r},t)}{\sum_{\mathbf{r}\in\text{well}} |\mathbf{r}-\mathbf{r}_{\text{center}}|}$$

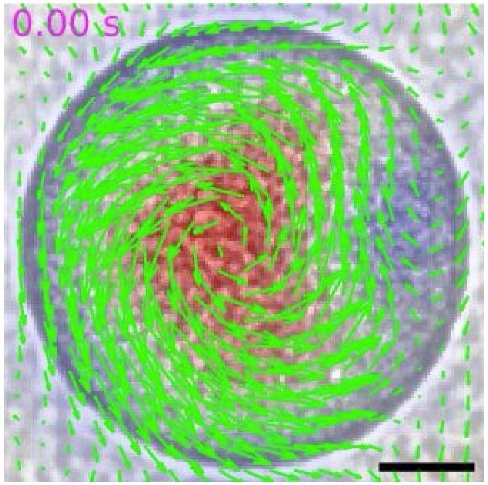
stable single vortex



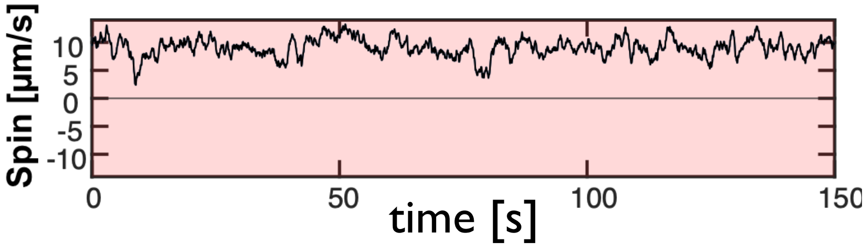
***R* = 44.6 μm**

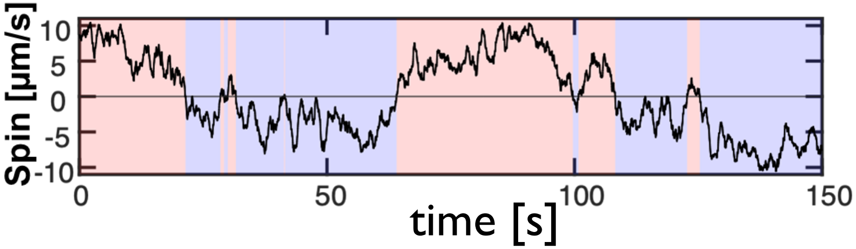
increasing radius

reversing vortex pair



***R* = 46.7 μm**

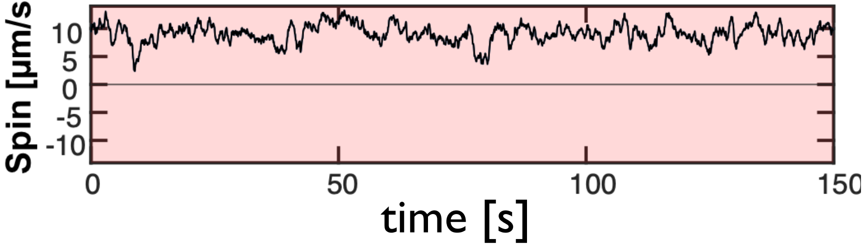




Detecting the vortex reversals

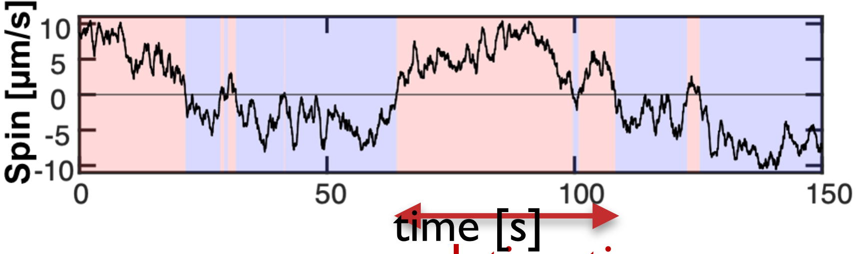
stable single vortex

***R* = 44.6 μm**



reversing vortex pair

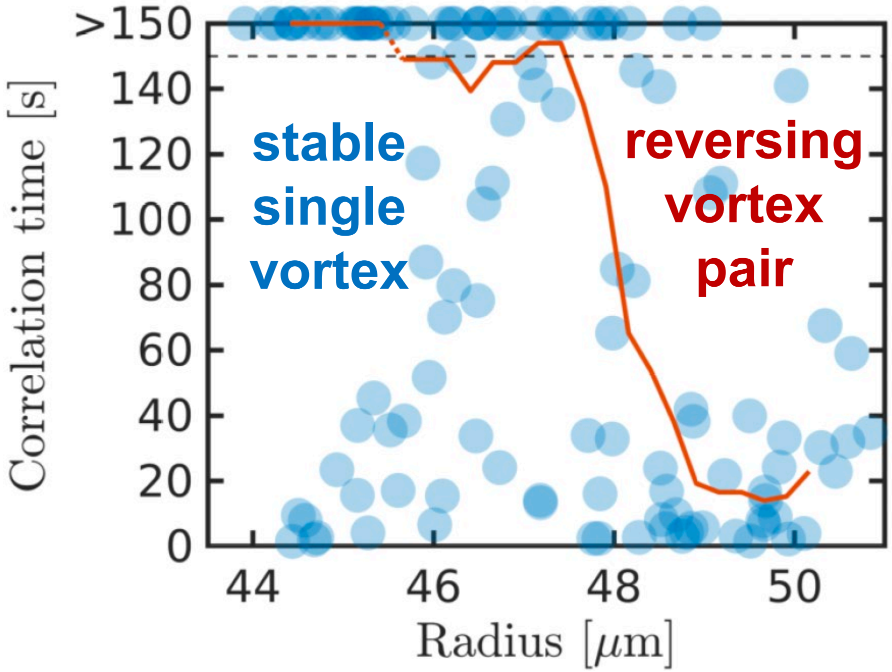
***R* = 46.7 μm**



correlation time

determined from $\overline{S_i(t)S_i(t+\tau)}$

correlation time vs radius



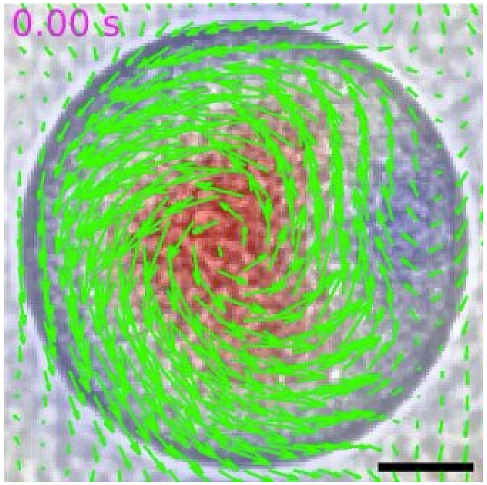
blue: each well

red: moving median

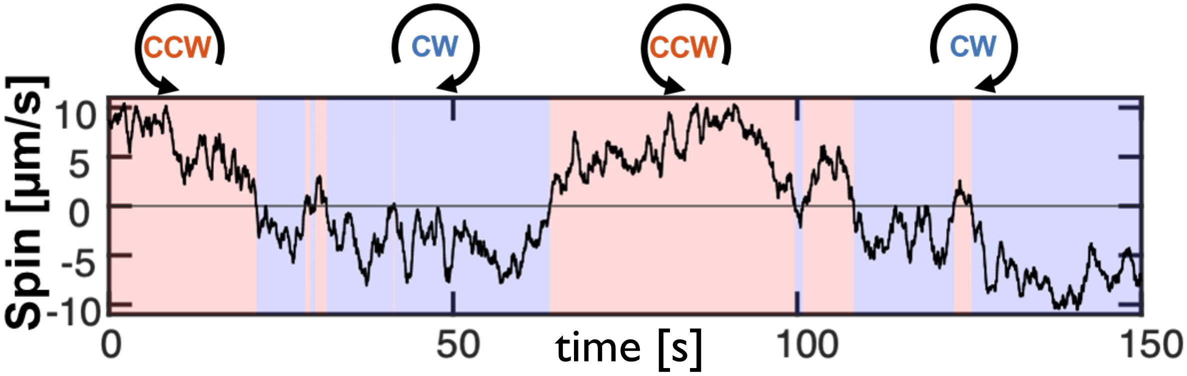
Transition is clearly detected

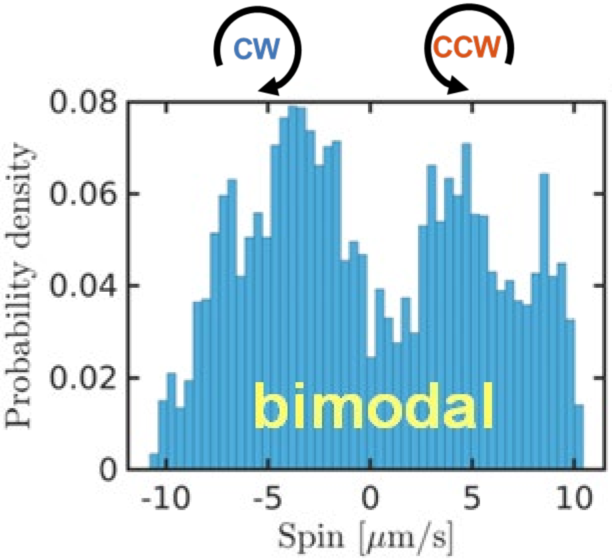
Vortex reversals: regular or irregular?

reversing vortex pair



***R* = 46.7 µm**





- Reversal looks rather regular & periodic...?
- Bimodal distribution of CW & CCW

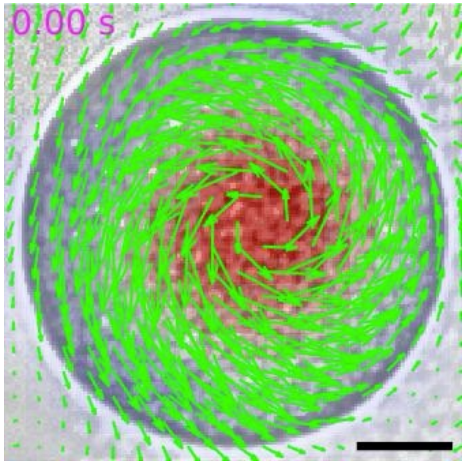
Vortex reversal = periodic (?) switching of CW/CCW states

periodicity will be justified later

What about the 4-vortex state?

