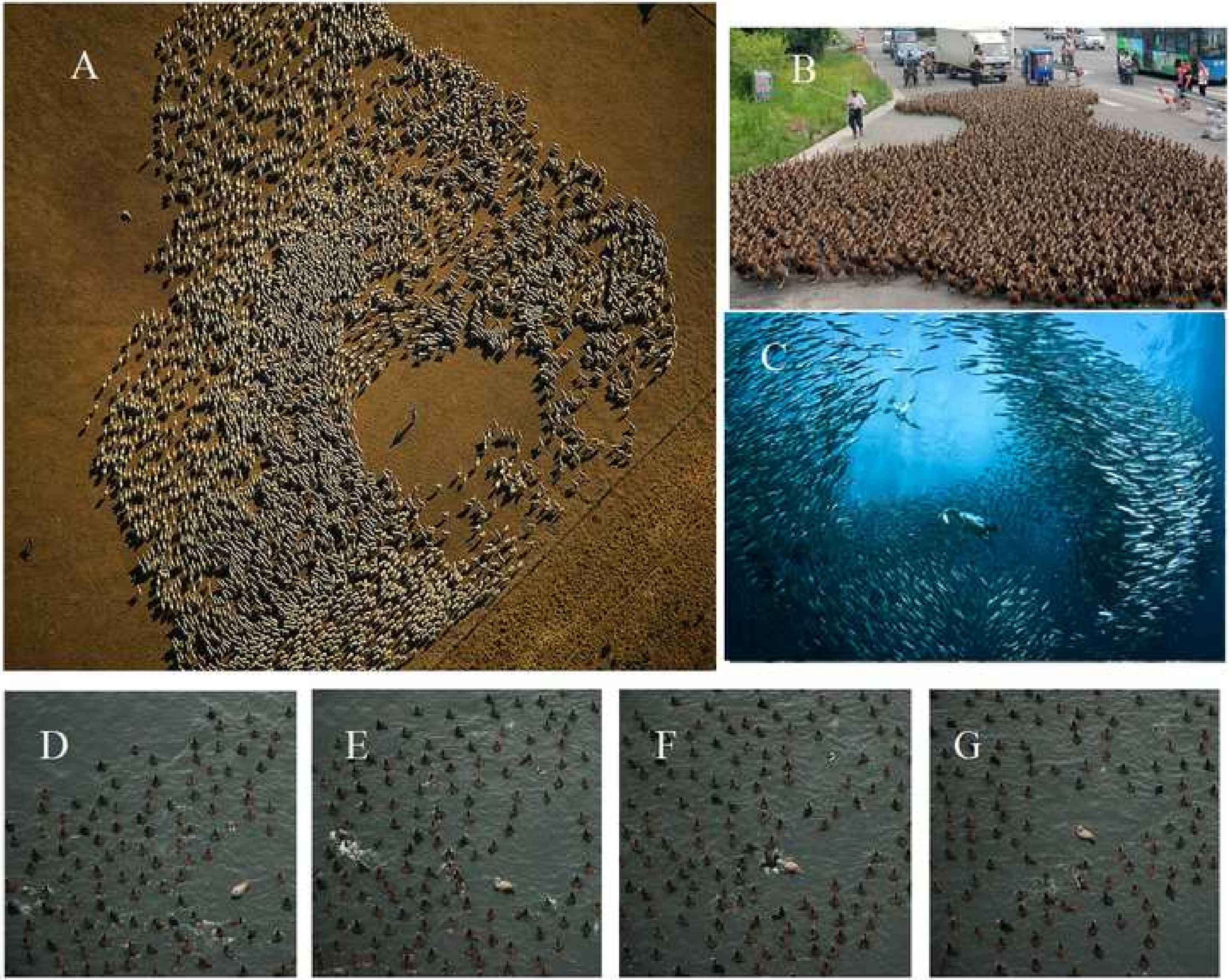
Predator-swarm interactions

- Hypothesis: swarming behaviour is an evolutionary adaptation that confers certain benefits on the individuals or group as a whole [Parrish,Edelstein-Keshet 1999; Sumpter 2010, Krause&Ruxton2002, Penzhorn 1984]
- Benifits:
  - efficient food gathering [Traniello1989]
  - heat preservation in penguins huddles [Waters,Blanchette&Kim 2012]
  - ***predator avoidance*** in fish shoals [Pitcher&Wyche 83] or zebra [Penzhorn84]
    - evasive maneuvers,
    - confusing the predator,
    - safety in numbers
    - increased vigilance
- Counter-hypothesis: swarming can also be detrimental to prey
  - Makes it easier for the predator to spot and attack the group as a whole [Parrish,Edelstein-Keshet 1999].