R = 44.6 μm

1 vortex

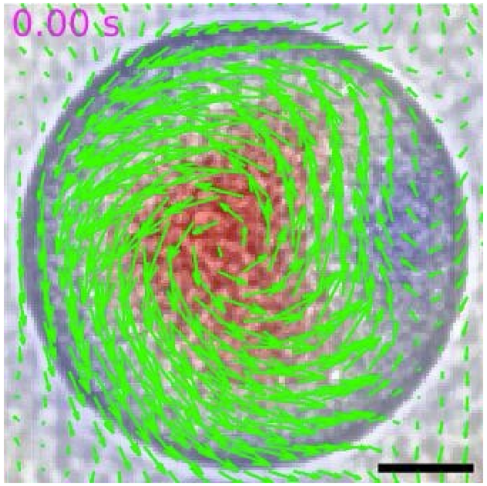


x4 fast 20 μm

stable for long time

R = 46.7 μm

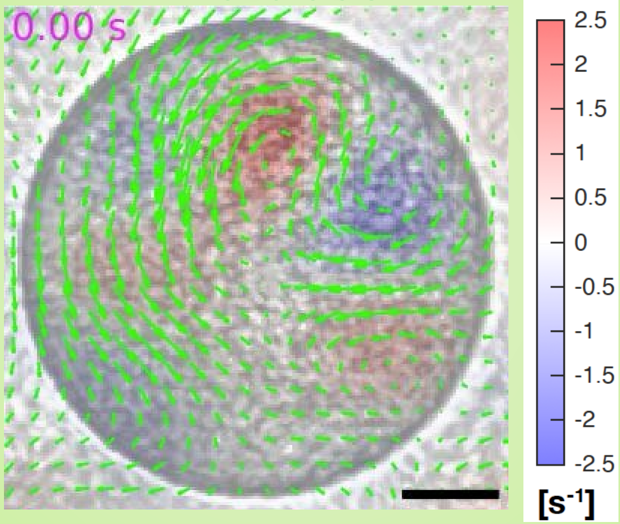
2 vortices



reversals

R = 48.8 μm

4 vortices



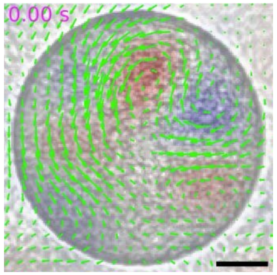
pulsations

Now let's characterize this!

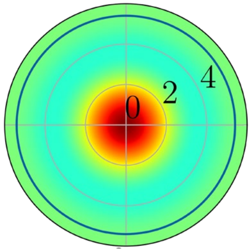
Multipole expansion of 4-vortex state

Decompose $\boldsymbol{v}(r,\theta)$ into angular Fourier modes: $\int d\theta e^{-in\theta}\boldsymbol{v}(r,\theta) + \mathrm{c.c.}$

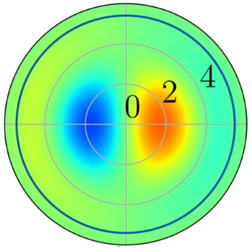
original **n=0** **n=1** **n=2**



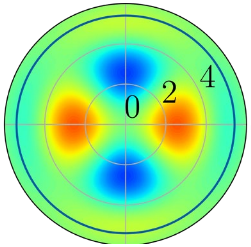
$=A_0(t)$



$+A_1(t)$



$+A_2(t)$



$+\cdots$

1-vortex mode **2-vortex mode** **4-vortex mode**

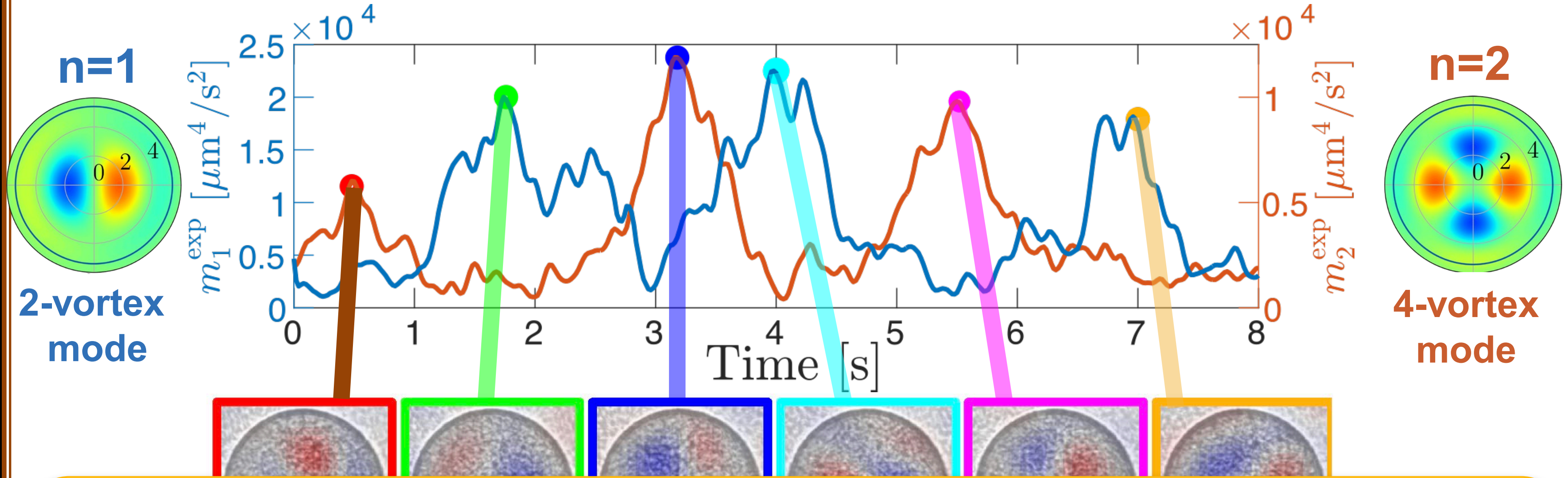
Calculate kinetic energy of each mode

$$m_n^{\mathrm{exp}}(t) = \int_0^R dr r \left| \frac{1}{2\pi} \int d\theta e^{-in\theta} \boldsymbol{v}(r,\theta;t) \right|^2$$

to evaluate its contribution

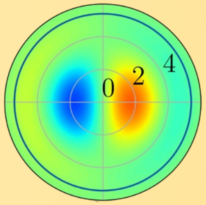
Multipole expansion of 4-vortex state

Kinetic energy of *n*th mode: $m_n^{\text{exp}} = \int_0^R dr r \left| \frac{1}{2\pi} \int d\theta e^{-in\theta} \boldsymbol{v}(r,\theta) \right|^2$



4-vortex state = anti-phase oscillation of

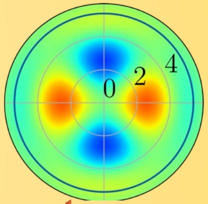
n=1



2-vortex mode

&

n=2



4-vortex mode

Summary so far: Route to turbulence (exp't)


radius R

R = 44.6 µm **1 vortex**

R = 46.7 µm **2 vortices**

R = 48.8 µm **4 vortices**

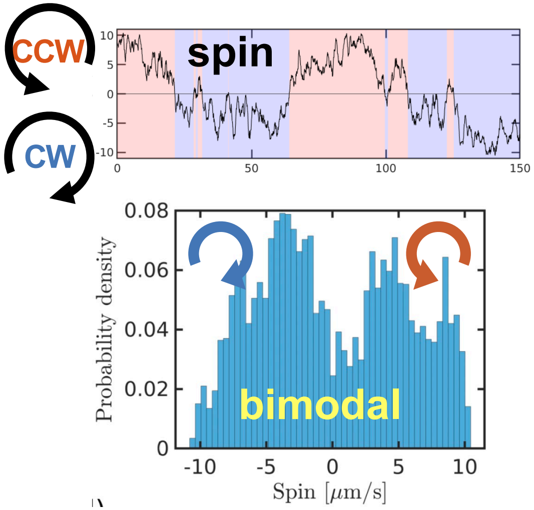
Can we understand these transitions theoretically?

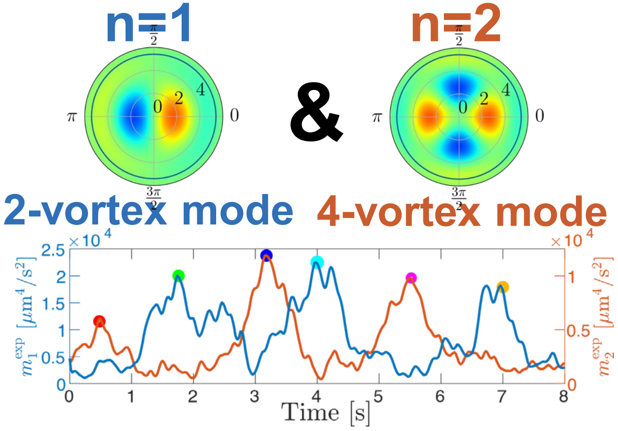
stable for long time

regular reversals

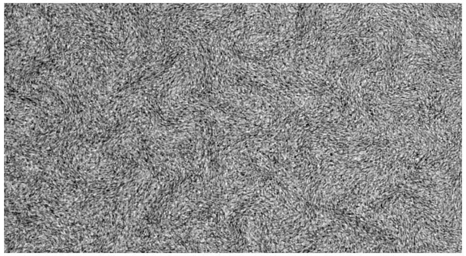
pulsations

Anti-phase oscillation





Model for bacterial turbulence?



Hydro descriptions of bacterial turbulence w/o confinement.

Two phenomenological models in the literature.

Toner-Tu-Swift-Hohenberg (TTSH) equation

Wensink+, PNAS 2012
Dunkel+, New J Phys 2013

$$\begin{cases} \nabla\cdot\boldsymbol{v}=0 \\ \partial_t\boldsymbol{v}+\underbrace{\lambda(\boldsymbol{v}\cdot\nabla)\boldsymbol{v}}_{\text{active stress}}=-\nabla p+\underbrace{a\boldsymbol{v}-b|\boldsymbol{v}|^2\boldsymbol{v}}_{\text{propulsion}}\underbrace{-\Gamma_0\nabla^2\boldsymbol{v}-\Gamma_2\nabla^4\boldsymbol{v}}_{\text{vortex formation}} \end{cases}$$

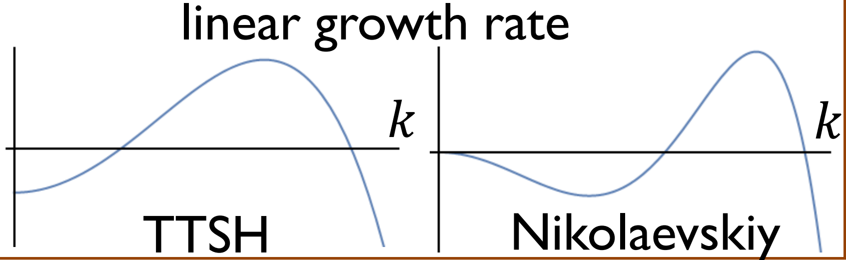
$\uparrow \nabla\cdot(\boldsymbol{v}\boldsymbol{v})$

Nikolaevskiy equation

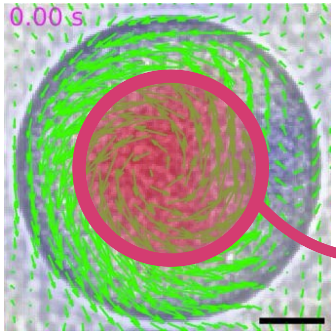
Beresnev & Nikolaevskiy, Physica D 1993
Słomka & Dunkel, PNAS 2017

$$\begin{cases} \nabla\cdot\boldsymbol{v}=0 \\ \partial_t\boldsymbol{v}+(\boldsymbol{v}\cdot\nabla)\boldsymbol{v}=-\nabla p+\Gamma_0\nabla^2\boldsymbol{v}\underbrace{+\Gamma_2\nabla^4\boldsymbol{v}}_{\text{energy input}}+\Gamma_4\nabla^6\boldsymbol{v} \end{cases}$$

In both models, vortices have a characteristic size.



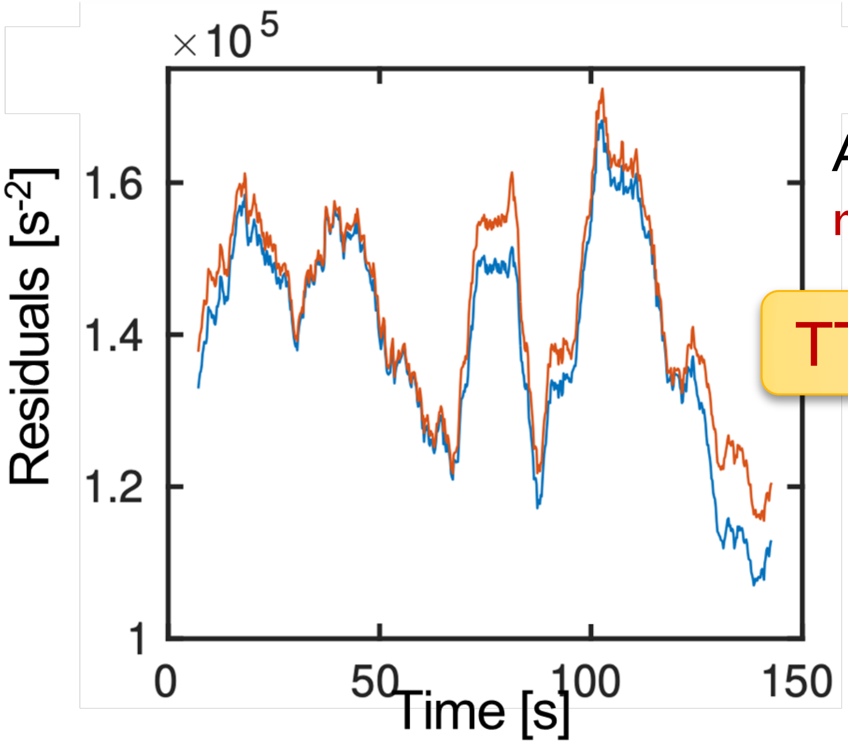
Experimental test



We only used area far from boundary

For each equation, we

- determined all coefficients by least squares from exp't data
- evaluated the residual for each time t



Always,
residual(Nikolaevskiy) > residual(TTSH)

TTSH outperforms Nikolaevskiy!

In the following, we use TTSH only.

Boundary conditions

TTSH equation (non-dimensionalized)

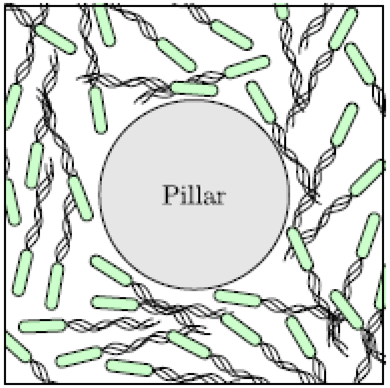
$$\boxed{\partial_t \vec{v} + \lambda \vec{v} \cdot \nabla \vec{v} = -\nabla q + a\vec{v} - b|\vec{v}|^2 \vec{v} - \left(1 + \nabla^2\right)^2 \vec{v}}$$

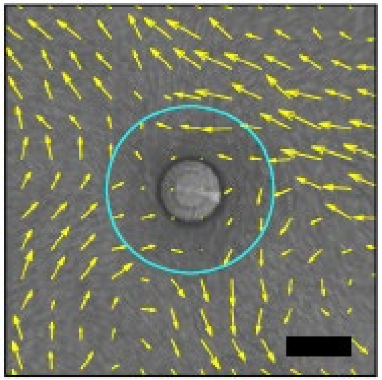
higher-order derivative

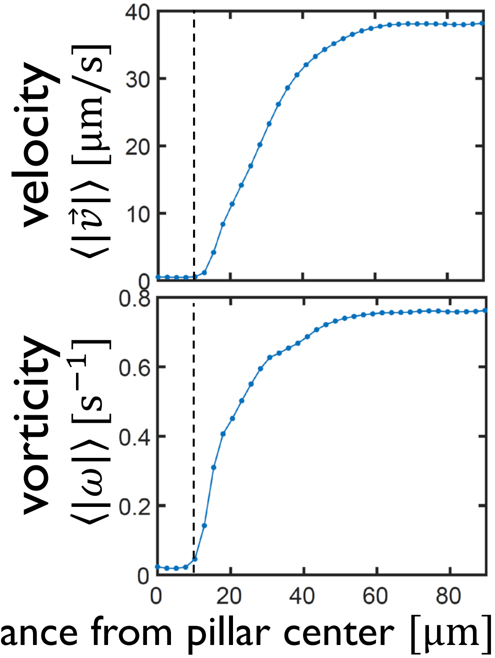
→ more boundary conditions needed

Boundary conditions were experimentally inferred.