A
B
C
D
E
F
G

Minimal model of predator-swarm interaction

- [Chen, K, J. Royal Soc. Interface 2014]:

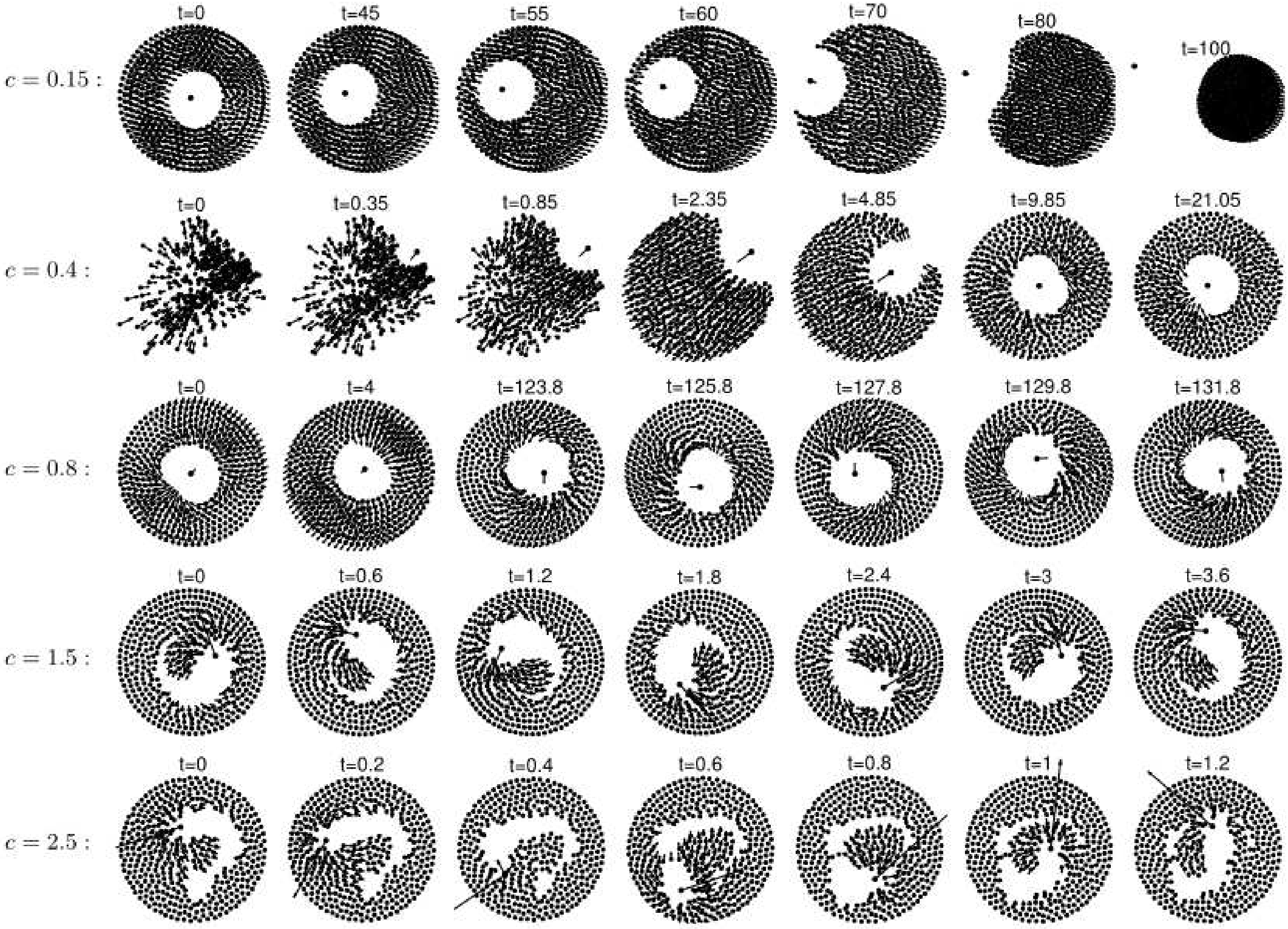
$$\underbrace{\frac{dx_j}{dt}}_{\text{Prey}} = \frac{1}{N}\sum_{k=1,k\neq j}^{N}\left(\underbrace{\frac{x_j-x_k}{|x_j-x_k|^2}}_{\substack{\text{prey-prey}\\ \text{repulsion}}} - \underbrace{a\left(x_j-x_k\right)}_{\substack{\text{prey-prey}\\ \text{attraction}}}\right) + b\underbrace{\frac{x_j-z}{|x_j-z|^2}}_{\substack{\text{prey-predator}\\ \text{repulsion}}} \tag{1}$$

$$\underbrace{\frac{dz}{dt}}_{\text{Predator}} = \frac{c}{N}\sum_{k=1}^{N}\underbrace{\frac{x_k-z}{|x_k-z|^p}}_{\substack{\text{predator-prey}\\ \text{attraction}}}. \tag{2}$$

- We take prey-prey and prey-redator interactions to be ***Newtonian***
  - makes the analysis possible!

- c : predator ”strength”. We will use it as control parameter.

- p : predator ”sensitivity”.