[Reinken, Nishiguchi, ... Comm Phys 3, 76 (2020)]







$\vec{v} = 0$ & $\omega = 0$

at boundary

Daiki Nishiguchi

Boundary conditions

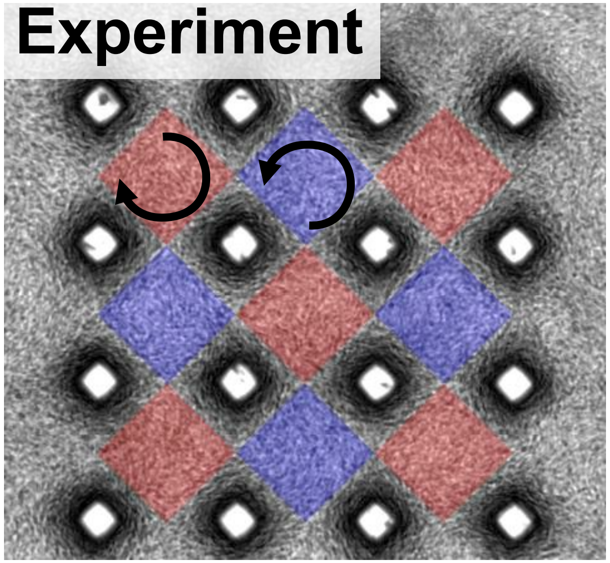
TTSH equation (non-dimensionalized)

$$\boxed{\partial_t \vec{v} + \lambda \vec{v} \cdot \nabla \vec{v} = -\nabla q + a\vec{v} - b|\vec{v}|^2\vec{v} - \left(1 + \nabla^2\right)^2 \vec{v}}$$

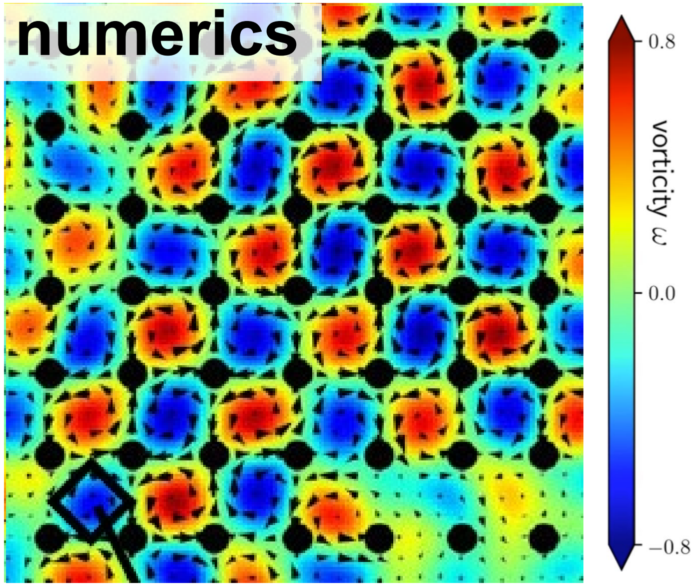
with $\vec{v} = 0$ & $\omega = 0$ at boundary.

This reproduced non-trivial vortex lattice order observed with pillar array.

[Reinken, Nishiguchi, ... Comm Phys 3, 76 (2020)]



red: ↻ blue: ↺ x0.5 speed

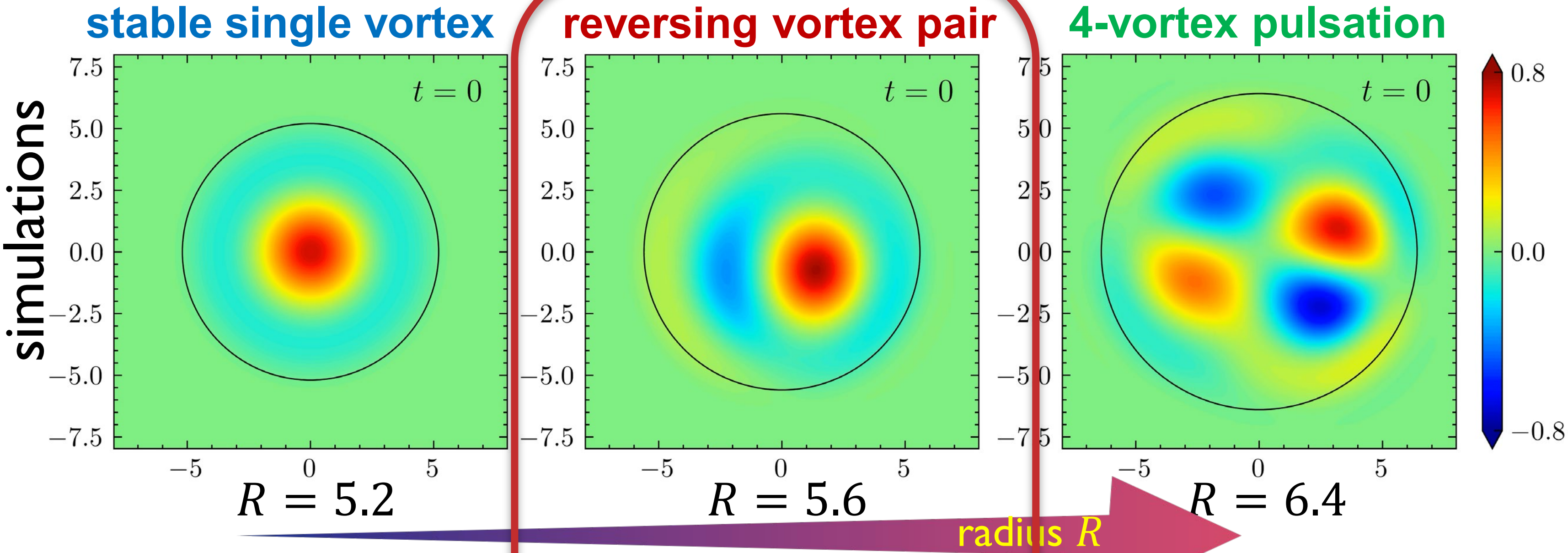


Let’s use this for circular wells & inspect the route to turbulence!

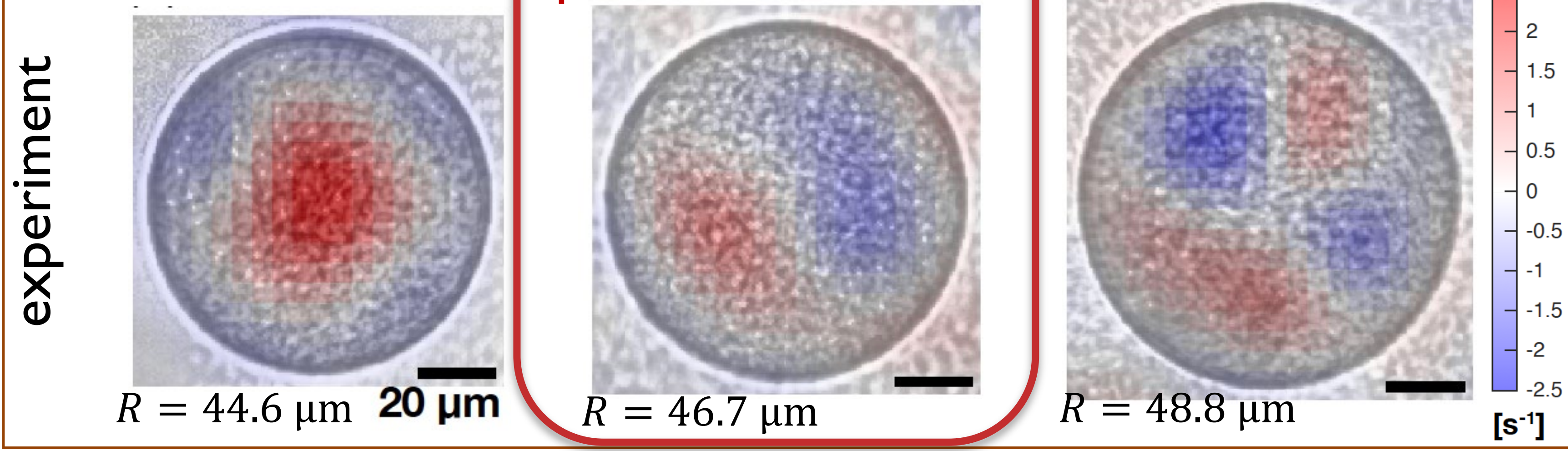
Circular well simulations

Sora Shiratani
(see also arXiv:2304.03306
for computation method)