$c = 0.15$:
t=0
t=45
t=55
t=60
t=70
t=80
t=100
$c = 0.4$:
t=0
t=0.35
t=0.85
t=2.35
t=4.85
t=9.85
t=21.05
$c = 0.8$:
t=0
t=4
t=123.8
t=125.8
t=127.8
t=129.8
t=131.8
$c = 1.5$:
t=0
t=0.6
t=1.2
t=1.8
t=2.4
t=3
t=3.6
$c = 2.5$:
t=0
t=0.2
t=0.4
t=0.6
t=0.8
t=1
t=1.2

Continuum limit

Coarse grain:

$$\rho\left(x\right)=\frac{1}{N}\sum_{j=1}^{N}\delta(x-x_j)$$

Let $N \to \infty$ we get

$$\rho_t(x,t)+\nabla\cdot(\rho(x,t)v(x,t))=0 \tag{3}$$

$$v(x,t)=\int_{\mathbb{R}^2}\left(\frac{x-y}{|x-y|^2}-a\left(x-y\right)\right)\rho(y,t)dy+b\frac{x-z}{|x-z|^2} \tag{4}$$

$$\frac{dz}{dt}=c\int_{\mathbb{R}^2}\frac{y-z}{|y-z|^p}\rho(y,t)dy. \tag{5}$$

The key to the story: $\frac{x-y}{|x-y|^2} = \nabla_x \ln|x-y|$.

$$v(x,t) = \int_{\mathbb{R}^2} \Bigg(\underbrace{\frac{x-y}{|x-y|^2}}_{\nabla_x \ln|x-y|} \quad -a\,(x-y) \Bigg) \rho(y,t)dy + b\left(\underbrace{\frac{x-z}{|x-z|^2}}_{\nabla_x \ln|x-z|} \right)$$

$$\begin{aligned} \nabla_x \cdot v &= \int_{\mathbb{R}^2} [2\pi\delta(x-y) - 2a]\rho(y)dy + 2\pi b\delta(x-z) \\ &= 2\pi\rho(x) - 2aM \end{aligned}$$

Define characterisitic coordinates:

$$\frac{dX}{dt} = v(X,t); \quad X(X_0,0) = X_0. \tag{6}$$

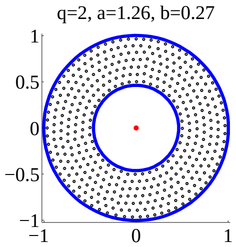
Along characteristics,

$$\frac{d\rho}{dt} = \frac{\partial\rho}{\partial t} + (\nabla_x\rho)v = -\left(\nabla_x \cdot v\right)\rho \tag{7}$$

$$= (2aM - 2\pi\rho)\rho \tag{8}$$

- Conclusion 1: $\rho \to aM/\pi$ as $t \to \infty$
  - $\rho \to \text{const}$ ***regardless of the swarm shape!***
- Conclusion 2: Radial steady state is an annulus of constant density!

Ring state (“confused” predator)



- Define

$$R_1 = \sqrt{b/a};\ R_2 = \sqrt{(1+b)/a}. \tag{9}$$

  The system (3-5) admits a steady state for which $z = 0$, ρ is a positive constant inside an annulus $R_1 < |x| < R_2$, and is otherwise.

- ***Main result:*** The ring is stable whenever $2 < p < 4$ and

$$\frac{ba^{\frac{2-p}{2}}}{(1+b)^{\frac{2-p}{2}}} =: c_0 < c < c_{hopf} := \frac{a^{\frac{2-p}{2}}}{b^{\frac{2-p}{2}} - (1+b)^{\frac{2-p}{2}}}. \tag{10}$$

- Increasing c past c_{hopf} ***triggers hopf bifurcation!***

Key calculation 2

- The density quickly approaches a constant, so the swarm is fully characterised by the motion of its boundaries.

- To determine its stability, it's enough perturb the boundary and the predator at the center:

$$\text{Inner boundary: } x = R_1 e^{i\theta} + \varepsilon_1 e^{\lambda t} \tag{11}$$

$$\text{Outer boundary: } x = R_2 e^{i\theta} + \varepsilon_2 e^{\lambda t} \tag{12}$$

$$\text{Predator: } z = 0 + \varepsilon_3 e^{\lambda t} \tag{13}$$

- Get a 3x3 eigenvalue problem

$$\left(R_2^2 - R_1^2\right)\lambda \begin{pmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \end{pmatrix} = A \begin{pmatrix} \varepsilon_1 \\ \varepsilon_2 \\ \varepsilon_3 \end{pmatrix} \tag{14}$$

where

$$A = \begin{pmatrix} -b-1 & b & 1 \\ -b-\frac{b}{1+b} & b & \frac{b}{1+b} \\ -c\left(\frac{b}{a}\right)^{\frac{2-p}{2}} & c\left(\frac{1+b}{a}\right)^{\frac{2-p}{2}} & c\left[\left(\frac{b}{a}\right)^{\frac{2-p}{2}} - \left(\frac{1+b}{a}\right)^{\frac{2-p}{2}}\right] \end{pmatrix}.$$

Implications

$$c_{hopf} = \frac{a^{\frac{2-p}{2}}}{b^{\frac{2-p}{2}} - (1+b)^{\frac{2-p}{2}}}, \quad 2 < p < 4 \tag{15}$$

- c_{hopf} is an increasing function of b (prey-predator repulsion)
  - increasing b makes it harder for the predator to catch the prey.

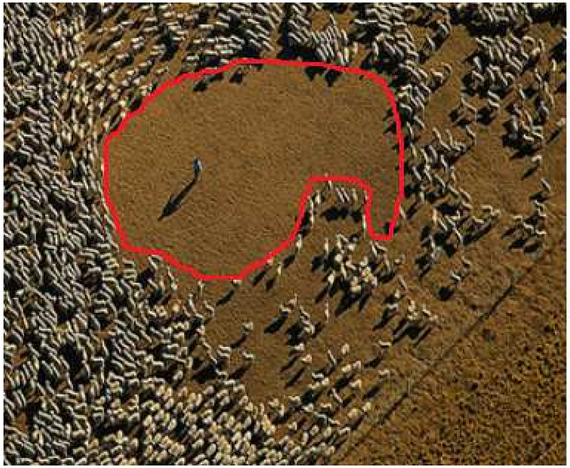
- c_{hopf} is a decreasing function of a (prey-prey attraction strength)
  - increasing a makes it easier for the predator to catch the prey.

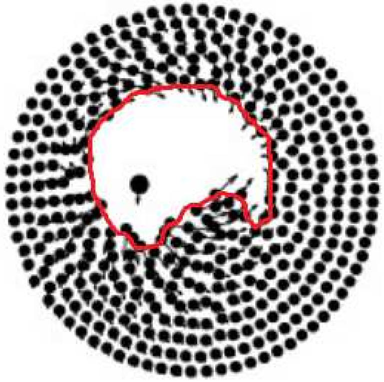
  - Swarming behaviour makes it ***easier*** for predator to catch prey (i.e. swarming is bad for prey)!

  - Example: in [Fertl&Wursig95] the authors observed groups of about 20-30 dolphins surrounding a school of fish and blowing bubbles underneath it in an apparent effort to keep the school from dispersing, while other members of the dolphin group swam through the resulting ball of fish to feed.

  - Swarming may be result of other factors such as food gathering, ease of mating, energetic benifits, or even constraints of physical environment are responsible for prey aggregation.

- When c crosses c_{hopf}, chasing dynamics result. But the prey may still escape!
  - Linear stability is a precursor to capturing the prey, but is insufficient to explain the capturing process itself!
  - Further (non-linear) analysis is needed to explain prey capture.
  - Chasing dynamics “look similar” to shephard chasing sheep:





Boundary evolution method

- Because of choice of nonlinearity, the density approaches a ***constant*** for large t
- So in principle, tracking the boundary is sufficient to track the whole swarm!
- Since density is constant:

$$v(x,t) = \frac{a}{\pi}\int_D \left(\frac{x-y}{|x-y|^2} - a\,(x-y)\right) dy + b\frac{x-z}{|x-z|^2} \tag{16}$$

- Integrate by parts, using constant density $\rho = a/\pi$,

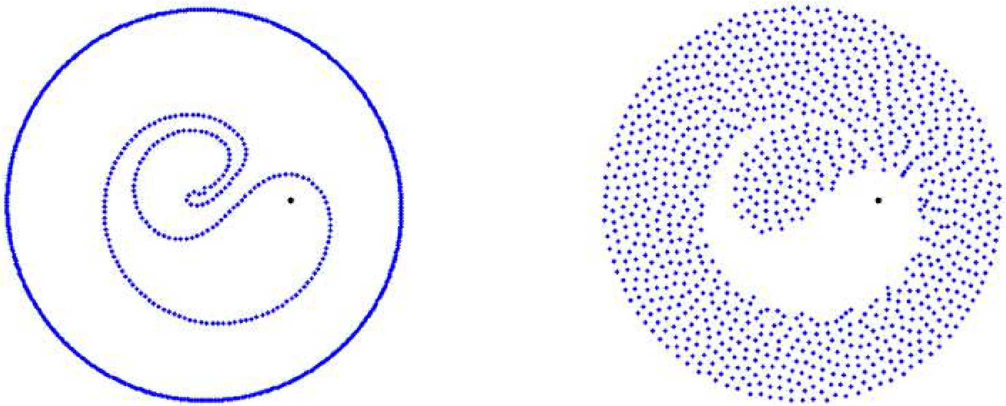
$$\begin{aligned} v(x) &= \frac{a}{\pi}\int_D \left(\frac{x-y}{|x-y|^2} - a\,(x-y)\right) dy + b\frac{x-z}{|x-z|^2} \\ &= \frac{a}{\pi}\int_{\partial D} \left(-\ln|x-y| + \frac{a}{2}|x-y|^2\right) \hat{n}\,dS(y) + b\frac{x-z}{|\;x-z\;|^2} \end{aligned}$$

$$\begin{aligned} \frac{dz}{dt} &= \frac{ca}{\pi}\int_{\mathbb{R}^2} \frac{y-z}{|y-z|^p} dy \\ &= \frac{ca}{\pi}\int_{\partial D} \frac{|y-z|^{2-p}}{2-p} \hat{n}\,dS(y). \end{aligned}$$

- Discretize ∂D and evolve both predator and ∂D according to the above.