Let's analyze

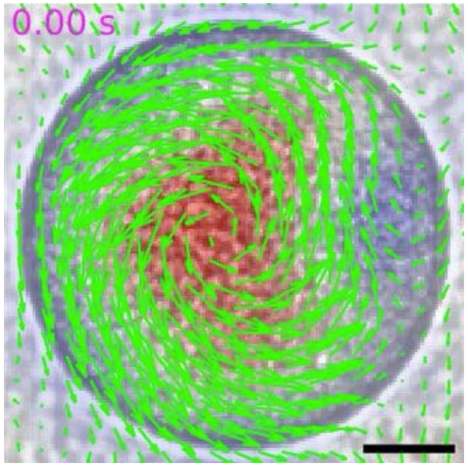


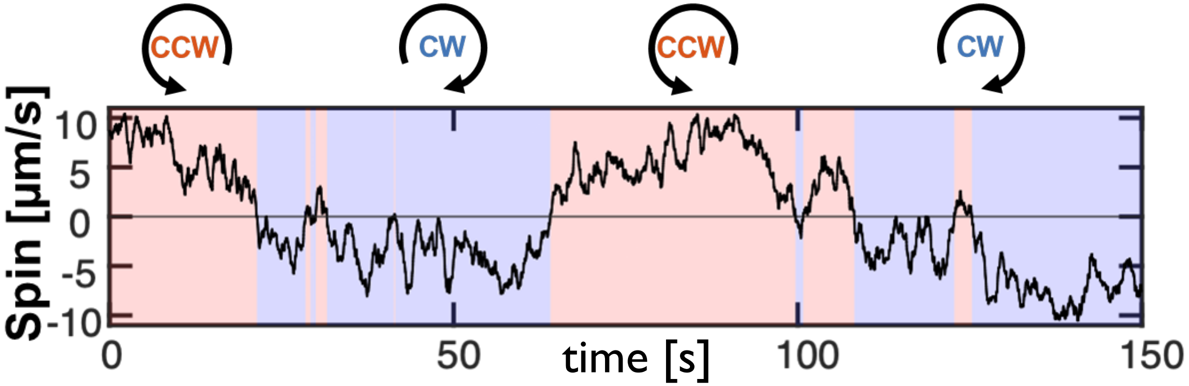
Consistent with experiments!



Reversing vortex pair

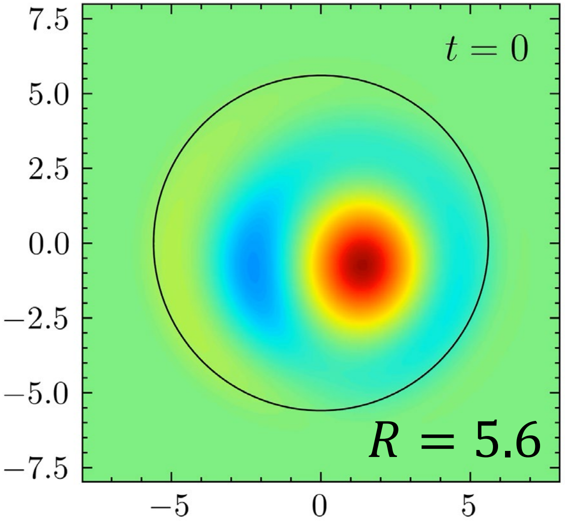
Experiment



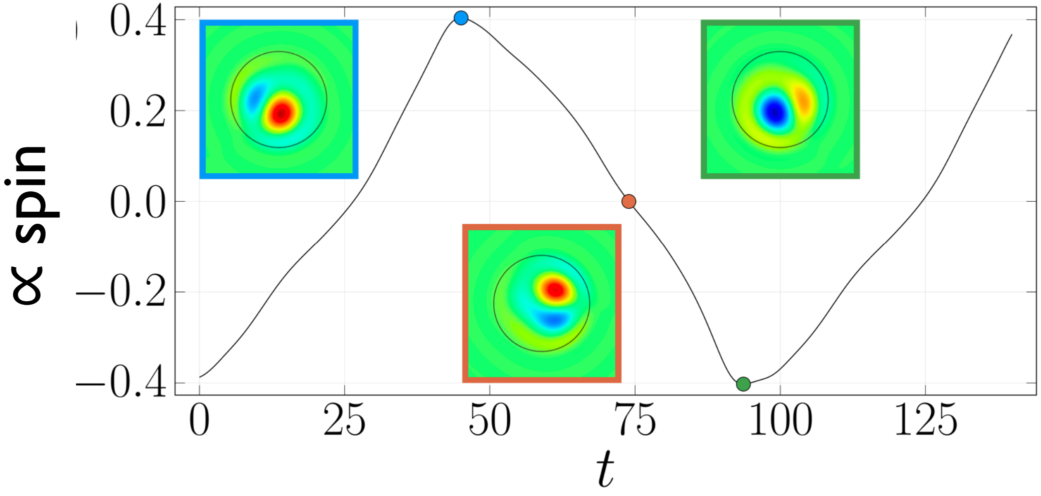


Seemingly regular reversals in experiment.

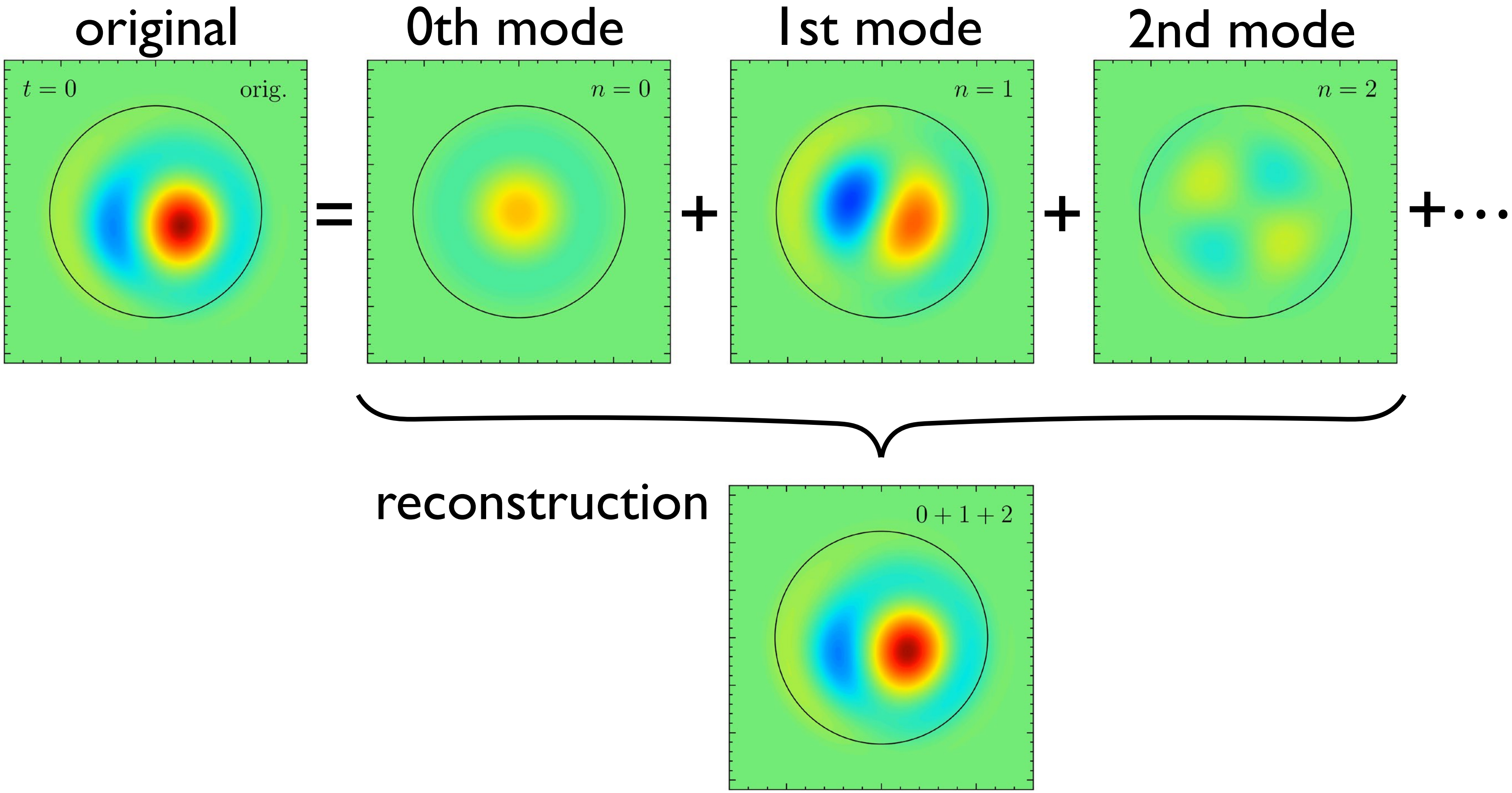
Simulation



Limit cycle was obtained in simulations!



Multipole expansion of reversing vortex pair



original

0th mode

1st mode

2nd mode

reconstruction

- First 3 modes are relevant (having comparable amplitudes)
- Can we describe them analytically?