- Note: the entire calculation is along the curve (so only 1D integrals!!)

- Use Forward Euler to update to points on the boundary.
  - This was found to be unstable, regardless of the choice of time step Δt. The is because the points along the boundary tend to cluster together as time evolves. This is a result of the points being pushed back along the boundary and aggregating at the tail.
  - Solution: reparameterize based on arc length at every time step.



Predator inside an infinite sea of prey

- Recall the steady state is an annulus of radii $R_1 = \sqrt{\frac{b}{a}} \qquad R_2 = \sqrt{\frac{1+b}{a}}$with the predator at the center.

- Take the double-limit $a \to 0$ and $b = O(1)$; then note that $R_2 \to \infty$ while R_1 remains $O(1)$. Discarding the $O(a^2)$ terms as well as the exterior boundary, we obtain

$$v(x) = \frac{1}{\pi} \int_{-\partial D_i} -a \ln |x-y| \hat{n} dS(y) + b \frac{x-z}{|x-z|^2} \tag{17}$$

where D_i is the interior boundary.

- Rescale space to make $a = b$, rescale time $t = a\hat{t}$ and dropping the hat we get

$$v(x) = \frac{1}{\pi} \int_{\partial D_i} \ln |x-y| \hat{n} dS(y) + \frac{x-z}{|x-z|^2}. \tag{18}$$

- Couple this with some law of motion for the predator z :
  - Moving in a straight line
  - Moving in a circle

Predator moving in straight line

Predator moving in straight line

Assume predator moving east with a constant speed ω along the x-axis:

$$z = \omega t \tag{19}$$

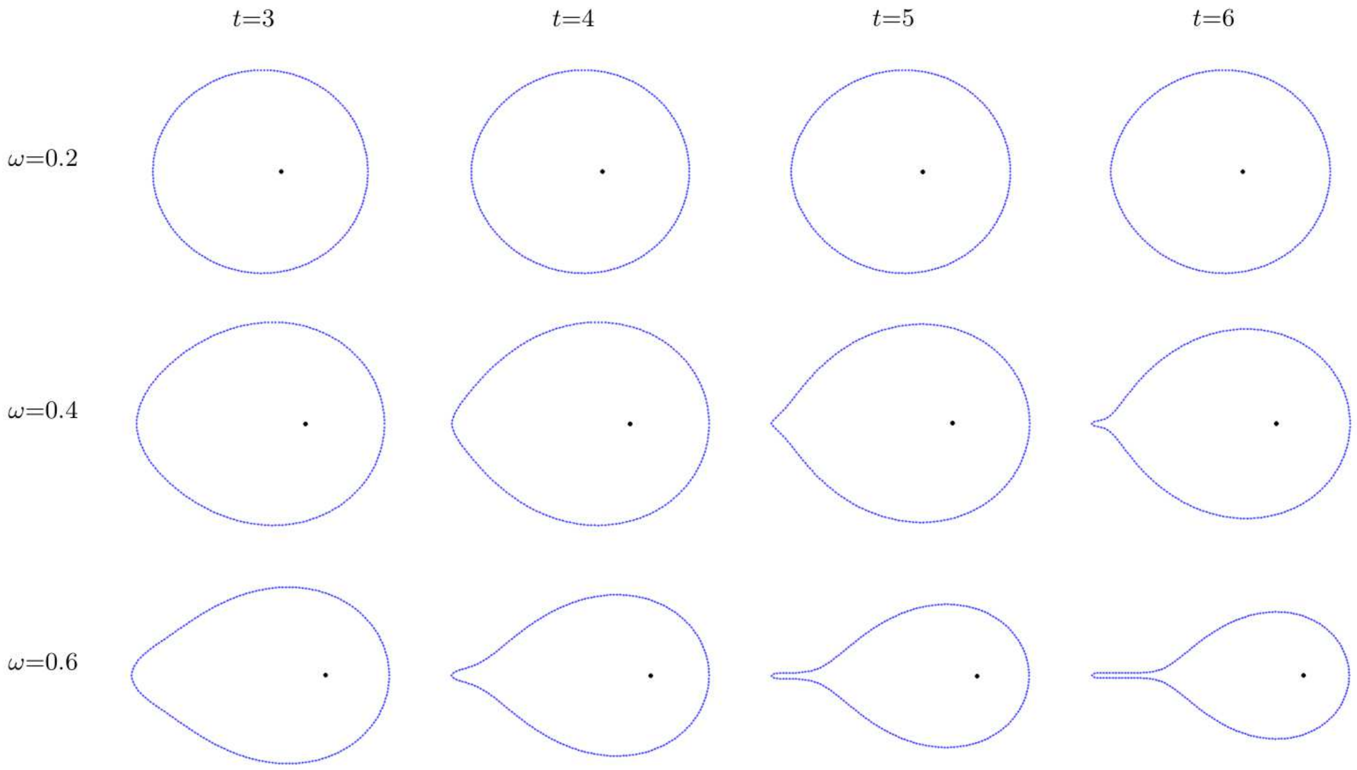
- Moving frame coordinates:

$$x = \tilde{x} + \omega t \tag{20}$$

- Dropping tilde, we get

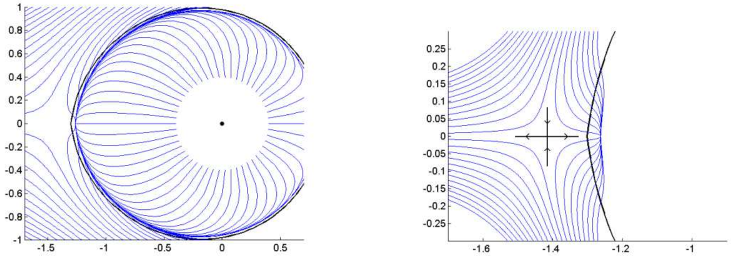
$$v(x) = \frac{1}{\pi} \int_{\partial D_i} \ln |x - y| \, \hat{n} dS(y) + \frac{x}{|x|^2} - \omega \tag{21}$$

- The "steady state" satisfies $v = 0$ on ∂D_i. To compute the steady state, evolve in time until convegence.

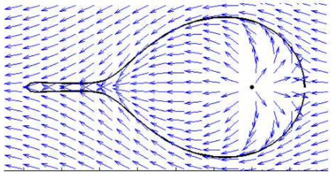


- **Open question:** what can we say about steady state ***analytically?***

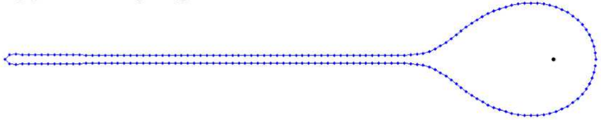
ω=0.2



$\omega = 0.5$

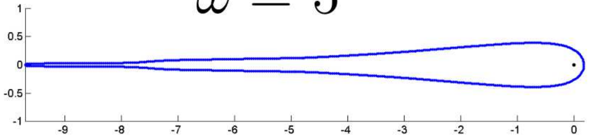


$t = 8.0$

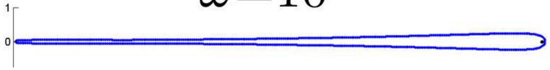


$t = 24.0$

$\omega = 5$



ω=10



- An “infinite” tail forms when $\omega > \omega_c \approx 0.25$. Conjecture: it is a result of a saddle point colliding with the boundary.

- The predator approaches the boundary as ω increases. (precursor to catching prey?) **Open question 2:** ***Do the asymptotics of large*** ω. ***Can you show the predator remains inside the boundary for any*** ω?