Theory

Igor S. Aranson

TTSH vorticity eq.

$$\boxed{\partial_t \omega + \lambda \vec{v} \cdot \nabla \omega = a\omega - b[\nabla \times (|\vec{v}|^2 \vec{v})]_z - (1+\nabla^2)^2 \omega}$$

linearized

$$\boxed{\partial_t \omega = a\omega - (1+\nabla^2)^2 \omega}$$

general solutions

Bessel function

$$\omega = \sum_{n=-\infty}^{\infty} \omega_n e^{\lambda_n t} \quad \text{with} \quad \omega_n = (C_n^+ J_n(k_n^+ r) + C_n^- J_n(k_n^- r))e^{in\theta} + \text{c.c.}$$

$$k_n^{\pm} = \sqrt{1 \pm \sqrt{a - \lambda_n}}$$

$$v_n^\theta = -\left(\frac{C_n^+}{2k_n^+}\Delta J_n(k_n^+ r) + \frac{C_n^-}{2k_n^-}\Delta J_n(k_n^- r) + nC_n^0 r^{n-1}\right)e^{in\theta} + \text{c.c.}$$

$$\left(\Delta J_n(x) \equiv J_{n-1}(x) - J_{n+1}(x)\right)$$

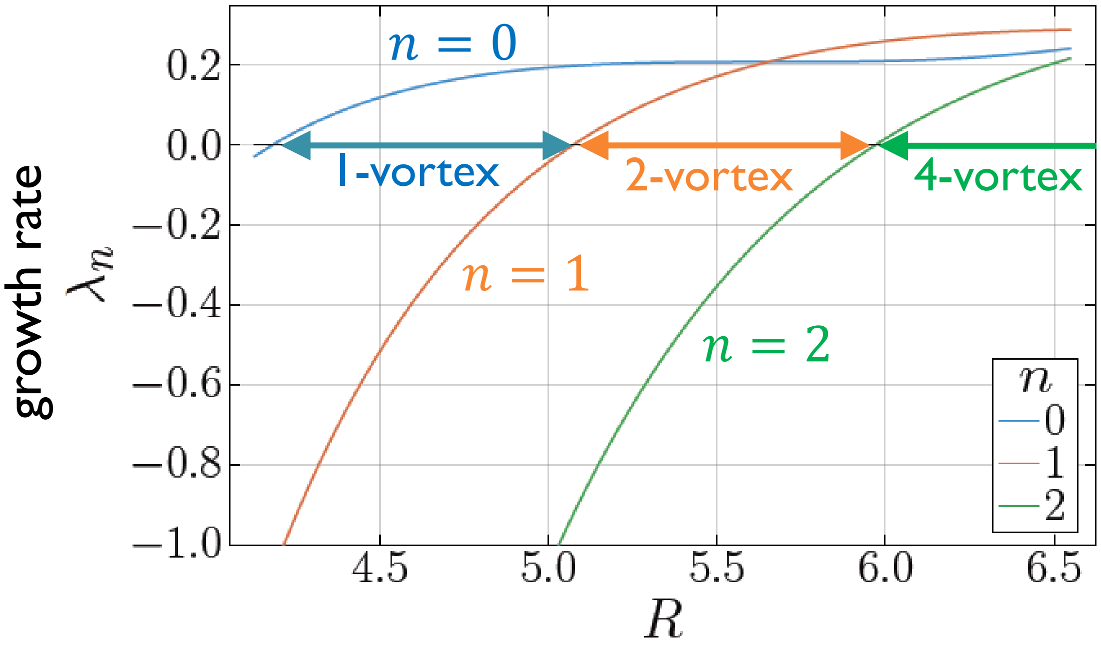
$$v_n^r = \frac{in}{r}\left(\frac{C_n^+}{(k_n^+)^2}J_n(k_n^+ r) + \frac{C_n^-}{(k_n^-)^2}J_n(k_n^- r) + C_n^0 r^n\right)e^{in\theta} + \text{c.c.}$$

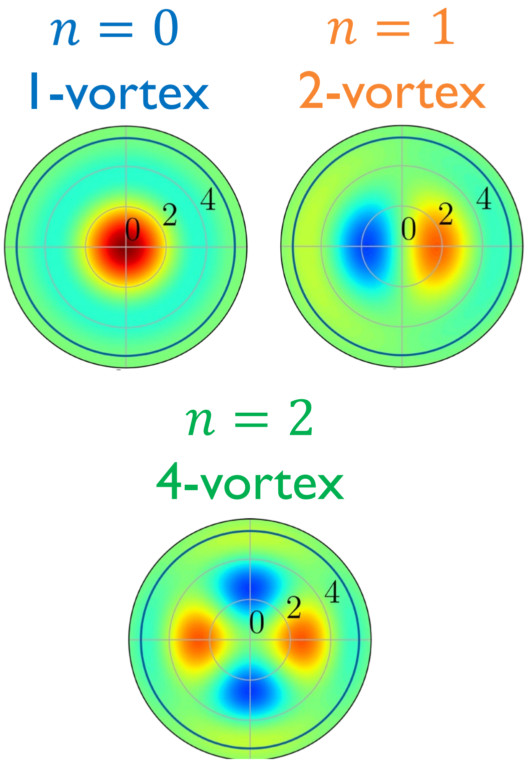
BC: $\vec{v}_n = 0$ & $\omega_n = 0$ at $r = R$ → $\lambda_n, k_n^{\pm}, C_n^{\pm}$ determined

Linear growth rate λ_n vs radius R

Transitions qualitatively accounted for

by linear instability of $n = 0{,}1{,}2$ modes



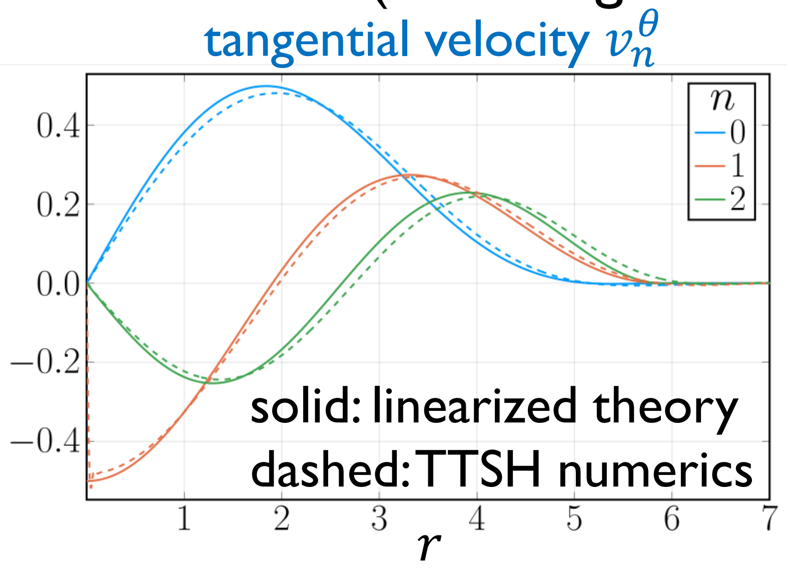


NB) Actual transition points are altered

by nonlinear effects (described later)

Spatial structure of vortices

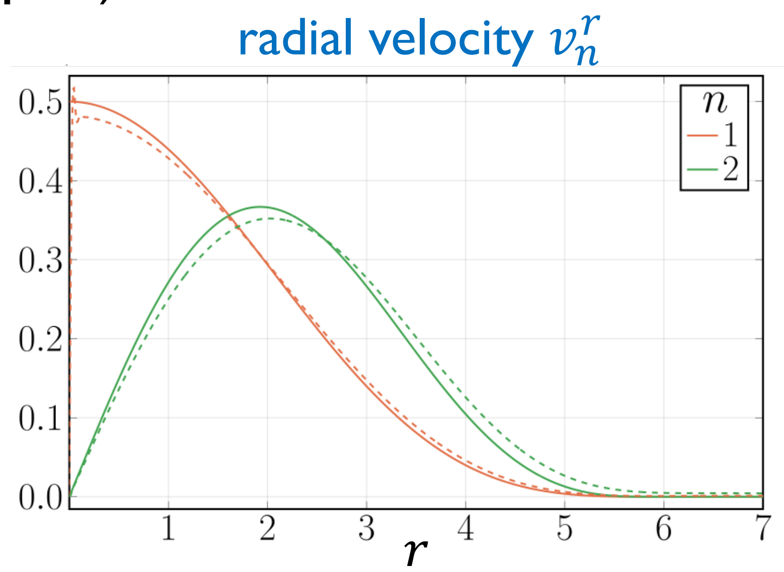
Simulations (reversing vortex pair)



tangential velocity v_n^θ

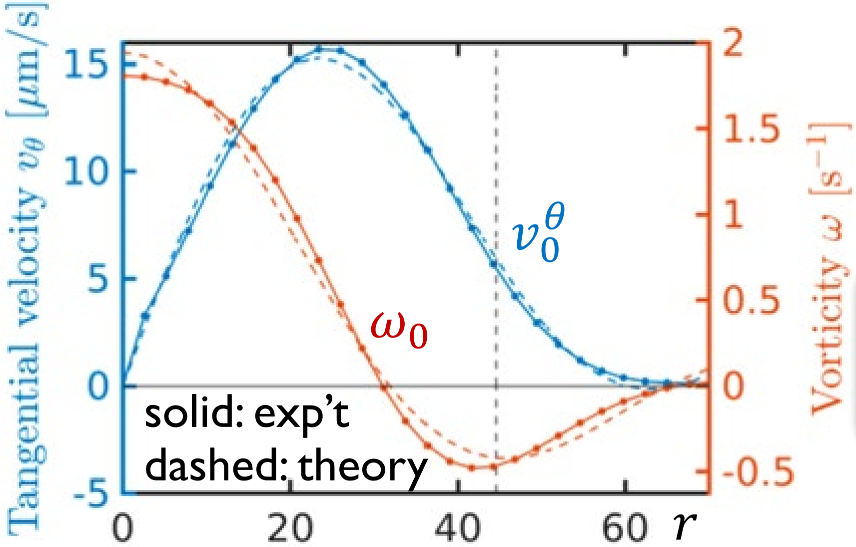
solid: linearized theory

dashed: TTSH numerics



radial velocity v_n^r

Experiment
(single vortex)



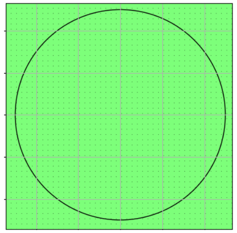
solid: exp't

dashed: theory

remarkable agreement!