Predator moving in a circle

Predator moving in a circle

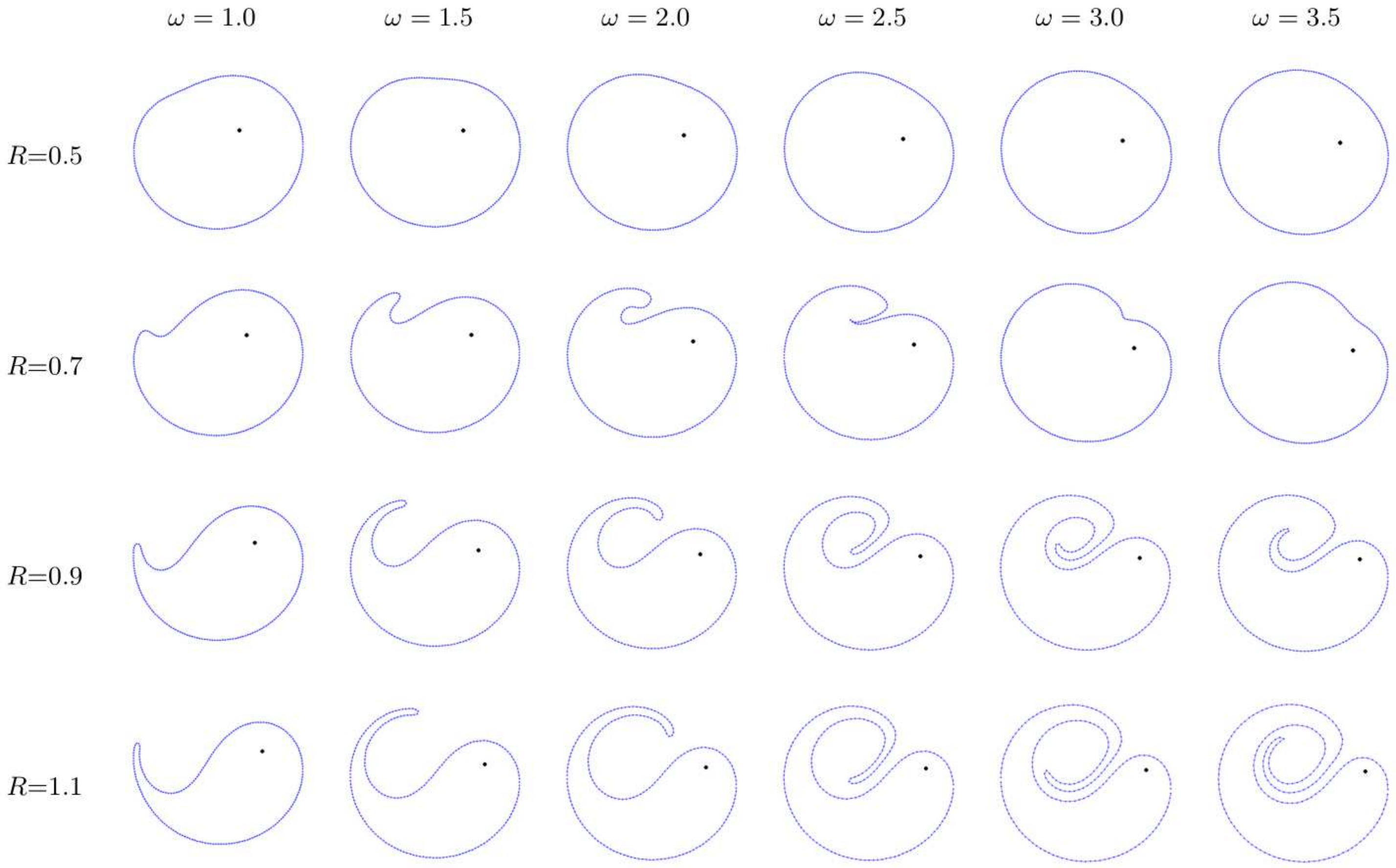
- Assume the predator is moving with angular velocity ω along a circle of radius R :

$$z = Re^{i\omega t}$$

- Go into rotating frame, $x = \tilde{x}e^{i\omega t}$, drop tilde:

$$v(x) = \frac{1}{\pi}\int_{\partial D_i} \ln|x-y|\,\hat{n}dS(y) + \frac{x-R}{|x-R|^2} - i\omega x.$$

- Predator moving in a line corresponds to the limit $R \to \infty$.


$\omega = 1.0$
$\omega = 1.5$
$\omega = 2.0$
$\omega = 2.5$
$\omega = 3.0$
$\omega = 3.5$
R=0.5
R=0.7
R=0.9
R=1.1

Increasing ω

- As ω is increased, the tail starts to “wiggle”.

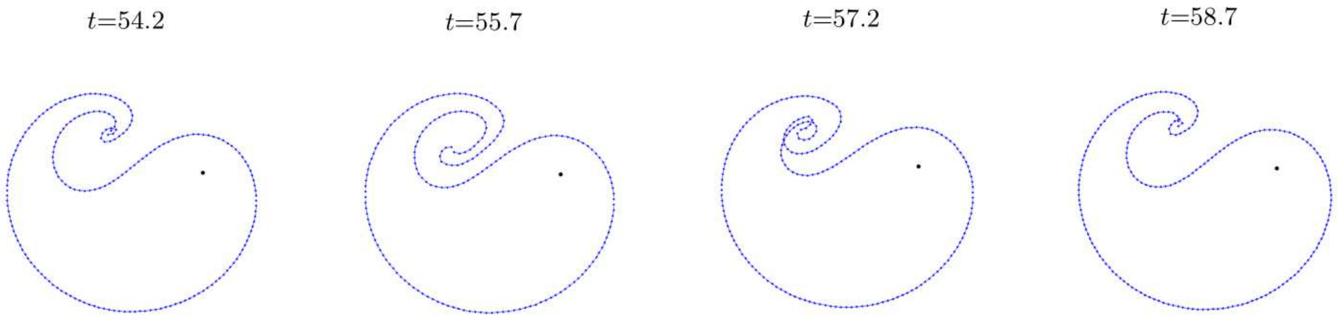
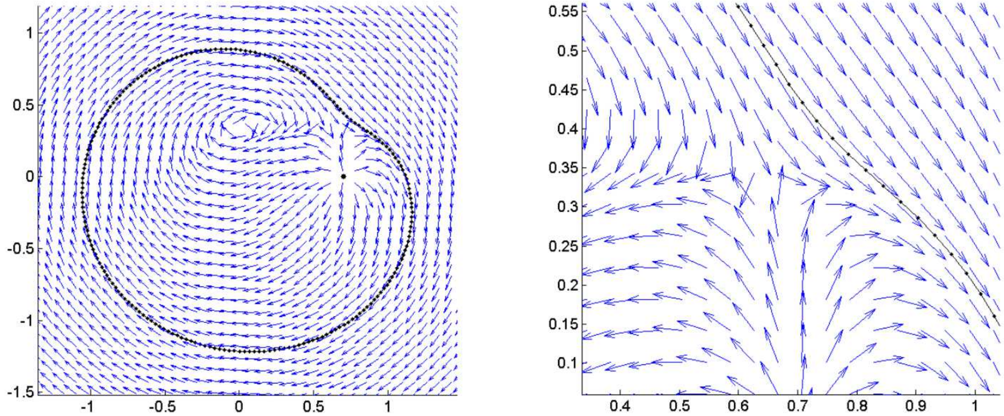


Figure 7: Moving tail for model (14). Parameters are $n = 200$, $\omega = 2.0$, $R = 0.9$, and time as given.