Dynamics

Mode decomposition



$$\omega(r,\theta,t) \simeq \underbrace{\underbrace{C(t)\omega_0(r)}_{\text{1-vortex}} + [\underbrace{A_1(t)e^{i\theta}\omega_1(r)}_{\text{2-vortex}} + \underbrace{A_2(t)e^{2i\theta}\omega_2(r)}_{\text{4-vortex}} + \mathrm{c.c.}]}_{\text{Bessel (eigenfunctions of linearized equation)}}$$

plugging it into TTSH

Time evolution equations (ODEs) for mode coefficients

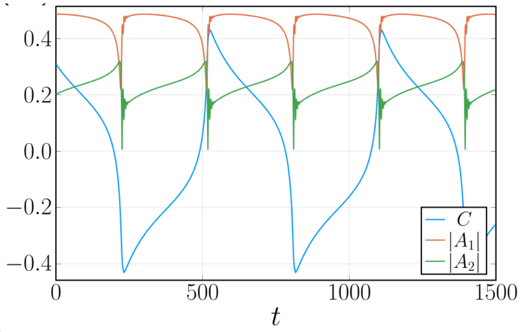
$$\partial_t C = \lambda_0 C - c_1 C^3 - c_2 C|A_1|^2 - c_3 C|A_2|^2 - 2c_4 \mathrm{Re} A_2 A_1^{2*}$$

$$\partial_t A_1 = \lambda_1 A_1 - b_1 A_1|A_1|^2 - b_2 A_1 C^2 - b_3 A_1 |A_2|^2 - b_4 C A_2 A_1^* + \delta_1 A_1 C + \gamma_1 A_2 A_1^*$$

$$\partial_t A_2 = \lambda_2 A_2 - a_1 A_2|A_2|^2 - a_2 A_2 C^2 - a_3 A_2 |A_1|^2 - a_4 C A_1^2 + \delta_2 A_2 C + \gamma_2 A_1^2$$

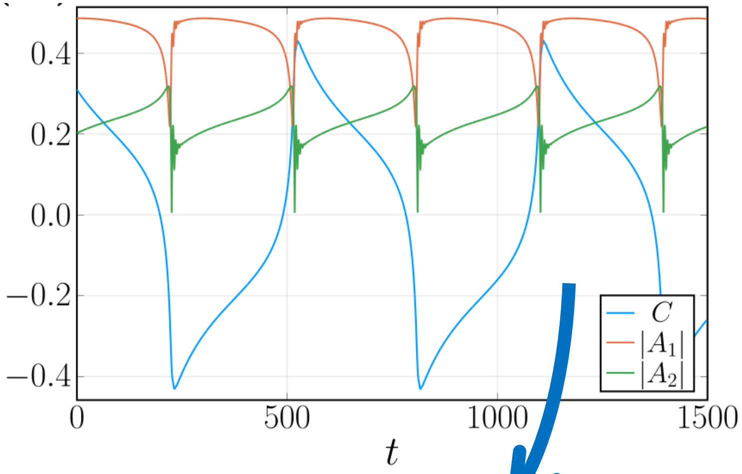
solving numerically

Time evolution of the coefficients in 2-vortex state

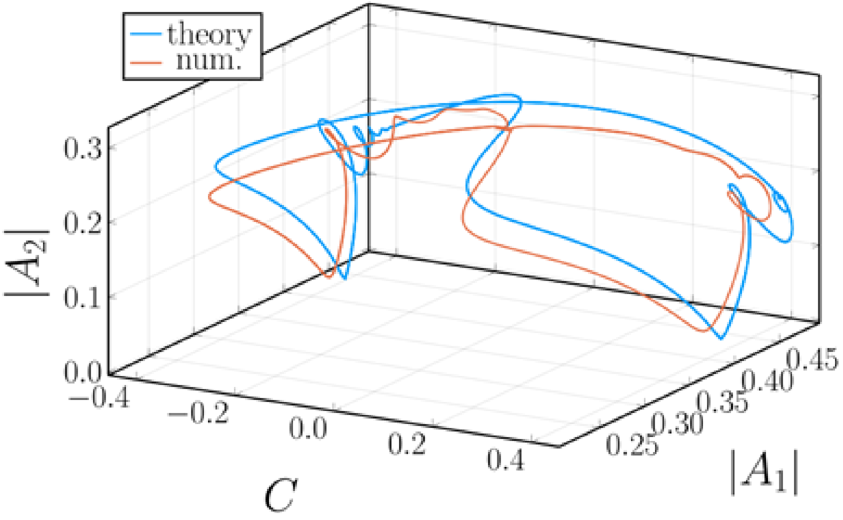


- Limit cycle solution!
- $\begin{cases} C > 0 & \mathrm{CCW} \\ C < 0 & \mathrm{CW} \end{cases}$ ∴ Periodic reversal of vortex pair!

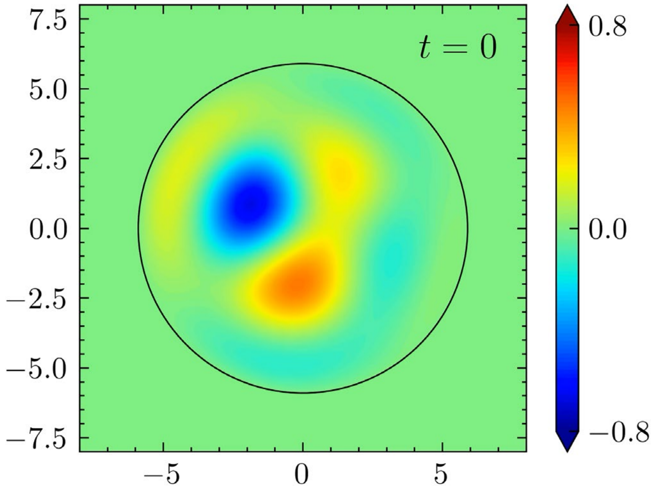
Reversing vortex pair



trajectories in phase space

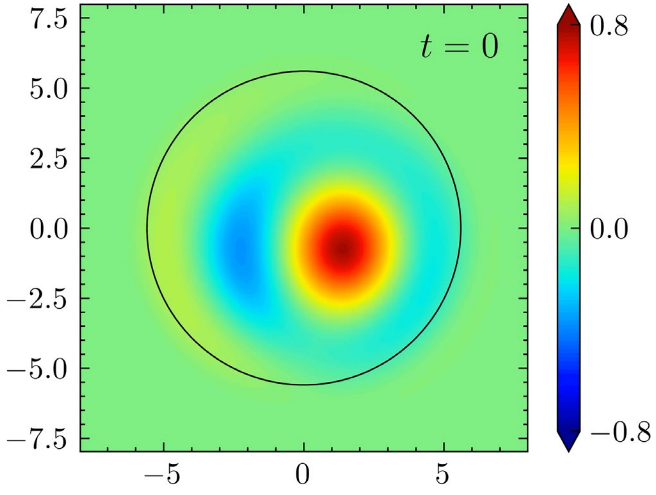


theory



$\approx$

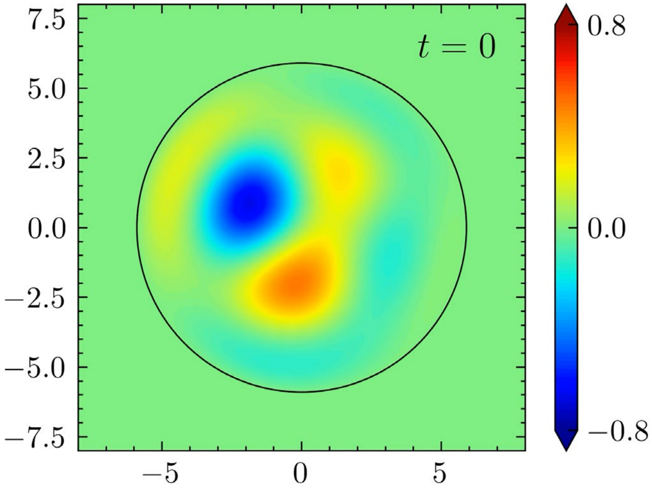
numerics



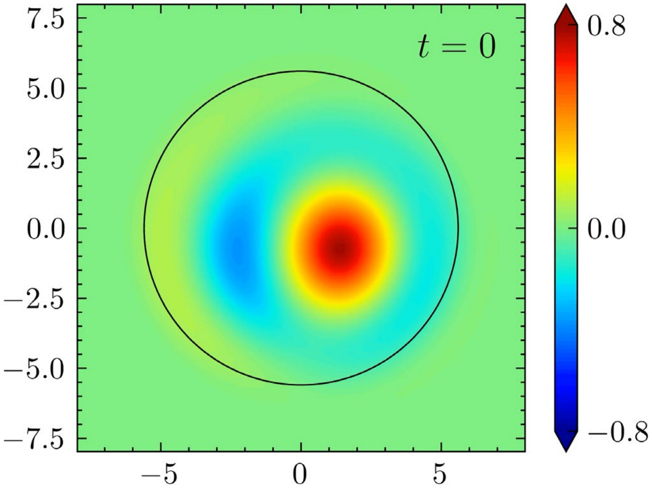
Reversing vortex pair to 4-vortex pulsations