Topological changes

- Formation of the tail and its development is indicated by changes in vector field.



(a) (b)

Figure 10: Vector field plot of the steady state for (17) with $\omega = 3.5, R = 0.7$ and $n = 200$. (a) Full image. (b) Close up of vector dynamics.

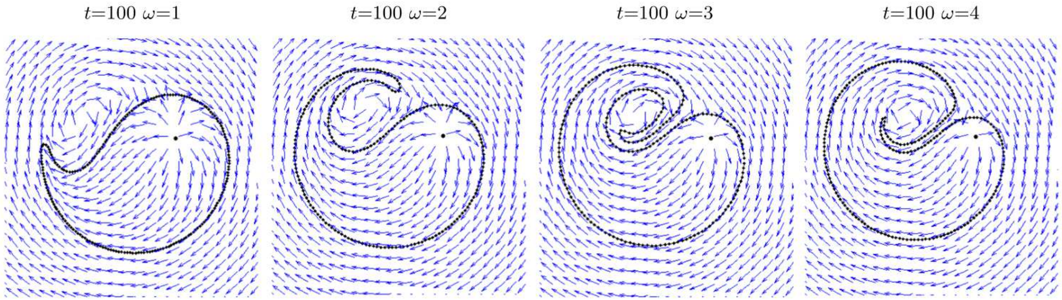


Figure 9: Vector field plots of (17) with $\omega = 0.01t$, $R = 9$, and x_1 fixed to remain at the rightmost point. Parameters were $n = 200$ and t as given.

Conclusions

- We presented an ***analytically tractable*** model of predator-prey interactions.
- Many open questions remain. The most important one: find shape of inner boundary for a predator moving in a straight line in the infinite sea of prey.
- Many models of collective animal behaviour found in literature include terms such as zone of alignment, angle of vision, acceleration etc. These terms may result in a more “realistic-looking” motion, although it can be difficult in practice to actually measure precisely how “realistic” it is. Moreover the added complexity makes it very difficult to study the model except through numerical simulations. Our minimal model shows that these additional effects are not necessary to reproduce complex predator-prey interactions.

Good open problem

- Take D'Orsogna et.al. model with Newtonian repulsion, linear attraction force:

$$
\begin{aligned}
x_i' &= v_i \\
v_i' &= \left(\alpha - \beta\left|v_i\right|^2\right) v_i + \sum_{j \neq i} \left(\frac{1}{\left|x_i - x_j\right|^2} - \gamma \right) (x_i - x_j)
\end{aligned}
$$

- Continuum limit:

$$
\begin{aligned}
\rho_t + \nabla \cdot (\rho u) &= 0 \\
u_t + \nabla u\, u &= \left(\alpha - \beta\left|u\right|^2\right) u + \int \rho(y) \left[\frac{1}{\left|x - y\right|^2} - \gamma \right] (x - y)\, dy
\end{aligned}
$$

- Exercise: It has an explicit milling “steady state” given by

$$u = \begin{cases} \frac{\vec{x}^{\perp}}{r}\sqrt{\frac{\alpha}{\beta}} & \text{inside an annulus } A : a < |\vec{x}| < b \\ ?????, & \text{outside said annulus} \end{cases};$$

$$\rho(x) = \begin{cases} \rho_0 & \text{inside an annulus } a < |x| < b \\ 0, & \text{outside said annulus} \end{cases}$$

$$a^2 = \frac{\alpha}{\beta\gamma}; \qquad b^2 = \frac{1}{\gamma} + \frac{\alpha}{\beta\gamma}.$$

- Numerical simulations show that this s.s. is stable for “thick” annulus but unstable for “thin” annulus:

- $Movie:\ \beta = 1,\ \ \gamma = 0.2,\ \ \alpha = 0.1 + 3.6(1 - t/400)(t/400)$ (i.e. alpha goes from 0.1 to 1 then back to 0.1)

- **Open question: Find the instability thresholds!!!**

References

- Papers and movies (http://mathstat.dal.ca/˜tkolokol/papers)
  - Yuxin Chen and Theodore Kolokolnikov, A minimal model of predator-swarm dynamics, Journal of the Royal Society Interface 11:20131208 (2014)
  - Hayley. Tompkins and T. Kolokolnikov, Swarm shape and its dynamics in a predator-swarm model, to appear, SIAM Undergraduate Research Online.

Thank you!