theory

numerics

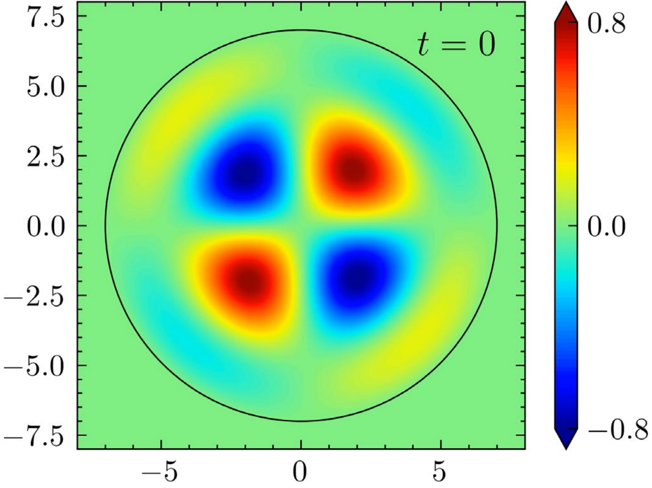


≈



4-vortex pulsations also reproduced!

increasing radius



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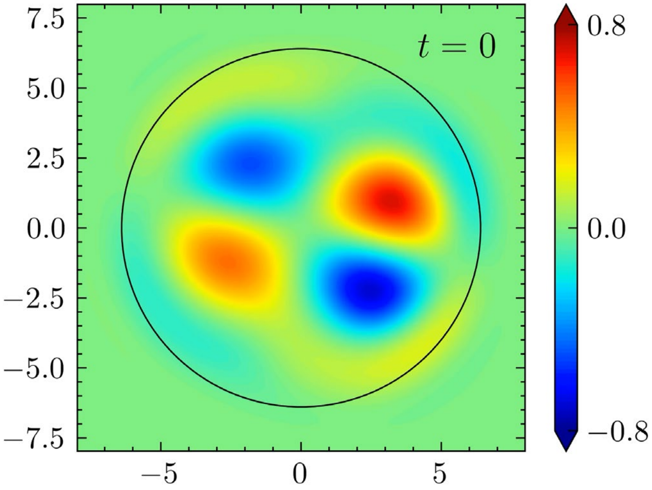
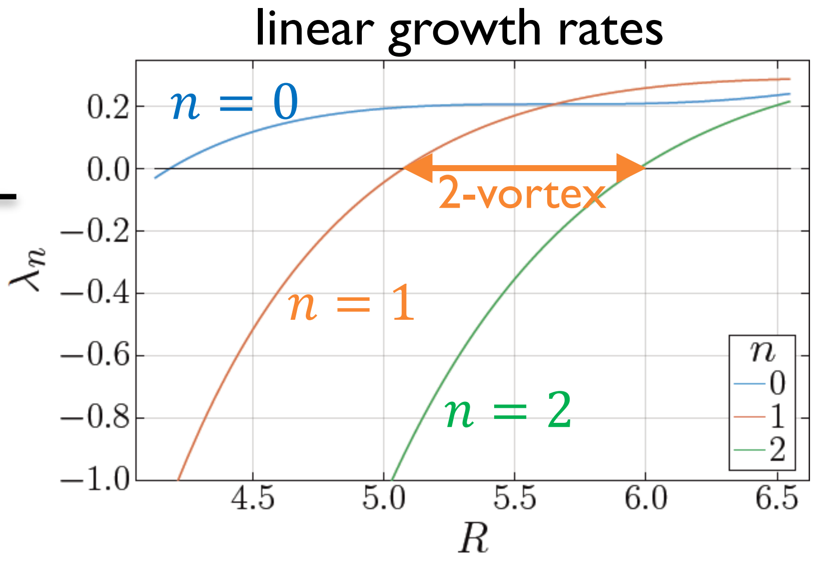


Coupling of the 3 modes


linear growth rates

but we showed $n = 2$ mode is essential for vortex reversing.

What activates this mode?

Time evolution equations (ODEs) for mode coefficients

$$\partial_t C = \lambda_0 C - c_1 C^3 - c_2 C|A_1|^2 - c_3 C|A_2|^2 - 2c_4 \mathrm{Re} A_2 A_1^{2*}$$

$$\partial_t A_1 = \lambda_1 A_1 - b_1 A_1|A_1|^2 - b_2 A_1 C^2 - b_3 A_1|A_2|^2 - b_4 C A_2 A_1^* + \delta_1 A_1 C + \gamma_1 A_2 A_1^*$$

$$\partial_t A_2 = \lambda_2 A_2 - a_1 A_2|A_2|^2 - a_2 A_2 C^2 - a_3 A_2|A_1|^2 - a_4 C A_1^2 + \delta_2 A_2 C + \gamma_2 A_1^2$$

damping

The rest can be activating!

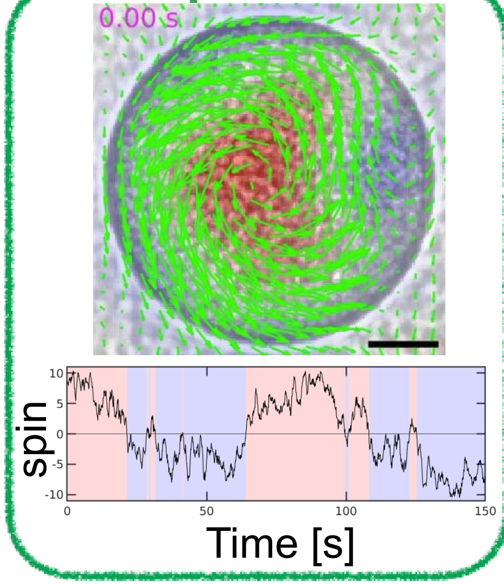
- We obtain $\delta_2, \gamma_2 \propto \lambda$ of $\lambda\left(\vec{v} \cdot \vec{\nabla}\right)\vec{v}$

→ active stress is crucial for the reversing vortex state!

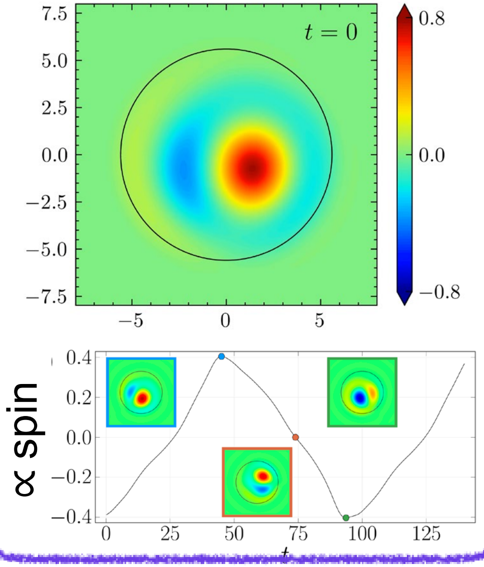
- In our theory, limit cycle was obtained only for $\lambda \gtrsim 3.75$.
- Experiment: $\lambda \approx 4.2$. Consistent!

Summary: Reversal is a precursor of active turbulence

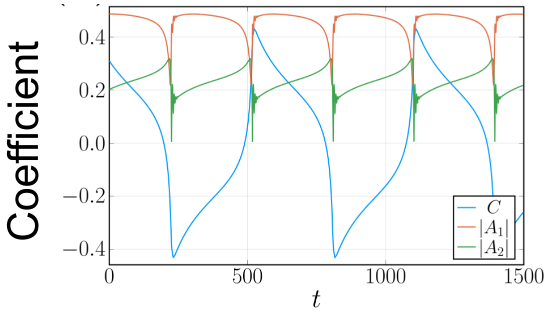
bacteria experiment



TTSH numerics

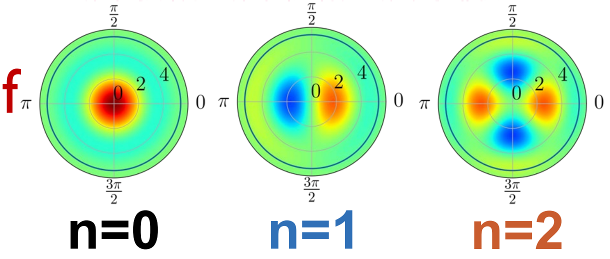


analytical theory



ODEs for the first 3 azimuthal modes obtained & account for the instability!

Underlying mechanism = orchestration of



- Active stress brings this orchestration.
- Bifurcation is generic.

→ Expected to arise in other active turbulence systems too!

Ref: **arXiv: 2407.05269** (main) & 2304.03306 (numerical detail)